Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain

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A B S T R A C T

Tooth wear analysis techniques (mesowear and microwear) are employed to analyze dietary traits in proboscideans, perissodactyls and artiodactyls from 33 Pleistocene localities in Britain. The objectives of this study are to examine the variability in each taxon, to track dietary shifts through time, and to investigate resource partitioning among species.

The integration of mesowear and microwear results first allowed us to examine dietary variability. We identified differences in variability among species, from more stenotopic species such as Capreolus capreolus to more eurytopic species such as Megaloceros giganteus and Cervus elaphus. Broad dietary shifts at the community level are seen between climatic phases, and are the result of species turnover as well as dietary shifts in the more flexible species. The species present at each locality are generally spread over a large part of the dietary spectrum, and resource partitioning was identified at most of these localities. Mixed feeders always coexist with at least one of the two strict dietary groups, grazers or browsers. Finally, for some species, a discrepancy is observed between meso- and microwear signals and may imply that individuals tended to die at a time of year when their normal food was in short supply.

1. Introduction

The objective of this study is to use tooth wear (mesowear and microwear) to analyze dietary traits in a wide range of herbivorous mammals, using samples from Pleistocene localities in Britain. We examine the variability in each taxon, track dietary changes through time, and investigate niche partitioning among species.

Tooth microwear and mesowear techniques are powerful tools for gaining insight into local and global environmental trends (Merceron et al., 2004, 2007; Rivals et al., 2010; Semprebon et al., 2004a). Ungulate tooth mesowear and microwear in particular have served as useful proxies for geographical and/or temporal variability in diet and vegetation structure through the Cenozoic (Mihlbachler et al., 2011; Semprebon and Rivals, 2007, 2010; Semprebon et al., 2016). Improvements in these techniques have revealed correlations with vegetation and climate as well as aspects of niche utilization (Calandra et al., 2008; Rivals et al., 2012). Over the past decade, integrated studies of microwear and mesowear have been undertaken for the inference of paleodiet (Rivals and Semprebon, 2006; Rivals et al., 2007a). The combination of the two techniques provides dietary information on two different timescales: mesowear averages the diet over few months (Fortelius and Solounias, 2000), while microwear reveals the diet in the last days of an animal’s life (Grine, 1986). While the results obtained from the two methods are usually in agreement (Semprebon and Rivals, 2007, 2010), discrepancies are sometimes observed (Rivals, 2012; Rivals et al., 2009a). Such differences, related to the temporal resolution of each method (Davis and Pineda Munoz, 2016) are not limitations but are informative of temporal (often seasonal) variation in diet (Sánchez-Hernández et al., 2016). The value of combining various dietary proxies has recently been highlighted by Loffredo and DeSantis (2014), who recommend caution when interpreting dietary traits based on dental mesowear alone. The same must also be valid for microwear because it is sensitive to short-term shifts in diet.

We focus on large mammals in Britain because of their rich fossil record and secure stratigraphic framework (Lister, 1992, 1997;
2.2. Tooth mesowear analysis

Suitable for microwear analysis, with taphonomic alterations which damaged the original micro-nivation of the epoxy casts under the stereomicroscope, specimens where both buccal cusps were broken or damaged, 910 original and the Cruickshanks private collection.

Collections: Natural History Museum (London), British Geological Survey (Keyworth), Colchester and Ipswich Museums Service (Ipswich), Torquay Museum, Norfolk Museums Service (Norwich), and the Cruickshanks private collection.

A total of 1491 specimens were moulded and screened to assess their suitability for tooth wear analyses. After excluding teeth where both buccal cusps were broken or damaged, 910 original specimens were suitable for mesowear analysis. After an examination of the epoxy casts under the stereomicroscope, specimens with taphonomic alterations which damaged the original micro-wear pattern were discarded, leaving a total of 815 specimens suitable for microwear analysis.

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 relative amounts of attritive and abrasive dental wear (due to tooth-tooth and tooth-food-tooth contact, respectively). Mesowear is scored macroscopically from the buccal side of upper molars, preferably the paracone of M2 (Fortelius and Solounias, 2000). A diet with low levels of abrasion (high attrition) maintains sharpened apices on the buccal cusps as the teeth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices, are omitted from mesowear analysis. Cusp sharpness is sensitive to ontogenetic age among young individuals (which have not yet developed substantial wear facets) and among dentally senescent individuals. However, for intermediate age groups, which usually comprise the majority of individuals in a fossil collection, mesowear is found to be less sensitive to age and more strongly related to diet (Rivals et al., 2007b) and therefore suitable for dietary reconstruction.

In this study, the standardized method (mesowear ‘ruler’) introduced by Mihlbachler et al. (2011) is 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). Using the mesowear ruler as a reference, cusps equal to or sharper and higher in relief than reference cusp 0 were assigned a value of 0. Cusps that were morphologically intermediate between reference cusp 0 and reference cusp 1, or equal to reference cusp 1 were assigned a value of 1, and so forth. The average value of the mesowear data from a single sample of fossil dentitions corresponds to the ‘mesowear score’ or MWS (Mihlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher to reduce inter-observer error, corresponding to the recommendations of Loffredo and DeSantis (2014).

Mesowear was applied to Rhinocerotidae, Equidae, Cervidae, and Bovidae because of their suitable tooth morphology when using the Fortelius and Solounias (2000) method. Recently, Saarinen et al. (2015) has developed a new approach to analysing proboscidean tooth surfaces and his data on British Pleistocene proboscideans complements that of the present study (Saarinen and Lister, in press; Saarinen et al., in press).

