



Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation

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ABSTRACT

Ungulate diets may vary following differences in vegetation, and their body size is affected by a complex set of ecological and physiological variables. Here we analyse Middle and Late Pleistocene British and German ungulate palaeocommunities to test whether there are significant correlations of diet and body size of ungulate species with vegetation openness. We also evaluate the role of interspecific interactions on the diet and body mass of the ungulate species. We use mesowear for dietary analyses and regression equations for estimating body mass from skeletal measures. The results show a correlation between ungulate mesowear and non-arboreal pollen percentages of the localities, but there are marked differences between species. Body masses of rhinoceroses (Rhinocerotidae) and deer (Cervidae) are on average higher in open environments, whereas aurochs (*Bos primigenius*) does not show clear connection of body size with vegetational conditions, and bison (*Bison* spp.) and wild horses (*Equus ferus*) have on average smaller mean size in more open ecosystems, possibly because of high population densities and resulting resource limitations. It is evident that the correlation of body size and vegetation openness is not straightforward and is likely to reflect the varying effects of population density, ecological adaptations and environmental conditions on body size in different species.

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INTRODUCTION

The composition of living herbivorous mammal communities generally reflects vegetation patterns: grazing and grass-dominated mixed-feeding species are more abundant in grassland environments than in forest environments, which are characterised by browsers and browse-dominated mixed-feeders (Gordon and Prins, 2008). However, diets within individual ungulate species can vary considerably in open versus closed environments and in different ungulate assemblages following the availability of resources, as well as resource competition with, and resource facilitation by, other ungulate species (e.g., Langvatn and Albon, 1986; Hobbs et al., 1996; Latham, 1999; Arsenaault and Owen-Smith, 2002; Stewart et al., 2002). Variation of body size in herbivorous mammal species is also probably influenced, at least in part, by open versus closed habitats and by the quality and abundance of vegetation, in ways that may vary with species' adaptations (Jarman, 1974; Langvatn and Albon, 1986; Guthrie, 1990; Bro-Jørgensen, 2008). In this study we analyse local patterns of diet of some of the most abundant ungulate species from Middle and Late Pleistocene mammal localities of Western and Central Europe in order to explore their relationship with vegetation reconstructions. We also examine whether body size is correlated with vegetation type and diet. Moreover, we compare the patterns of diet and body size across ungulate species to evaluate the role of different ecological strategies and potential resource competition between the species.

Several recent studies have demonstrated dietary variation in fossil ungulate species from localities with different environmental conditions. For example, Kahlke and Kaiser (2011) used mesowear analysis on the Middle Pleistocene rhinoceros *Stephanorhinus hundsheimensis* in Germany. The population from the cool-climate of Süssenborn has, on average, a mesowear signal indicating a more abrasive diet than that of the interglacial of Voigtstedt. Kaiser (2004) did a similar analysis for the Late Miocene populations of the equid *Hippotherium primigenium* from Höwenegg and Eppelsheim, Germany. He noted that the population from Höwenegg had a mesowear signal indicating browsing diet roughly similar to that of the modern Sumatran rhinoceros (*Dicerorhinus sumatrensis*), whereas the population from Eppelsheim had a dietary signal resembling that of the common waterbuck (*Kobus ellipsiprymnus*), which is a grazer. Palaeoenvironmental data indicate that Höwenegg was probably a subtropical

mesophytic forest, which is supported by the overall composition of the mammal fauna, whereas Eppelsheim would likely have included at least seasonally abundant grassy vegetation, which is supported by palaeobotanic finds (Kaiser, 2004). Another example is the study by Rivals et al. (2015a) showing intraspecific variation in the diets of proboscidean species *Anancus arvernensis*, *Mammuthus rumanus* and *M. meridionalis* between Early Pleistocene localities in Europe, based on tooth microwear analysis.

It can be hypothesised that differences in the diets of local fossil populations of a species reflect differences in local vegetation, and probably also the presence of competitors. We have included all the most common species of large ungulates from several British and German Middle and Late Pleistocene localities (see Table 1) to test the correlation of their dietary signals with environmental proxy data obtained from pollen records. Non-arboreal pollen percentages (NAP %) can be used as rough estimates of vegetation openness (Svenning, 2002), although they do not allow precise quantitative estimates of the extent of open landscape, or productivity (Sugita et al., 1999). It can be predicted that the broad dietary composition of the ungulate community is correlated with the degree of openness of vegetation, although it is likely that some species are so specialized in utilizing certain kinds of plant material that their diet does not vary greatly across localities with different plant communities, and they would be absent if their preferred food were missing.

Correlations of ungulate body mass with environmental characteristics can also be predicted but they are likely to be complex. Body size is affected by a variety of physiological and ecological variables, and it may be difficult to separate their effects on the body size of individual species (e.g., Jarman, 1974; Peters, 1983; West et al., 1997; Gillooly et al., 2002; Haskell et al., 2002; Damuth, 2007). Body size has been postulated to relate to temperature, via its effects on heat conservation (e.g., Bergmann, 1847; Peters, 1983), but as a general explanation of mammalian size variation this idea has been strongly criticized (Geist, 1987; Lister, 1992). For herbivorous mammals, more likely determinants include habitat structure, social structure (e.g., Jarman, 1974), and the availability and abundance of their optimal food (e.g., Langvatn and Albon, 1986). In particular, large body size could be associated with open environments for a number of reasons. First, because of mostly seasonally harsh climates but long sunshine hours

and fertile soils created by glacial erosion, the open environments of glacial Europe comprised seasonally highly productive plant communities with low chemical defences, thus providing abundant and good-quality sources of food for herbivores (Guthrie, 1990; Zimov et al., 1995; Geist, 1998). Second, large body size enables the processing of large quantities of this often digestively challenging plant food, and also increases resistance to seasonal shortages of food and water (Peters, 1983; Lindstedt and Boyce, 1985; Clauss et al., 2003) during the harsh winters of glacial episodes. Third, large size may help in predator avoidance because of its benefit for energy-efficient locomotion in open environments (Peters, 1983). Fourth, it has been suggested that ungulates tend to form larger groups in open environments and increasing competition for mates among males, which could lead to selection for larger body size (Geist, 1971). Finally, it has been suggested that smaller body sizes could be beneficial in closed environments because of easier maneuverability (Bro-Jørgensen, 2008). However, the relationship between body size and vegetational environment is likely to be complex: body size could also be smaller in open habitats, especially in gregarious ungulate species, because their tendency to form larger groups in open environments could in fact result in increased population densities (Khan et al., 1996; Borkowski, 2000). This could limit the resources available for each individual, resulting in smaller body size via intraspecific competition (e.g., Wolverton et al., 2009). It might also be hypothesised that a shift to suboptimal diet forced by vegetational change or competition might adversely affect the body size of individuals in a local population. Here we examine these relationships by comparing body masses of key ungulate species across localities with vegetation reconstructed from pollen data and with their diets using mesowear analysis.

