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

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ABSTRACT

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 paleodiets (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;

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Schreve, 2001a; Currant and Jacobi, 2011; Preece and Parfitt, 2012; Penkman, 2013). Details of the localities and dating evidence are given in the references cited in Table 1. The geographical position of the British Isles also made its fauna particularly sensitive to climatic changes, with repeated taxic turnover of mammals between cold and warm phases. Together these factors provide considerable potential for examining dietary shifts and niche partitioning among herbivorous mammal species.

2. Material and methods

2.1. Material

The material studied was selected from 33 Pleistocene localities in Britain spanning the last 2.6 Myr (Fig. 1; Table 1). We analysed large herbivorous mammals among the Proboscidea (Gomphotheriidae and Elephantidae), Perissodactyla (Rhinocerotidae, Equidae, Tapiridae), and Artiodactyla (Cervidae and Bovidae). In addition, we studied the mammal assemblage from the Red Crag Nodule Bed, of Late Pliocene age (ca. 3.0–2.6 Ma).

Specimens were sampled in 2010 and 2012 from the following 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 microwear 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 tooth 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 mm^2 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