2.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the cleaning, moulding, casting, and examination protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004b). The low-magnification microwear technique has been questioned in relation to repeatability and inter-observer error (DeSantis et al., 2013; Mihlbachler et al., 2012). Such problems may arise when observers are not properly trained in the microwear method or when comparing data that were collected by different researchers. To avoid this problem, 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 incident 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 in a square area of 0.16 mm² using an ocular reticule. We used the classification of features defined by Solounias and Semprebon (2002) and Semprebon et al. (2004b) 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 they are wide, but have straight, parallel sides. These categories are subdivided as follows:

- Pits are classified as small pits, large pits, or puncture pits. Large pits are deeper, less refractive (always dark), generally at least twice the diameter of small pits, and often have less regular outlines than do small pits. Puncture pits are large and very deep pits with crater-like features with regular margins, and they appear dark due to low refractivity.

Scratches are divided into fine scratches (i.e., narrow scratches that appear relatively shallow and have low refractivity), coarse (i.e., wide scratches that are also relatively deep but have high refractivity), and hypercoarse (i.e., very deep and trenchlike features which are wider than the other types of scratches). The presence of some other features is recorded qualitatively. Cross scratches are oriented approximately perpendicularly to the majority of scratches observed on the enamel (Solounias and Semprebon, 2002). Gouges are features which have ragged, irregular edges and are much larger (approximately 2–3 times as large) and deeper than large pits. They are relatively dark features with...
Table 1


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<tr>
<th>Locality</th>
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<th>Reference</th>
<th>Taxa</th>
<th>Mesowear</th>
<th>Microwear</th>
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<td>5–7</td>
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<tr>
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<td>1.8,9</td>
<td>Bos/Bison</td>
<td>29.207</td>
<td>0.10</td>
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The presence or absence of these features in a microscopic field was recorded. In addition, scratch textures were assessed using the scratch width score (SWS) which is obtained by giving a score of '0' to a tooth with predominantly fine scratches, '1' to one with a mixture of fine and coarse types of textures, and '2' to one with predominantly coarse scratches. Individual scores for a sample of teeth are then averaged to get the SWS.

In artiodactyls and perissodactyls, scratches and pits were counted in two areas on the paracone of the upper molars and the protoconid of the lower molars. In proboscideans, the area was selected on a loph in the center of the worn part of the occlusal surface. The results were compared with a database constructed from extant ungulate taxa (Solounias and Semprebon, 2002; Rivals et al., 2010). Using average scratch and pit data, it is possible to discriminate between the dietary categories of browser (i.e., eating woody and non-woody dicotyledonous plants) versus grazer (i.e., eating grass). Mixed-feeding ungulates can best be separated from browsers or grazers by calculating the percentage of individuals in a population possessing scratch numbers that fall between 0 and 17 in the 0.16 mm² area (%0–17) (Semprebon and Rivals, 2007). Thus, for extant ungulates, the percentages of individuals in the low-scratch range are generally as follows: grazers have 0.0–22.2% of individuals with scratches between 0 and 17; mixed feeders have 20.9–70.0% of individuals with scratches between 0 and 17; and leaf-dominated browsers have 72.7–100.0% of individuals with scratches between 0 and 17 (Semprebon and Rivals, 2007).

### Results

#### Species’ dietary traits

Dietary traits in Proboscidea, Rhinocerotidae, Equidae, Cervidae, and Bovidae are here examined by combining tooth mesowear and }

![Fig. 1. Geographic position of the localities sampled.](image-url)
microwear analyses. Mesowear and microwear results for each locality and species are summarized in Table 1. Raw data for all the specimens sampled are given in the Supplementary Online Data.

3.1.1. Proboscidea

Proboscidea are represented in the British Pleistocene fossil record by one species of Gomphotheriidae (*Anancus arvernensis*) and five species of Elephantidae (*Mammuthus rumanus*, *Mammuthus meridionalis*, *Mammuthus trogontherii*, *Mammuthus primigenius*, and *Palaeoloxodon antiquus*).

The gomphothere *Anancus arvernensis* is present in the Early Pleistocene Red Crag and Norwich Crag Formations. Tooth microwear patterns are different between the two samples. In the Red Crag, all individuals have low numbers of scratches and quite high numbers of pits and, thus, fall within the range of extant leaf browsers based on these two variables alone (Fig. 2A). They also show the presence of large pits, puncture pits, and gouges, suggesting that they may have included seeds and fruits in their diet (Rivals et al., 2015a). In the Norwich Crag, *A. arvernensis* has a higher number of scratches but an intermediate number of pits (Fig. 2A). The scratch numbers (%0-10) classify the sample as grass-dominated mixed feeders (Fig. 3). It also has somewhat more gouging present which might again be related to fruit and seed consumption. This microwear pattern has also been observed in Early Pleistocene *Anancus* from Chilhac (France) and the Eastern Scheldt in the Netherlands (Rivals et al., 2015a). In Africa, *Anancus*

![Fig. 2. Bivariate plots of the average numbers of pits and scratches in (A) *Anancus arvernensis* and *Palaeoloxodon antiquus* and (B) the *Mammuthus* lineage. Bars correspond to standard error of the mean (±1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).](image-url)
was also reported to be opportunistic and to feed both on browse and grass (Zazzo et al., 2000; Lister, 2013).

The earliest member of the mammoth lineage in Europe, *Mammuthus rumanus* from the Red Crag proper, has a microwear pattern similar to that of the co-occurring gomphothere (*Anancus arvernensis*), with low numbers of scratches and quite high numbers of pits, indicating leaf browsing (Fig. 2B). Large pits most likely indicate the presence of grit ingested together with the plants.