MATERIALS AND METHODS

Localities and Collections

Middle and Late Pleistocene localities from Britain and Germany were chosen for this study because terrestrial Pleistocene deposits in these regions are extensive and stratigraphically well understood (e.g., Schreve and Bridgland, 2002), and there are many localities with both mammal and pollen records. The ungulate fossil material was studied by Juha Saarinen in the collections of the Natural History Museum of London (NHML),

Torquay Museum (TM), the Sedgwick Museum of Geology, Cambridge (SMC), University Museum of Zoology, Cambridge (UMZC), Ipswich Museum (IM), British Geological Survey at Keyworth (BGS), Staatliches Museum für Naturkunde, Stuttgart (SMNS), Staatliches Museum für Naturkunde, Karlsruhe (KMNS) and the Quaternary Palaeontology Research Station of the Senckenberg institute, Weimar (IQP).

To ensure adequate sample sizes, only localities rich in Middle or Late Pleistocene large mammal remains were chosen. Even so, not all species are represented by statistically significant samples. Analyses of the total ungulate faunas were performed only for localities where key species representing more than one ecological guild (specialised browsers, specialized grazers and/or more generalistic mixed-feeders) were present. All species with large enough sample sizes (at least >3, mostly >10) were included in the locality-based analyses. Thus, while taphonomic biases should be borne in mind, we expect the results to adequately reflect the ecomorphological profiles of the faunas.

With the exception of pigs and hippopotamuses, all the ungulate species (Perissodactyla and Artiodactyla) with sufficient sample sizes were included (Table 1). Suidae was excluded because in the Middle and Late Pleistocene of Europe it is represented only by the wild boar (*Sus scrofa*), the fossils of which are rare, and the original mesowear scoring method of Fortelius and Solounias (2000) cannot be applied to bunodont teeth. *Hippopotamus* was excluded from the dietary analyses for the same reason, although it probably had a significant role in some interglacial mammal communities, such as the Ipswichian of Barrington, England (Gibbard and Stuart, 1975; Turner, 1975; Stuart, 1976; Stuart and Gibbard, 1986).

Mesowear Analysis

As a proxy for diet, we utilise the mesowear method. This is based on the abrasiveness of plant material consumed by herbivorous mammals and its effect on tooth wear. At present it is understood that low abrasiveness of diet (e.g., dicotyledonous leaves) allows attrition (tooth-to-tooth wear) to dominate, leading to high and sharp tooth cusps, whereas more abrasive components (especially grass) cause the cusps to wear down, becoming lower and rounder. Highly abrasive diet typical for grazers causes low and blunt wear relief on the teeth. This method has been successfully applied to fossil ungulate teeth (e.g., Kaiser, 2004; Muhl-

bachler and Solounias, 2006; Rivals et al., 2007; Croft and Weinstein, 2008; DeMiguel et al., 2008; Kahlke and Kaiser, 2011; Mithlbackler et al., 2011) and is grounded in studies of modern ungulates of known diet (e.g., Fortelius and Solounias, 2000; Clauss et al., 2007). Morphological adaptations improving wear resistance of herbivorous mammal teeth, such as increased molar crown height (hypsodonty), reflect the conditions under which they evolved and have been shown to be adaptive both to environmental factors (such as precipitation and erosion rates, which regulate the accumulation of mineral particles on plant material), as well as to dietary factors (abrasive food items, mainly grass). The mesowear signal, on the other hand, has been demonstrated to show a purely dietary signal (non-abrasive vs. abrasive plant material, or browse vs. grass) (Louys et al., 2012; Kaiser et al., 2013; Kubo and Yamada, 2014). Mesowear analysis will thus provide a robust proxy for ungulate diet irrespective of abiotic environmental and climatic effects.

Mesowear scoring was undertaken following Fortelius and Solounias (2000). Second upper molars were predominantly used, while first or third upper molars were chosen in some cases for increasing sample sizes. Lower molars of Cervidae were used only in a couple of cases to complement the data, when the mesowear was clearly high and sharp, in which case it would be sharp in upper molars as well (see Kaiser and Fortelius, 2003). For analysing dietary signals between the localities, mesowear scores were transformed into univariate values on a scale from 1 (low abrasiveness of diet, attrition-dominated tooth wear) to 3 (high abrasiveness of diet, abrasion-dominated tooth wear) by using the following method:

1. The shape of the cusps was coded as a numeric value from 1 to 3 (1 = sharp, 2 = rounded, 3 = blunt) and the height of the cusps as 1 or 3 (1 = high, 3 = low).
2. In the sample of teeth of a species from a locality, "shape value" was calculated as the arithmetic mean of the shape values and "height value" as the arithmetic mean of the height values.
3. The mesowear value for the sample was calculated as the arithmetic mean of its "shape value" and "height value".

Note that this method of calculating mesowear as a univariate value is similar in principle to those used by Rivals et al. (2007) and Kaiser (2011), but instead of using numeric values from 0 to 3 to reflect the combined cusp height and shape of each individual and then averaging across the sample, we obtain sample averages of cusp height

and shape separately and then combine to calculate the final mesowear value. This was done because it more closely follows the original methodology, as introduced by Fortelius and Solounias (2000), allowing for all combinations of cusp shape and relief. To validate this approach, we calculated univariate mesowear values from the original mesowear data for extant species used by Fortelius and Solounias (2000) and tested them by using the same statistical approaches as used by these authors. We performed hierarchical clustering analysis to see if our mesowear values cluster the modern species into biologically meaningful dietary groups, and discriminant analyses to test how well our mesowear values classify the modern species into the "traditional" dietary classes of browsers, mixed-feeders and grazers (see Fortelius and Solounias, 2000). The results of those tests support our approach and are given in Appendix 1.

Body Size

Previous studies of body size variation in Pleistocene mammals have compared individual skeletal measurements (e.g., Lister, 1994) or body mass estimates (e.g., Alberdi et al., 1995) in a single genus or species. Body mass estimates based on regression equations between bone measurements and body masses across a given modern mammal group (e.g., Damuth and McFadden, 1990) provide a way of combining body size data obtained from several skeletal or dental measures. The benefits of this approach are that body mass is a universal measure of size comparable between organisms of different body plan, and that it enables large, statistically significant amounts of material to be analysed.