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**Fig. 3.** Low scratch percentages (%0–17) and dietary changes in (A) *Anancus arvernensis* and *Palaeoloxodon antiquus* and (B) the *Mammuthus* lineage through geological time. The grey areas correspond to the range of values for the extant mixed feeders.

**Fig. 4.** Bivariate plot of the average numbers of pits and scratches in Rhinocerotidae. Bars correspond to standard error of the mean (±1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).
(Semprebon and Rivals, 2007), which would indicate that it frequented open habitats (Rivals et al., 2015a).

Early Pleistocene *Mammuthus meridionalis* samples show a relatively high variability in microwear pattern, although most are identified as grass-dominated mixed feeders. Some samples have high numbers of scratches which plot in the grazing morphospace, such as at Overstrand, West Runton, and East Runton (Fig. 2B). The samples from Norwich Crag and Mundesley are intermediate in terms of scratches; their low-scratch percentage indicates grass-dominated mixed feeding (Table 1). Finally, the sample from Bacton shows low numbers of scratches which indicates browse-dominated mixed feeding (Figs. 2B and 3).

*Mammuthus trogontherii* and *Mammuthus primigenius* show microwear patterns with intermediate to high numbers of scratches (Fig. 2B), indicating a range from mixed feeding to grazing. None of our samples of *M. trogontherii* or *M. primigenius* was found to have exclusive browsing traits, although *M. trogontherii* from West Runton, Overstrand and Sidestrand (early Middle Pleistocene) and Ilford (MIS 7) are identified as browse-dominated mixed feeders (Fig. 2B). At West Runton, the tooth microwear results are supported by paleoenvironmental evidence for mixed environments with woodland as well as open grassland areas (Lister and Stuart, 2010).

*Palaeoloxodon antiquus*, present at nine Middle Pleistocene localities, shows microwear patterns with sample means ranging from 13.4 to 19.5 scratches in the 0.16 mm² area (Fig. 2A). The %0e17 values range from 33.3 to 83.3% (Table 1). Such values indicate diets ranging from the mixed feeders to leaf browsers (Fig. 3). These observations are in agreement with the association of the species with temperate, forested or mixed vegetational, conditions (Stuart, 1982). The absence of grazing *P. antiquus* is consistent with the finding that in Britain it is absent from cold stages with generally open habitat (Schreve, 2001a; Stuart, 1982). Nonetheless, grass-dominated mixed feeding habit was identified previously in microwear analysis of *P. antiquus* from the Middle Pleistocene of Megalopolis in Greece (Rivals et al., 2012).

### 3.1.2. Rhinocerotidae and Tapiridae

The Rhinocerotidae are represented in the British Pleistocene by four species of *Stephanorhinus* (*Stephanorhinus etruscus*, *Stephanorhinus hundsheimensis*, *Stephanorhinus kirchbergerensis* and *Stephanorhinus hemitoechus*) and, in the late Middle to Late Pleistocene, by *Coelodonta antiquitatis*.

The low-crowned *Stephanorhinus etruscus* from the Red Crag Nodule Bed and East Runton, shows low mesowear scores (MWS = 1.3) and low numbers of scratches (Table 1). At the two localities, the mesowear and microwear patterns both indicate that *S. etruscus* had dominant browsing habits (Figs. 4 and 5). In the Red Crag Nodule Bed it shows a higher number of pits and most of the individuals have large pits, while at East Runton average number of pits is lower and no individuals have large pits (Table 1). Considering that higher numbers of pits indicate grit consumption (Hoffman et al., 2015) the rhinoceros population from the Red Crag Nodule Bed occupied more open environments on average than at East Runton.

In the early Middle Pleistocene, *S. hundsheimensis* shows higher mesowear scores (MWS between 1.8 and 4.0) than *S. etruscus*. It also shows intermediate and low numbers of scratches (Table 1). Both proxies suggest browsing and mixed-feeding dietary habits. The mesowear scores show that *S. hundsheimensis* was restricted to the mixed-feeding ecospace, varying from browse-dominated to graze-dominated mixed feeding (Fig. 5). Tooth microwear supports a similar pattern for the samples from Pakefield and Boxgrove. However there is a discrepancy at West Runton and Westbury, where microwear suggests a browsing diet. This is presumably linked to different levels of temporal resolution into diet afforded...
by each technique, with mesowear providing a long term perspective and microwear seasonal and/or episodic dietary trait(s), and assuming also clumped (probably seasonal) mortality of the sample. In any case it is clear that S. hundsheimensis was a highly flexible feeder. This generalist adaptation has already been evidenced in the Middle Pleistocene of Germany, where dental mesowear indicated the presence of both grazing and browsing populations (Kahlke and Kaiser, 2011).

Merck’s rhinoceros, S. kirchbergensis, and the narrow-nosed rhinoceros, S. hemitoechus, co-occurring during the late Middle Pleistocene, show different tooth-wear patterns.

S. kirchbergensis shows low mesowear scores, low numbers of scratches (and high %0–17), and higher percentages of individuals with large pits (over 57%) (Table 1). They also tend to have wider scratches as reflected by the scratch width score (SWS), and most of them have more gouging. According to mesowear scores and number of scratches, S. kirchbergensis was browser or mixed feeder (Figs. 4 and 5). The presence of large pits and gouges, as well as larger scratches, suggests the consumption of fruits and seeds (Semprebon et al., 2004a, 2011). The sample from Grays Thurrock stands out because of its higher number of pits (Fig. 4). It plots (Semprebon et al., 2004a, 2011). The sample from Grays Thurrock stands out because of its higher number of pits (Fig. 4). It plots

S. hemitoechus shows high mesowear scores and high numbers of scratches (and low %0–17) compared to S. kirchbergensis (Table 1). It shows low percentages of individuals with large pits (Table 1). The mesowear and microwear patterns indicate grazing and mixed feeding dietary traits (Fig. 5), both indicating an adaptation to more open habitats than S. ursicus or S. hundsheimensis.

Throughout the Middle Pleistocene, S. kirchbergensis and S. hemitoechus show clear dietary differences: S. kirchbergensis has more browsing dietary traits, while S. hemitoechus has more grazing traits (Fig. 5). Nonetheless, each of these two species maintains a certain degree of dietary flexibility, as also reported in Germany and some localities in the UK for these two species, based on dental mesowear (van Asperen and Kahlke, 2015). In S. hemitoechus we observed a difference between the two proxies for the sample from Clacton (MIS 11), where mesowear suggests longer-term grazing while microwear indicates shorter-term browse-dominated mixed-feeding.

Finally, the woolly rhinoceros Coelodonta antiquitatis, at Crayford and Slade Green (MIS 7–6), shows a high mesowear score pointing toward a high proportion of grass in its diet (Fig. 5). The microwear pattern, however, with intermediate number of scratches, suggests a mixed-feeding diet with the inclusion of browse, at least during parts of the year (Figs. 4 and 5). At Kent’s Cavern (MIS 3), C. antiquitatis has the highest mesowear scores of all the rhinoceros samples analysed, and also high numbers of scratches (and low %0–17). Here, both mesowear and microwear patterns provide evidence of a strict grazing diet (Figs. 4 and 5).

Considering the Rhinocerotidae as a whole, and its history during the British Quaternary, we observe a broad temporal shift into more abrasive diets. This was achieved largely by taxonomic replacement, with the more specialized grazing species, Stephanorhinus hemitoechus and later Coelodonta antiquitatis, appearing during the Middle Pleistocene.

Tapiridae are present at the oldest locality, Red Crag Nodule Bed (Late Pliocene). Because tooth mesowear cannot be applied to bunodont teeth, the samples from these two groups were examined exclusively through microwear analysis. The sample of tapir (Tapirus sp.) shows a microwear pattern with low number of scratches and high number of pits, characteristic of browsers. Moreover, this sample shows that all individuals have large pits and gouges, as well as high numbers of puncture pits, indicating fruit-eating (Table 1).

3.1.3. Equidae

All the species of Equidae available in the collections were sampled: Hipparion sp. in the Red Crag Nodule Bed, the Early Pleistocene horses Equus bressanus and Equus stenonis, the early Middle Pleistocene Equus altidens, and the Middle and Late Pleistocene Equus ferus (including Equus mosbachensis). However, at some localities some species could not be included in this study.

![Fig. 6. Bivariate plot of the average numbers of pits and scratches in Equidae. Bars correspond to standard error of the mean (±1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).](image-url)
because of small sample size (few specimens, or specimens discarded for taphonomic reasons). *Equus suessenbornensis* is not included at all for the same reasons.

*Hipparion* sp. from the Red Crag Nodule Bed shows a mesowear score indicating grazing. However, it is one of the lowest mesowear scores recorded for all the Equidae sampled in this study (Table 1). The microwear pattern, with low numbers of scratches, indicates leaf browsing at the time of death (Figs. 6 and 7). Microwear analysis on various species has shown that hipparions were not exclusively grazers, but had broad dietary traits (Hayek et al., 1992) which is supported by the discrepancy between mesowear and microwear in this study.

Tooth microwear and mesowear patterns indicate intra- and inter-specific variability in horse feeding traits (Figs. 6 and 7). Mesowear scores of all samples are relatively high (MWS > 3.5), indicating high abrasiveness and hence grazing (Fig. 7). Tooth microwear shows a trend toward more grazing through the Pleistocene, from browser-dominated mixed-feeding traits in the Early Pleistocene horses from East Runton, to mixed-feeding and grazing traits in the Middle and Late Pleistocene populations. However, this shift across most of the microwear dietary spectrum needs to be viewed in the context of the temporal resolution of the microwear method. Tooth microwear only reflects the diet of the last days or week, consequently it is more sensitive to short-term changes in diet than mesowear. The biggest differences between meso- and microwear are found in the oldest sample at East Runton, mesowear suggesting a mostly grazing diet but microwear revealing that *Equus bressanus* could also browse.

Microwear patterns in Middle Pleistocene horses show a diversity of dietary traits, from browser-dominated mixed-feeding to grazing. The discrepancy with the mesowear data indicates a difference in diet at the time of death, especially from the populations from West Runton and Boxgrove (early Middle Pleistocene), as well as Brundon, Stoke Tunnel, and Stutton (MIS 7), all of interglacial age. Finally, the strongest grazing signal is found at the Late-glacial interstadial locality of Gough’s Cave (MIS 2), where both mesowear and microwear indicate an almost exclusive focus on grass in the horses’ diet.

In sum, tooth mesowear confirms the largely grazing habit of horses through the Pleistocene in Britain, but microwear suggests a frequent browsing element, especially for Early Pleistocene and some Middle Pleistocene populations. Browse-dominated mixed-feeding horses are known from tooth wear in Middle Pleistocene assemblages at Schöningen in Germany (Kuitems et al., 2015; Rivals et al., 2015b) and Deutsch-Altenburg 1 in Austria (Rivals, 2012). It is not possible to distinguish if this is low herbaceous browse or tree/shrub browse. DNA analysis of stomach contents of one horse (*E. ferus*) from Late Pleistocene Siberia revealed a high proportion of forbs (low-growing browse) in this animal’s last food, with sub-sidary grass, but no shrub or tree browse (Willerslev et al., 2014).