For the body mass analyses only postcranial bone measurements were used as these are generally the best predictors of body mass (e.g., Damuth and McFadden, 1990), and the addition of dental measurements would require separate analysis as they have different scaling relationships with body size (Damuth and McFadden, 1990). The measurements comprise antero-posterior and medio-lateral diameters of epiphyses and diaphyses of metapodials, tibiae, radii, humeri and femora. Measurement protocols follow Scott (1990). The measurements were taken with digital calipers with 0.1 mm precision. Body mass estimates were based on the regression equations of Scott (1990) for all species except for Rhinocerotidae, and Fortelius and Kappelman (1993) for Rhinocerotidae, based on body masses and skeletal measurements of a range of extant species. Given the

TABLE 1. Localities used in this study with their ages, species analysed and NAP %.

Locality	Country	Age	Species analysed in this study	Locality used in community-level analyses	Minimum NAP %	Maximum NAP %	Mean NAP %	Reference for age	Reference for pollen record
Star Carr	UK	MIS 1	<i>B. primigenius</i> , <i>C. elaphus</i> , <i>C. capreolus</i> , <i>A. alces</i>	yes	15.0	42.0	25.3	Innes et al., 2011; Penkman et al., 2011	Clark, 1954
Late-glacial localities (pollen zone III)	Ireland	MIS 2, Allerød-interstadial	<i>M. giganteus</i>	yes	45.0	93.0	74.8	Watts, 1997; Barnosky, 1986	Watts, 1977
Gough's Cave	UK	MIS 2, Bølling interstadial (GI-1e)	<i>E. ferus</i> , <i>C. elaphus</i>	yes	89.0	94.0	91.7	Currant and Jacobi, 2001; Jacobi and Higham 2009	Leroi-Gourhan, 1986
Whitemoor Haye	UK	MIS 3	<i>C. antiquitatis</i>	no	82.3	96.7	89.5	Schreve et al., 2013	Schreve et al., 2013
Kent's Cavern (cave earth)	UK	MIS 3	<i>E. ferus</i> , <i>B. priscus</i> , <i>C. elaphus</i> , <i>R. tarandus</i> , <i>M. giganteus</i> , <i>C. antiquitatis</i>	no				Bocherens and Fogel, 1995; Currant and Jacobi, 2001	
Isleworth	UK	MIS 5a-d	<i>B. priscus</i> , <i>R. tarandus</i>	no	86.9	94.0	90.4	Penkman et al., 2011; Bates et al., 2014	Kerney et al., 1982
Wretton (Devensian strata)	UK	MIS 5a-d	<i>B. priscus</i> , <i>R. tarandus</i>	no	80.0	98.0	89.0	Lewin and Gibbard, 2010	West et al., 1974
Villa Seckendorff	Germany	MIS 5a-d	<i>E. ferus</i> , <i>E. hydruntinus</i> , <i>B. priscus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>M. giganteus</i> , <i>C. antiquitatis</i>	no				Ziegler, 1996	
Aufhausener Höhle	Germany	Last glacial (Würmian)	<i>E. ferus</i> , <i>C. antiquitatis</i>	no				Kley, 1966	
Upper Rhine valley localities: Brühl (Koller), Otterstadt, Edingen, Ketsch, Lampertheim in der Tanne	Germany	Late Pleistocene	<i>B. primigenius</i> , <i>C. elaphus</i> , <i>C. capreolus</i> , <i>D. dama</i> , <i>A. alces</i> , <i>S. kirchbergensis</i> , <i>C. antiquitatis</i>	no				Koenigswald and Beug, 1988; Dietrich and Rathgeber, 2012	

TABLE 1 (continued).

Locality	Country	Age	Species analysed in this study	Locality used in community-level analyses	Minimum NAP %	Maximum NAP %	Mean NAP %	Reference for age	Reference for pollen record
Reilingen	Germany	MIS 5e?	<i>S. hemitoechus</i>	no				Ziegler and Dean, 1998	
Taubach	Germany	MIS 5e	<i>E. ferus</i> , <i>B. priscus</i> , <i>C. elaphus</i> , <i>C. capreolus</i> , <i>S. kirchbergensis</i>	no				Brunnacker et al., 1983; van Kolfschoten, 2000	
Barrington	UK	MIS 5e	<i>B. priscus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>D. dama</i> , <i>S. hemitoechus</i>	yes	89.0	94.0	91.5	Ashton et al., 2011	Gibbard and Stuart, 1982
Joint Mitnor Cave	UK	MIS 5e	<i>B. priscus</i> , <i>C. elaphus</i> , <i>D. dama</i> , <i>S. hemitoechus</i>	no				Ashton et al., 2011	
Kirkdale Cave	UK	MIS 5e	<i>B. primigenius</i>	no				Ashton et al., 2011	
Hoe Grange quarry	UK	MIS 5e	<i>B. priscus</i> , <i>B. primigenius</i> , <i>D. dama</i>	no				Ashton et al., 2011	
Brundon	UK	MIS 7	<i>E. ferus</i> , <i>B. priscus</i> , <i>B. primigenius</i>	no				Ashton et al., 2011	
Ilford	UK	MIS 7	<i>E. ferus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>C. capreolus</i> , <i>S. kirchbergensis</i> , <i>S. hemitoechus</i>	yes	18.0	72.0	44.6	Ashton et al., 2011; Penkman et al., 2011	West et al., 1964
Crayford	UK	MIS 7	<i>E. ferus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>S. kirchbergensis</i> , <i>C. antiquitatis</i>	no				Ashton et al., 2011; Penkman et al., 2011	
Aveley (zone II B)	UK	MIS 7	<i>B. primigenius</i>	no	9.2	57.9	28.2	Ashton et al., 2011; Penkman et al., 2011	West, 1969
Grays Thurrock	UK	MIS 9	<i>E. ferus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>D. dama</i> , <i>M. giganteus</i> , <i>S. kirchbergensis</i>	yes	12.0	26.0	19.2	Ashton et al., 2011; Penkman et al., 2011	Gibbard, 1994
Steinheim a.d. Murr, Grube Sammet	Germany	MIS 10	<i>E. ferus</i> , <i>B. priscus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>M. giganteus</i>	yes				Schreve and Bridgland, 2002	
Steinheim a.d. Murr, Grube Sigrist	Germany	MIS 11	<i>E. ferus</i> , <i>C. elaphus</i>	no				Schreve and Bridgland, 2002	

TABLE 1 (continued).