### 3.1.4. Cervidae

Pleistocene cervids have a high taxonomic diversity in Britain. Eleven taxa of cervids were sampled and examined.

In the Red Crag Nodule Bed, the cervids are attributed to three size categories (Lister, 1999): most specimens belong to a medium-sized deer (*cf. Cervus pardinensis*), a few to a large-sized deer (*cf. Cervus perrieri*) and one to the small-sized *cf. Procapyreolus cusanus*. *P. cusanus* was discarded from the study because of its small sample size. For the two other size categories, the dietary proxies are internally consistent (Figs. 8A and 9A). For the medium-sized deer (*cf. Cervus pardinensis*), mesowear score is intermediate (MWS = 2.14) and microwear pattern is also characterized by intermediate number of scratches. The two proxies suggest mixed-feeding traits. The large-sized deer (*cf. Cervus perrieri*) has a lower mesowear score (MWS = 1.50) and lower number of scratches; it is
Cervus, categorized as browse-dominated mixed feeder.

At East Runton, the dietary signal is shifted towards more browsing, as indicated by lower mesowear scores and higher numbers of scratches in Cervulaces gallicus and Eucladoceros spp. (Figs. 8C and 9B). It is important to note that the sample of Eucladoceros from East Runton includes three species (Lister, 1996) which cannot be morphologically separated on teeth on our current understanding. Few studies are available for comparison, but mesowear analysis on Eucladoceros sp. from the Early Pleistocene of Italy also indicates browsing habits (Strani et al., 2015).

In the Middle Pleistocene, cervids are diverse and abundant at most of the localities (Table 1), especially during the early Middle Pleistocene. Some of the genera persist into a less diverse Late Pleistocene cervid assemblage.

Among the Megacerini, early Middle Pleistocene jaws and maxillae from West Runton have provisionally been allocated to three species (Lister et al., 2010): ‘species A’ (cf. Megaloceros savini), ‘species B’ (cf. Præmegaceros verticornis) and ‘species C’ (cf. Præmegaceros dawkinsi). Among the teeth we sampled, only two specimens could provisionally be attributed to one of these species. The other specimens were not identifiable (isolated teeth) or not suitable for microwear. The two specimens allocated to ‘species B’ (NHM M17538 and M17741) belong to different individuals (Lister et al., 2010). Their microwear patterns show the same average number of scratches (see raw data available in the online Supplementary Material), suggesting a similar browsing diet for the two individuals. Among the unidentified megacerine specimens from West Runton, some have a similar pattern to ‘species B’ and others are different. Considering the West Runton megacerine sample as a whole, it plots among the browse-dominated mixed feeders (Fig. 8C).

At Pakefield, all megacerine material was provisionally referred to ‘species A’ (cf. M. savini) (Lister et al., 2010) and all specimens fit within the browsing species (Fig. 8C). For the unidentified megacerine in correlated deposits at Kessingland, mesowear indicates grazing dietary traits while microwear suggests the incorporation of some browse during parts of the year. At Boxgrove, the specimens were referred to ‘species B’ (cf. Præmegaceros verticornis) and plot among the browse-dominated mixed feeders. The individual variation observed at these localities does not permit us to detect any pattern among the three species found in the early Middle Pleistocene.

In the late Middle to Late Pleistocene, Megaloceros giganteus has tooth-wear patterns indicating a wide range of dietary behaviour including grazing, leaf browsing and mixed feeding, but generally tending toward mixed feeding and grazing (Figs. 8C and 9B). The samples of M. giganteus from Grays Thurrock (MIS 9) and Ilford (MIS 7) show an average annual signal corresponding to mixed feeding, but microwear suggests a shift toward more grass at the time of mortality.

The Middle and Late Pleistocene red deer (Cervus elaphus) shows a wide range of mesowear and microwear values (Figs. 8A and 9A) compared to other cervids, corresponding to significant dietary plasticity (Lister, 1984). Globally, the two proxies point toward a preference for mixed feeding and leaf browsing. However some discrepancies between the mesowear and microwear data indicate periodic shifts in individual diet, in particular at Boxgrove, Grays Thurrock, and Gough’s Cave. Previous tooth microwear and mesowear analyses on red deer from European localities of the same age range revealed a similar pattern, with high variability in dietary traits (Rivals et al., 2009b).

The Middle and Late Pleistocene fallow deer, Dama roberti (Breda and Lister, 2013) and Dama dama (including D. d. clactoniana and D. d. dama) have tooth wear patterns pointing toward browsing. Dama cf. roberti from the early Middle Pleistocene of Westbury sub Mendip, and Dama dama from Swanscombe (MIS 11) are the only two Dama samples which provide a mixed-feeding signal from mesowear, but the tooth microwear indicates pure leaf browsing. This would suggest seasonal mixed feeding for those...
samples. A similar result, showing mixed feeding from mesowear and leaf browsing from microwear, has been reported for *D. d. clactoniana* from the Middle Pleistocene of Caune de l’Arago in France (Rivals et al., 2008). All the other populations of *D. roberti* and *D. dama* have consistent mesowear and microwear patterns indicating leaf browsing (Figs. 8B and 9A) and are likely to be related to foraging in closed habitats, as also suggested by studies of stable isotopes at various localities in the Middle Pleistocene of

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**Fig. 9.** Low scratch percentages (%0−17), mesowear scores (MWS), and dietary changes in Cervidae through geological time. (A) *Cervus* and *Dama*. (B) Other species. The grey areas correspond to the range of values for the extant mixed feeders (see Fig. 5).
Atapuerca, Spain (García García et al., 2009).