Locality	Country	Age	Species analysed in this study	Locality used in community-level analyses	Minimum NAP %	Maximum NAP %	Mean NAP %	Reference for age	Reference for pollen record
Clacton	UK	MIS 11	<i>E. ferus</i> , <i>B. primigenius</i> , <i>C. elaphus</i> , <i>D. dama</i> , <i>S. hemitoechus</i>	yes	5.0	67.0	27.3	Schreve, 2001; Penkman et al., 2011	Bridgland et al., 1999
Swanscombe (lower loam)	UK	MIS 11	<i>E. ferus</i> , <i>B. priscus</i> , <i>B. primigenius</i> , <i>D. dama</i> , <i>M. giganteus</i> , <i>S. hemitoechus</i>	yes	11.0	66.0	31.6	Schreve, 2001; Penkman et al., 2011	Conway, 1996
Hoxne	UK	MIS 11	<i>E. ferus</i> , <i>C. elaphus</i>	no	12.1	37.3	23.5	Schreve, 2000; Penkman et al., 2011	Mullenders, 1993
Frankenbacher Sande	Germany	>MIS 11	<i>E. mosbachensis</i> , <i>B. schoetensacki</i>	no				Van Asperen, 2010	
Boxgrove (horizons 5 and 4 c)	UK	MIS 13	<i>E. ferus</i> , <i>B. schoetensacki</i> , <i>C. elaphus</i> , <i>D. roberti</i> , <i>Megacerini</i> sp., <i>S. hundsheimensis</i> , <i>S. cf. megarhinus</i>	yes	5.0	12.0	8.5	Roberts and Parfitt, 1999	Roberts, 1986
Pakefield (pollen zone Cr II)	UK	MIS 15 or MIS 17	<i>B. schoetensacki</i> , <i>S. hundsheimensis</i>	no	20.0	57.0	33.3	Penkman et al., 2011	West, 1980
Mauer	Germany	MIS 15	<i>E. mosbachensis</i> , <i>B. schoetensacki</i> , <i>C. elaphus</i> , <i>C. latifrons</i> , <i>S. hundsheimensis</i>	yes	2.7	55.0	25.7	Wagner et al., 2011	Urban, 1992
Süssenborn	Germany	MIS 16	<i>E. sussenbornensis</i> , <i>E. altidens</i> , <i>B. schoetensacki</i> , <i>C. elaphus</i> , <i>C. sussenbornensis</i> , <i>C. latifrons</i> , <i>Megacerini</i> sp., <i>S. hundsheimensis</i>	no				Kahlke et al., 2010; Kahlke and Kaiser, 2011	
Voigtstedt	Germany	MIS 17	<i>C. elaphus</i> , <i>C. sussenbornensis</i> , <i>Megacerini</i> sp., <i>S. hundsheimensis</i>	yes	1.0	22.0	11.5	Maul et al., 2007; Kahlke and Kaiser, 2011	Erd, 1970
West Runton	UK	MIS 17	<i>Equus</i> sp., <i>B. schoetensacki</i> , <i>C. elaphus</i> , <i>D. cf. roberti</i> , <i>Capreolus</i> sp., <i>Megacerini</i> sp., <i>S. hundsheimensis</i>	yes	5.0	55.0	44.6	Stuart and Lister, 2010; Maul and Parfitt, 2010	Field and Peglar, 2010

generally good statistical power of these predictive equations, we consider it justified to use them for individual body mass estimates within the species (not just at the inter-specific level). Relative body size, on a scale of 0 to 1, was calculated by dividing the mean body masses of the species at a given locality by the largest mean body mass of the species across localities.

Pollen Data

Non-arboreal pollen (NAP) percentages were obtained from original published values where available, but in some cases they were estimated visually from pollen diagrams (Table 1). Pteridophyte spores and aquatic plants were excluded. Pollen from forest shrubs (such as *Corylus* and *Salix*) were considered “arboreal” because they do not indicate an open environment.

Connecting the pollen records with large ungulate assemblages from a given locality can be challenging. In a few cases, pollen samples have been obtained from sediment preserved in the bones of large mammals, for example from the Ipswichian of Barrington, England (Gibbard and Stuart, 1975). At other sites, the stratigraphic origin of the mammal fossils within a specific pollen zone is known, and NAP % values of that zone were used in the analyses. In further cases, the stratigraphic relation between the pollen and mammal fossils is unclear, with potential for false association (Sutcliffe, 1975). In such cases, minimum, maximum and mean NAP % were determined for the pollen sequences from the locality and examined separately to take account of uncertainty in the correlation with the mammal fossils. It has been suggested that in some localities, Barrington and Swanscombe in particular, pollen records may give a biased picture of the original vegetation composition. For Barrington, its uniquely high NAP percentage compared to other UK mid-Ipswichian sites has been suggested to result from defecation by grazing hippopotamuses in the river where the deposits formed (Gibbard and Stuart, 1975). For Swanscombe, poor and selective pollen preservation makes the residual pollen profile unreliable (Turner, 1985). We discuss these cases separately in the cases where they may have an impact on the interpretations of our results.

For each mammal species, we also calculated the minimum, maximum and mean NAP percentages across localities in which they occur (Table 2). The localities with their ages, mammal species studied and pollen data collated for this study are

shown in Table 1. A map of the localities is shown in Figure 1.

Analyses

The following analyses were performed:

1. Linear correlation analysis of the minimum, maximum and mean NAP percentages with species' mean mesowear values, mean body masses and body size indices across localities. The species body mass – NAP comparisons were done using specimen-level body mass data rather than sample means.
2. Comparison of mean mesowear values with the presence/absence of other ungulate species to explore the role of interspecific relationships.
3. Pairwise correlations of mean body masses between species across localities.
4. Comparison of mean body masses of palaeopopulations of species across localities. This was undertaken by pairwise Wilcoxon tests, because normal distribution or equal variance could not be assumed for the body mass estimate data. This is the case in particular because of the effects of sexual dimorphism, combined with different social structures, on body size distributions within species.
5. Correlations of mean mesowear and mean body mass per species across localities.

Our approach does not take into account the possible effect of sexual dimorphism, which might cause some biases in sample mean body masses, if genders are unequally represented, especially likely if sample sizes are low. Postcranial bones are often impossible or difficult to assign to gender, and thus we could not assess the gender composition of samples, or analyse males and females separately. For perissodactyl species (horses and rhinos) sexual dimorphism in size is generally low and can be disregarded. For species known to be sexually dimorphic, especially artiodactyls such as *Cervus elaphus* and *Bison priscus*, sample sizes are mostly large enough to warrant an assumption that males and females are both represented, justifying the use of mean body mass as an estimate of population mean.

Many of the bone samples used here have been measured in studies of individual species variation by previous authors (e.g., Forsten, 1991, 1993, 1999; Lister, 1994; Lister et al., 2010; Breda et al., 2010; Van Asperen, 2010, 2013), but here we compare body mass estimates instead of linear bone dimensions, and compare results across species as well.