The Middle Pleistocene roe deer (*Capreolus capreolus*) has very low mesowear scores (between 0 and 0.5) and low numbers of scratches at West Runton, Boxgrove and Grays Thurrock. The two proxies, tooth mesowear and microwear, are in agreement and both indicate that the roe deer was a strict browser (Fig. 9C). It seems that *C. capreolus* had dietary habits which were not subject to seasonal changes.

Fig. 10. Bivariate plot of the average numbers of pits and scratches in Bovidae. Bars correspond to standard error of the mean (± 1 S.E.M.) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers (B) and grazers (G) from Solounias and Semprebon (2002) and Rivals et al. (2010).

Fig. 11. Low scratch percentages (%0–17), mesowear scores (MWS), and dietary changes in Bovidae through geological time. The grey areas correspond to the range of values for the extant mixed feeders (see Fig. 5).
Finally, the reindeer (*Rangifer tarandus*), which is represented in our samples only at Kent’s Cavern, shows a mixed feeding habit (Figs. 8C and 9B) which may be related to seasonal migration as seen in last-glacial and extant populations and reflected in antler shedding (Aaris-Sørensen et al., 2007), microwear (Rivals and Solounias, 2007) and stable isotopes (Britton et al., 2009, 2011; Drucker et al., 2012).

### 3.1.5. Bovidae

Bovidae are represented by the Late Pliocene *Parabos* sp., the Early Pleistocene *Leptobos* sp., and by two genera that are present in the Middle and Late Pleistocene: *Bos* and *Bison*. The separation of teeth of the latter two can be problematic, especially when both genera are present at a locality. In such cases, the samples are labelled here as *Bos/Bison*. Diagnostic specimens were identified as belonging to *Bos primigenius*, *Bison schoetensacki*, and *Bison priscus*.

The late Pliocene *Parabos* sp., from the Red Crag Nodule Bed, has a mesowear score plotting at the boundary between browsers and grazers (*MWS* = 2) and a tooth microwear pattern with low number of scratches (and high %0) that indicates browsing habits (Figs. 10 and 11). The discrepancy between the two proxies suggests general mixed feeding traits but a more browsing diet at the time of death.

The Early Pleistocene *Leptobos* sp. from East Runton shows mesowear similar to *Parabos* sp., indicating mixed feeding (Fig. 11). Only one tooth was suitable for microwear at that locality; its microwear pattern is consistent with mixed feeding.

The early Middle Pleistocene *Bison schoetensacki* from Mundesley, West Roniton, Pakefield and Westbury-sub-Mendip plot into the graze-dominated mixed feeding range of mesowear (Fig. 11). Microwear data are only available at West Runton and indicate grazing traits, at least at the time of death (Figs. 10 and 11), suggesting periodic shifts towards the consumption of more grass.

In the Middle and Late Pleistocene, where *Bos* and/or *Bison* are present, the mesowear shows a narrow range of variation (*MWS* = 2 to 3.28) while the microwear data cover the complete dietary spectrum, from grazing to browsing. To explore further, unidentified *Bos/Bison* samples were excluded and only the localities with identifiable *Bos primigenius* or *Bison priscus* were considered. In the interglacial assemblages of Ilford and Aveley (MIS 7), Grays Thurrock (MIS 9), and Clacton (MIS 11), the large bovid is *Bos primigenius*, which is notably a mixed feeder to browser. *Bison priscus*, scorable here only in Late Pleistocene localities, tends towards mixed feeding and grazing (Fig. 11). Tooth microwear confirms these patterns but the higher intraspecific ranges of variation suggest temporal variability in both *Bos*.

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**Fig. 12.** Low scratch percentages (30–17), mesowear scores (MWS), and dietary changes for all taxa in selected localities. Abbreviations: Aa – *Anancus arvernensis*; B/B – *Bos/Bison*; Bo – *Bos primigenius*; Bp – *Bos priscus*; Bs – *Bison schoetensacki*; Ca – *Coelodonta antiquitatis*; Ce – *Capreolus capreolus*; Ce – *Cervus elaphus*; Cpa – *Cervus parvidensinis*; Cpe – *Cervus perrieri*; Cg – *Cervulus gallicus*; C – *deer indet.*; Cervus?; Dd – *Dama dama*; Dr – *Dama roberti*; Ea – *Equus altidens*; Eb – *Equus bressanus*; Ef – *Equus ferus*; Es – *Equus stenonis*; Eucl. – *Eucladoceros sp.*; Ha – *Hippopotamus amphibius*; Hi – *Hipparian sp.*; Lep. – *Leptobos*; m – *megacerine sp.*; Mb – *Mammuthus borsoni*; Mg – *Megaloceros giganteus*; Mn – *Mammuthus meridionalis*; Mp – *M. primigenius*; Mt – *M. trogontherii*; Pa – *Palaeoloxodon antiquus*; Par. – *Parabos*; Pp – *Propotamochoerus provincialis*; P – *Paras*; Rb – *Rangifer tarandus*; Sb – *Sus arvernensis*; Se – *Stephanorhinus etruscus*; Sh – *S. hemitoechus*; Sk – *S. kirchbergensis*; Su – *S. hunshheimensis*; T – *Tapirus sp.*
primigenius and Bison priscus diets.

4. Discussion

4.1. Resource partitioning

Resource partitioning was examined at a selection of localities where tooth wear from at least three species was sampled and provided suitable data. Following this criterion, 12 localities were selected for a comparison of meso- and microwear patterns among all ungulates (Fig. 12).