There is considerable taxic turnover of mammals between the early and late Middle Pleisto-

TABLE 2. Mean mesowear and body mass values with sample sizes (n) and standard deviations (SD), and minimum, maximum and mean environmental NAP % of the most abundant ungulate species across all localities in which they occur. The species are arranged according to the mean NAP % of their environments from lowest (top) to highest (bottom).

Genus	sp.	n (mesowear)	Mean mesowear value	SD (mesowear)	Mesowear value range (of locality means)	n (body mass)	Mean body mass (kg)	Body mass range (kg)	Minimum NAP%	Maximum NAP%	Mean NAP%
<i>Alces</i>	<i>alces</i>	8	1.00	0	1.00	35	433	202 – 642	12	42	22
<i>Capreolus</i>	<i>capreolus</i>	22	1.07	0.08	1.00 – 1.17	53	35	22 – 51	12	42	23
<i>Stephanorhinus</i>	<i>hundsheimensis</i>	51	1.13	0.22	1.00 – 1.22	63	1348	999 – 1691	1	57	25
<i>Cervalces</i>	<i>latifrons</i>	13	1.11	0.16	1.00 – 1.23	19	914	593 – 1479	3	55	26
<i>Bison</i>	<i>schoetensacki</i>	22	1.46	0.04	1.42 – 1.50	78	835	314 – 1313	3	57	28
<i>Stephanorhinus</i>	<i>kirchbergensis</i>	52	1.03	0.07	1.00 – 1.17	25	1844	1381 – 2538	3	72	30
<i>Cervus</i>	<i>elaphus</i>	122	1.16	0.27	1.03 – 1.38	253	211	77 – 475	1	94	36
<i>Dama</i>	<i>dama</i>	42	1.12	0.08	1.04 – 1.17	124	87	39 – 145	5	94	39
<i>Equus</i>	<i>ferus</i>	174	2.35	0.29	2.00 – 2.45	462	499	301 – 883	5	94	40
<i>Bos</i>	<i>primigenius</i>	79	1.44	0.05	1.35 – 1.50	209	1121	389 – 2010	5	94	40
<i>Stephanorhinus</i>	<i>hemitoechus</i>	53	1.29	0.27	1.19 – 1.44	25	1522	1181 – 2384	5	94	49
<i>Megaloceros</i>	<i>giganteus</i>	48	1.38	0.22	1.10 – 1.69	91	687	329 – 1228	11	94	54
<i>Bison</i>	<i>priscus</i>	73	1.45	0.21	1.38 – 1.83	264	1011	363 – 1930	11	94	76
<i>Coelodonta</i>	<i>antiquitatis</i>	35	2.21	0.65	1.33 – 2.53	28	1905	1038 – 2958	82	97	90
<i>Rangifer</i>	<i>tarandus</i>	17	1.09	0.19	1.09	68	129	43 – 255	80	98	90

cene in Western Europe. Accordingly, Late Middle and Late Pleistocene localities were considered separately from early Middle Pleistocene localities when analysing the body mass, because many species are not common to the two intervals. Some localities for which pollen data were not available, but which have rich ungulate fauna with measurement data, are included in the discussion.

RESULTS

Vegetational Environments of the Mammals

Most of the common and abundant mammal species occur in a wide range of environments, from ones with predominantly closed vegetation (low NAP %, roughly 0 – 30 % NAP) to very open vegetation (high NAP %, roughly 70 – 100 % NAP) (Tables 1-2). Of these species, *Cervus elaphus* and *Equus ferus* are most clearly associated with both open and closed environments, as shown by the wide range of their associated NAP percentages. *Megaloceros giganteus* and *Bison priscus* are commonly associated with rather open environments (i.e., with mean NAP > 50 %), but occur also

in relatively low NAP localities. *Dama dama*, *Bos primigenius* and *Stephanorhinus hemitoechus* tend to be mostly associated with relatively closed environments, but their occurrence in the low NAP environment of Barrington, England, indicates variability in this regard as well. The early Middle Pleistocene “woodland” bison (*Bison schoetensacki*) and rhinoceros (*Stephanorhinus hundsheimensis*) are predominantly associated with closed environments as shown by their low mean environmental NAP %, but they also occur in semi-open environments (roughly 30 – 70 % NAP). Merck’s rhinoceros (*Stephanorhinus kirchbergensis*) is also mostly associated with low NAP environments, but it does occur in localities which indicate semi-open conditions, such as Ilford, England. European elk (moose) *Alces alces* and roe deer *Capreolus capreolus* have the lowest environmental NAP percentages, which supports the status of these species as forest-adapted specialists. The reindeer (*Rangifer tarandus*) and the woolly rhinoceros (*Coelodonta antiquitatis*) represent the other extreme, being clearly associated with open environments (NAP > 80 %), and they are more clearly



FIGURE 1. The localities included in this study from England and Ireland (1.1) and from Germany (1.2). The maps (1.1) and (1.2) are not to the same scale.

associated with glacial stages than any other species analysed in this study.

Mesowear

The overall mean and range of mesowear values of the most common species, together with their average environmental NAP percentages, are shown in Table 2. For full data see Appendix 2. There are clear interspecific differences in dietary strategies and their correspondence with environmental openness.

Species with low mesowear values are generally associated with relatively low NAP environments and species with high mesowear values with high NAP environments, but this is not always the case (Table 2). *Equus ferus* and *Rangifer tarandus* are the most striking exceptions to the pattern. *Equus ferus* has the highest mean mesowear values of all the species, corresponding with specialized grazing diet, but the species is not restricted to open environments. Conversely, *Rangifer tarandus* is a browse-dominated feeder with low mesowear values, but occupies environments with high NAP % (Table 2).

Variations in dietary niche breadth are also evident (Table 2). *Alces alces*, *Capreolus capreolus* and *Stephanorhinus kirchbergensis* have low mean mesowear values (close to 1) with relatively small variation, indicating browsing diets for these species. *Rangifer tarandus* also has a low mean mesowear value typical of browsers, but it shows higher variation than the other browsers. *Cervus elaphus*, *Dama dama* and *Stephanorhinus hund-*

sheimensis have relatively low (1.11 – 1.16) mean mesowear values, indicating browse-dominated mixed-feeding diet, but show significant local variation, especially *C. elaphus*. *Megaloceros giganteus* and *Stephanorhinus hemitoechus* have intermediate means (1.38 and 1.29, respectively) and high local variation, indicating generalized and flexible mixed-feeding. The large bovids, *Bison schoetensacki*, *Bison priscus* and *Bos primigenius* have intermediate mean mesowear values (1.44 – 1.46) indicating mixed-feeding diets with a significant component of grass, but there are differences in local variation among the species: *Bison schoetensacki* and *Bos primigenius* show low variation, *B. priscus* high. *Equus ferus* and *Coelodonta antiquitatis* have high, abrasion-dominated mean values (2.35 and 2.21, respectively), which suggests generally grazing diets, but they show some remarkable local variation.