4.1.1. General patterns

At all sites selected, mixed feeders are always present together with at least one of the two strict dietary groups, grazers and/or browsers (Fig. 12). The species present at each locality are spread over a large part of the dietary spectrum. In general, species at a locality are separated in their diets, i.e. there is evidence of resource partitioning among species. This is very clearly seen, for example, at Kent’s Cavern (MIS 3), where six species do not, with one exception, overlap in either microwear or mesowear scores.

There are exceptions, however, e.g., the clustering of three cervids and two rhinos at Grays Thurrock (MIS 9), or various cervid species at Boxgrove (cf. MIS 13). However, the discrepancy often observed between the two proxies (as described in section 3) suggests that resource partitioning could occur on a temporal or spatial basis. For example, the two rhinoceros species from Grays Thurrock have a very similar mesowear pattern indicating mixed feeding, while tooth microwear indicates that the preserved samples of the species represent animals which had different diets at the time of death. The same occurs at West Runton (cf. MIS 17) between Bison schoetensacci and Stephanorhinus hundsheimensis, at Ilford and Aveley (MIS 7) between Megaloceros giganteus and Bos primigenius, and at Kent’s Cavern (MIS 3) between Cervus elaphus and Bison priscus.

In a few cases, species have very similar tooth-wear patterns both in meso- and microwear, suggesting competition for the use of similar resources. In some case, competition could have been mitigated by grazing succession, although in the African test case (Fortelius and Solounias, 2000) tooth-wear differences were observed, as successive species take different plant parts. This pattern occurs at Boxgrove and West Runton between Capreolus capreolus and Dama roberti. It should be recognized, however, that the relatively coarse categorization into browsers and grazers may conceal differences of detail in the combination of plant taxa consumed by different mammal species.

4.1.2. Intra-group patterns

Some interesting patterns are evidenced among species in the main taxonomic groups when more than one species occurs at a locality.

Among Proboscidea, Palaeoloxodon antiquus is always found to be mixed-feeding to browsing (Fig. 12). Mammutus primigenius is strongly grazing in the last cold stage of Kent’s Cavern, as is its predecessor M. trogontherii in the early Middle Pleistocene of Pakefield. Very interestingly, however, remains attributed (Lister et al., 2005) to late M. trogontherii at Ilford (MIS 7), appear mixed-feeding. At this site, where both P. antiquus and M. trogontherii are present in the same horizon (Schreve, 1997), both are mixed-feeders but the former is more browse-dominated and the latter more graze-dominated (Fig. 12). See also discussion about Crayford, below.

For the Rhinocerotidae, as reported earlier, S. kirchbergensis shows lower mesowear scores and lower numbers of scratches (and higher %0–17) than S. hemitoechus at all localities where they co-occur (Table 1 and Fig. 12). The two species always plot in the expected direction, i.e. S. hemitoechus more grazing, S. kirchbergensis more browsing. At most localities S. kirchbergensis plots among the cervids (such as Cervus elaphus or Dama dama) while S. hemitoechus is often closer to Equus ferus (e.g. at Ilford and Aveley (MIS 7) and at Grays Thurrock (MIS 9); see comment about Crayford below).

Among cervids, Capreolus capreolus, Dama roberti and D. dama (as well as the unidentified megacerines where present) always display a strong browsing signal, while Cervus elaphus and Megaloceros giganteus tend more towards mixed-feeding (Fig. 12). When Dama and Cervus co-occur in the same assemblage, microwear and mesowear consistently indicate a more browsing diet for Dama than Cervus. This pattern is evidenced in the single assemblages sampled at West Runton, Boxgrove, Grays Thurrock and Joint Mitnor Cave (Figs. 9 and 12).

At East Runton, even though its widespread antlers suggest open habitat, Cervulaces gallicus appears as a browser, as proposed on the basis of the low-crowned teeth (Lister, 1981). Considering all these data, the paleoecology of C. gallicus can be proposed as an open-ground soft-leaf feeder (like the reindeer), although a lightly-wooded habitat, as proposed by Breda (2008), cannot be ruled out.

4.2. Implication for paleoecological interpretation at selected localities

The dietary spectrum of a herbivore community as a whole contributes to our understanding of the vegetational environments at a given locality, especially where direct palaeobotanical evidence is limited or lacking. Some examples, from sites with three or more species, are given below.

The Red Crag Nodule Bed or Basement Bed (ca. 3.0–2.7 Ma) is characterized by an exotic fauna including Tapirus arvernensis, Hipparion sp., Mammut borsoni, Propotamochoerus provincialis, and at least three species of deer. All examined species are mixed feeders or browsers, except the hipparions which have a mesowear signal typical of grazers, although the microwear indicates periodic browsing (Fig. 12). This browse-dominated community corresponds to pollen evidence for temperate forest (Head, 1998a).

At West Runton, all scorable species fit into the mixed feeding and browsing categories, corresponding to temperate climatic conditions during the Cromerian interglacial with an ecosystem dominated by forest, but also with some open areas (Lister and Stuart, 2010). No pure grazers are evidenced: even the stenonid horse Equus altidens has a browsing microwear signature, but its mesowear could not be scored, nor could that of the larger E. suessenhornensis.

At Swanscombe, where palaeobotanical evidence is limited, micro- and mesowear show that the fauna was mainly mixed-feeding. Notably, the horse has the lowest mesowear value (i.e., the least exclusively grass-eating diet) of all Equus ferus samples analysed here (Fig. 12). This corresponds to the correlation of the lower levels at Swanscombe to the first half of the Hoxnian interglacial, MIS 11 (Ashton et al., 2008) and the attribution of the fauna to predominantly forested conditions (Schreve, 2001b), though some grassy areas were available to the mixed-feeders.

Based on the composition of the mammalian assemblage, Schreve (1997) suggested that Grays (MIS 9) was more strongly wooded than Ilford and Aveley (MIS 7), where the faunas are characterized by a predominance of open-habitat or parkland species. The browsing to browse-dominated mixed-feeding clustering of the mesowear values for all species at Grays Thurrock except horse supports this conclusion.

Interpretation of the Crayford sites is complicated by uncertainty over the stratigraphic provenance of the material;
mammalian fossils were recovered from underlying gravels and overlying brickearths, but the origin of individual fossils is not always clear. Currant (1986) suggested that the cold elements of the fauna (Coelodonta antiquitatis and Ovibos moschatus) came from later (MIS 6) deposits than the main MIS 7 fauna, although accounts from the time of excavation report the former species from the underlying gravel and the latter from the overlying brickearth (Schreve, 1997). The tooth wear data indicate mixed-feeding or grazing for all species, suggesting a relatively open phase even in MIS 7. Equus ferus and Stephanorhinus hemitoechus both have a remarkably similar dietary profile to Coelodonta antiquitatis, and since the former two species are not doubted to have occurred in MIS 7, the attribution of the Crayford C. antiquitatis to MIS 7 cannot be excluded on dietary grounds. As discussed above, microwear in C. antiquitatis at Crayford suggests a mixed-feeding diet with the inclusion of browse, at least during parts of the year. This indicates the availability of significant numbers of trees or shrubs at that time, which confirms that the Crayford and Slade Green deposits may belong at least in part to the interglacial MIS 7 rather than to the cold stage MIS 6 (cf. Scott et al. 2011). The similarity in both meso- and microwear of Stephanorhinus hemitoechus, Equus ferus and C. antiquitatis may even suggest competition for the use of similar resources if all three species came from the same Crayford Gravels as indicated in contemporary reports (Schreve, 1997).

S. kirchbergensis, conversely, is reported only from the brickearth, and shows the same dietary differentiation from S. hemitoechus as at other localities (including those of MIS 7 age). Mammutthus trogontherii and Palaeoloxodon antiquus are graze-dominated and browse-dominated mixed feeders, respectively, as at Ilford (see above); both species apparently co-occurred in the Crayford Gravel although M. trogontherii also extended into the brickearth (Schreve, 1997).

Kent’s Cavern is a celebrated last cold stage site; the main cave-earth fauna is dated to ca. 40–20 ka (Higham et al., 2011). In Britain in general this period has been reconstructed as an open steppe-tundra, but there is also evidence for growth of boreal trees, at least at times (West, 2000), and this seems especially plausible for southern hilly country such as the vicinity of Kent’s Cavern where, however, direct palaeoethnological evidence is poor. The browse component in the mixed-feeding diets of Cervus elaphus and Megaloceros giganteus, and even Bison priscus from the Kent’s Cavern main cave earth supports the presence of trees, shrubs and/or dicotyledonous herbs in the area. The presence of some wooded areas around Kent’s Cavern is supported rather negative bone collagen δ13C values observed in Cervus elaphus remains (Bocherens and Fogel, 1995). It is an interesting and unanswered question whether the development of these plant types, and the animals that depended on them, was a permanent feature in this region or dates only to the short MIS 3 interstadials. The reindeer (Rangifer tarandus) has a strong browsing to browse-dominated mixed-feeding signature which indicates a diet of dicotyledonous plants. The scratch width and the proportion of large pits and gouges fits with extant caribou populations (Rivals and Solounias, 2007) which feed on low plants, including lichens and mosses, confirming the reindeer from Kent’s Cavern as an open-country animal.

5. Conclusion

The combination of mesowear and microwear provides a powerful tool for examining dietary flexibility and resource partitioning at different temporal scales. Mesowear provides a dietary signal integrated over several months at least, and allows us to contrast more eurytopic species (e.g. Megaloceros giganteus, ranging from grazing to browse-dominated mixed-feeding) to more stenotypic (e.g. Capreolus capreolus, always browsing). Broad dietary shifts in the faunas a whole are also evident between climatic phases (Section 4.2 above; Fig. 12), and result from both species turnover and dietary shifts in flexible species common to the sites.

Dental microwear provides an independent proxy that records relatively short-term diet. For stenotopic species (e.g. the browser Capreolus capreolus or the grazer Coelodonta antiquitatis) the two proxies tend to match. For other species, however, there is commonly a discrepancy between meso- and microwear signals that is clearly informative but not always easy to interpret. The discrepancy is not systematic in direction, e.g. M. giganteus shows a more grazing signal in mesowear than microwear at Kent’s Cavern (MIS 3), but a more browsing signal in mesowear than microwear at Ilford and Avoley (MIS 7) and Grays Thurrock (MIS 9). The differences can be extreme, e.g. Stephanorhinus kirchbergensis at Swancombe shows graze-dominated mixed-feeding in mesowear but 100% browsing in microwear. The microwear signal is clearly capturing one part of the individual’s mixed diet in the days to weeks leading up to the time of death. Since the microwear signal for a fossil sample is averaged over all available individuals, a consistent difference from the mesowear average implies that individuals tended to die at a time when they were eating mainly one element of their mixed diet. This is most easily interpreted as a seasonal effect, and since the model requires mortality to be concentrated in the season when a particular food was being taken, it may be that this food, or its level of productivitiy, was suboptimal and was taken at that season only because the optimal food was not available. In other words, the animals tended to die at a time of year when their normal food was in short supply so they were forced to eat suboptimal food. In rare cases, the microwear signal appears to be a small minority of the total diet indicated by mesowear. An example is the Hipparion from the Red Crag Basement Bed, whose diet is grazing on the basis of mesowear, but whose microwear indicates browsing around the time of death.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2016.06.007.

References


495–500.