Considering mammalian assemblages as a whole, their combined mean mesowear values in localities for which pollen records were available, show a statistically significant positive correlation with minimum, maximum and mean NAP % (Figure 2 and Table 3). Biases in the sampling of ungulate faunas and pollen may affect the correlation, which might in reality be stronger. For example, hippopotamus is not included in the mesowear signal from Barrington, which probably brings the mean lower than would be expected for the locally high NAP %. Considering individual mammalian families, Cervidae and Rhinocerotidae show statistically significant positive correlations of their mean mesowear

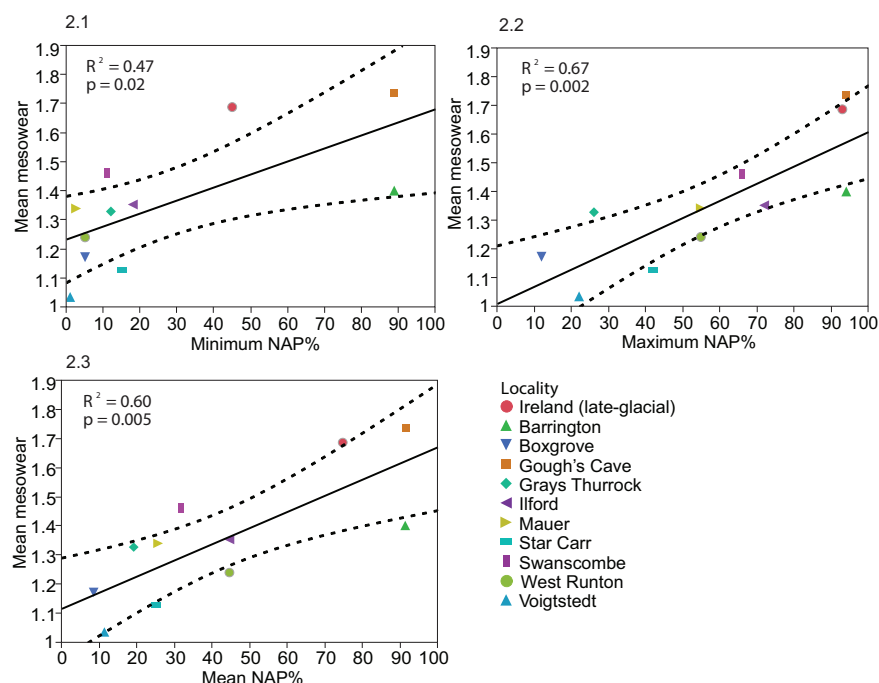


FIGURE 2. Linear regressions of mean mesowear values of the ungulates in the local palaeocommunities and NAP % in the pollen records of the localities with (1.1.) minimum NAP %, (1.2.) maximum NAP % and (1.3.) mean NAP %.

signal with the NAP %, Bovidae shows significant positive correlation only with maximum NAP %, and Equidae as a family does not show a significant correlation of mesowear with NAP % (Table 3).

Within individual species, mean mesowear values tend to show positive relationships with NAP % of the localities (Figures 3-4 and Table 4 bottom rows). All the species with sufficient data to analyse this, except *Cervus elaphus* and *Stephanorhinus hemitoechus* (but see Discussion), show positive R^2 between mesowear values and NAP % (Figures 3-4):

- *Megaloceros* and *Praemegaceros* spp., i.e., megacerine deer: statistically significant positive correlation of mesowear and minimum NAP % (Figure 3).
- *Megaloceros giganteus*: significantly higher mean mesowear value in the open late-glacial environment of Ireland, than in the relatively closed environment of Grays Thurrock (Figure 3).
- *Dama dama*: significant positive correlation of mean mesowear values with maximum NAP % (Figure 3).
- *Bison priscus/schoetensacki*: significant positive correlation of mean mesowear values with minimum, maximum and mean NAP %, despite the low number of cases (Figure 4).

- *Bos primigenius* and *Equus ferus*: positive R^2 values, which while non-significant at $p = 0.05$, are consistent with a positive relationship between NAP and mesowear (Figure 4).
- *Stephanorhinus hundsheimensis*: significant positive correlation of mean mesowear values with maximum and mean NAP % despite the low number of cases (Figure 4).
- *Stephanorhinus kirchbergensis*: higher mesowear value in the more open environment of Ilford than in the more closed environment of Grays Thurrock (Appendix 2).

These results show that ungulate species tend to shift their diet according to environment, even if species have different dietary adaptations, and that open-environment browsing (in *Rangifer tarandus*) as well as closed-environment grazing (in some populations of *Equus ferus*) are possible strategies. The specialised browser *Capreolus capreolus* does not show any differences in mesowear values between the localities, indicating that it did not shift its diet according to environment.

Cervus elaphus does not show any significant correlation of mesowear and NAP % (Figure 3). The lack of correlation in *Cervus elaphus* despite considerable local variation in mesowear values is the most significant exception and requires further consideration.

TABLE 3. Correlations of mean mesowear value of different ungulate groupings with NAP % in the localities. + = significant positive correlation, no = no correlation. Values indicating significant correlations are emboldened.

		Nr. of localities	Correlation	R ²	p
All ungulates	Min. NAP	11	+	0.47	0.02
	Max. NAP	11	+	0.67	0.002
	Mean NAP	11	+	0.6	0.005
Equidae	Min. NAP	8	no	0.09	0.46
	Max. NAP	8	no	0.16	0.33
	Mean NAP	9	no	0.09	0.47
Bovidae (<i>Bos</i> and <i>Bison</i>)	Min. NAP	7	no	0.11	0.46
	Max. NAP	7	+	0.62	0.03
	Mean NAP	8	no	0.24	0.25
Cervidae	Min. NAP	8	(+)	0.44	0.05
	Max. NAP	8	+	0.54	0.02
	Mean NAP	9	+	0.58	0.02
Rhinocerotidae	Min. NAP	8	+	0.59	0.02
	Max. NAP	8	+	0.93	<0.0001
	Mean NAP	8	+	0.82	0.0008

Comparisons of mean mesowear values of species in the presence/absence of other ungulate species are shown in Table 4. Most of the species, especially *Equus ferus* and *Bos primigenius*, show lower (more attrition-dominated) mesowear values in the presence of mammal species associated with closed environments (*Alces alces*, *Capreolus capreolus* and *Dama dama*) and higher (more abrasion-dominated) values in the presence of species associated with open environments (*Bison priscus*, *Megaloceros giganteus* and *Coelodonta antiquitatis*). However, *Cervus elaphus* shows an opposite pattern, having significantly more abrasion-dominated mesowear values in the presence of browsers associated with closed environments, especially *A. alces* (and *C. capreolus*, although not significantly so). This finding implies that *C. elaphus* included more grass in its diet when other browse-dominated feeders were present, which could explain the lack of correlation with vegetation patterns in this species (see Discussion).

Body Mass

Mean body masses of each species in the main localities are shown in Appendix 3. We did not find any correlation between body size and mesowear signal across localities in most of the species studied here (Appendix 4). The only statistically significant correlation is the negative correlation between body mass and mesowear in *Bison*

schoetensacki, implying that it had a larger body size when it consumed more browse. The cross-locality correlations of each species' mean body mass with that of other species, and with environmental NAP percentages, are shown in Table 5 (Appendix 5 for p-values). A general pattern is that some genera (*Equus ferus* and *Bison* spp.) show negative correlations of body mass with habitat openness, while others, such as *Cervus elaphus*, have positive correlation of mean body mass and habitat openness.

Cervidae. Mean relative body size indices across all cervid species analysed together have significant positive correlation with mean NAP % of localities ($R^2 = 0.5$, $p = 0.03$), implying that larger individuals and/or species are typical in open environments. However, there are important differences between species. Mean body mass of *Cervus elaphus* is positively correlated with NAP %, whereas *Megaloceros giganteus* does not show significant relationship and the pattern for *Dama dama* appears negative but could be unreliable, as discussed later (Figure 5, Table 5 and Appendix 5). For the other species of deer, intraspecific patterns could not be analysed due to insufficient data from localities with NAP %.

Mean body masses of *Cervus elaphus*, ranked by locality from oldest (right) to youngest (left), are shown in Figure 6, and pairwise comparisons between localities are shown in Appendix 6.

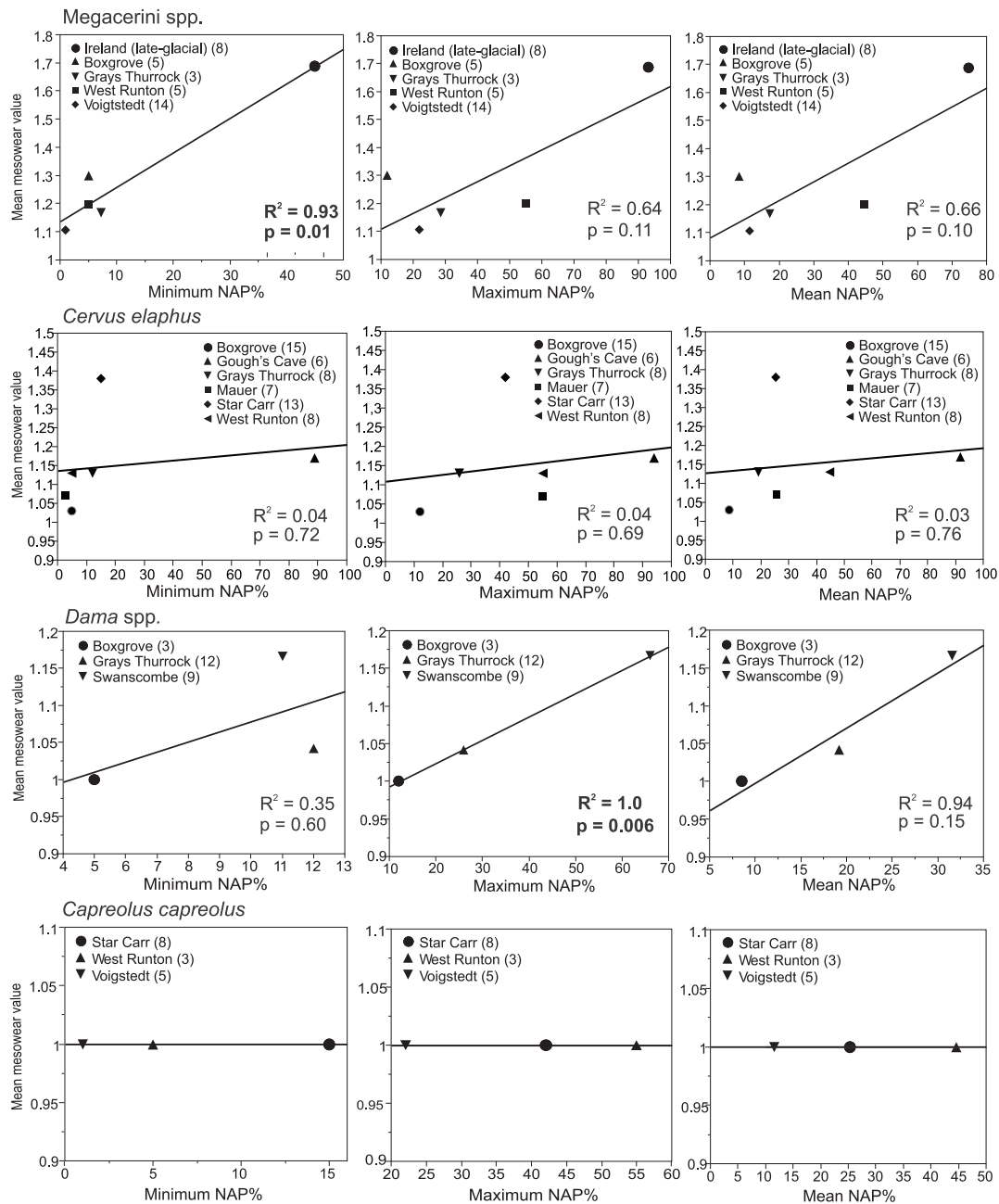


FIGURE 3. Linear regressions of mean mesowear values of deer (Cervidae) from localities with pollen records, and minimum, maximum and mean NAP % in the pollen records of the localities. Numbers of specimens per locality are given in brackets after the locality names. For Megacerini, the samples from Grays Thurrock and Ireland are *Megaloceros giganteus*; those from Boxgrove, West Runton and Voigtstedt combine *Praemegaceros verticornis*, *P. dawkinsi* and *Megaloceros savini*. For *Dama* the specimens from Boxgrove are *D. cf. roberti*; others are *D. dama*.

There is spatial and temporal variation, which appears to be connected with environmental variation. In the early Middle Pleistocene of Germany, the population from the relatively open environment of Süssenborn has significantly larger mean body mass than the interglacial population from Voigtstedt and larger mean body mass (though not

statistically significant) than the interglacial population from Mauer. The MIS 11 population from Clacton and the MIS 9 population from Grays Thurrock have mean body masses that are significantly below the average for *C. elaphus*. At Steinheim an der Murr, Germany, *C. elaphus* from the temperate mammal assemblage of Grube Sigrist (MIS 11) are

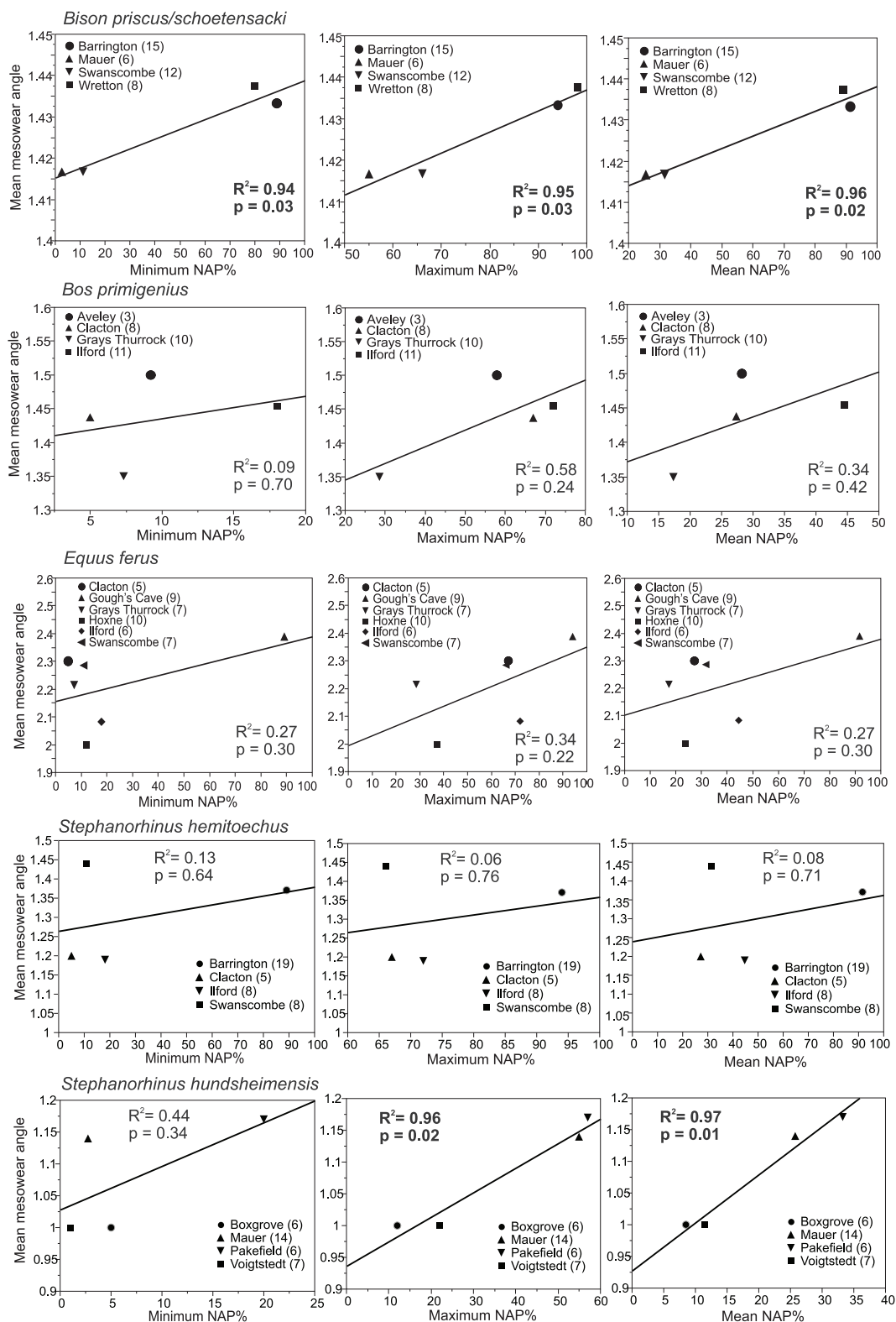


FIGURE 4. Linear regressions of mean mesowear values of Bovidae, *Equus ferus* and Rhinocerotidae from localities with pollen records, and minimum, maximum and mean NAP % in the pollen records of the localities. Numbers of specimens per locality are given in brackets after the locality names. *Bison* from Mauer is *B. schoetensacki*; from other localities, *B. priscus*.

TABLE 4. Means comparison of mesowear values of species in the presence/absence of other key ungulate species by paired Wilcoxon tests. M = mean mesowear value. Test statistics (Z and p-values) of the means differences are given for each presence/absence pair for each species (statistically significant values are emboldened). The species presence/absence data per locality were obtained from: Arnold-Bemrose and Newton (1905), Adam (1954), Lister (1984), Ziegler (1996), Schreve (1997), van Kolfschoten (2000) and Currant and Jacobi (2001).

	Cervus elaphus		Equus ferus		Bos primigenius		Bison priscus		Dama dama		Stephanorhinus hemitoechus	
	M		M		M		M		M		M	
<i>A. alces</i> present	1.26	Z = 2.14; p = 0.03	2.36	Z = 0; p = 1	1.35	Z = -2.24; p = 0.02	1.34	Z = -1.51; p = 0.13	1.04	Z = -1.67; p = 0.10		
<i>A. alces</i> absent	1.10		2.35		1.48		1.45		1.17			
<i>C. capreolus</i> present	1.26	Z = 1.46; p = 0.14	2.23	Z = -1.98; p = 0.05	1.44	Z = -1.10; p = 0.27	1.38	Z = -0.97; p = 0.33	1.12	Z = -0.52; p = 0.60	1.25	Z = -1.00; p = 0.32
<i>C. capreolus</i> absent	1.14		2.40		1.50		1.46		1.17		1.33	
<i>S. kirchbergensis</i> present	1.18	Z = 0.55; p = 0.58	2.27	Z = -1.24; p = 0.22	1.45	Z = -0.56; p = 0.57	1.38	Z = -1.07; p = 0.28	1.13	Z = -0.22; p = 0.83	1.25	Z = -1.00; p = 0.32
<i>S. kirchbergensis</i> absent	1.14		2.38		1.48		1.46		1.14		1.33	
<i>Dama dama</i> present	1.14	Z = -1.62; p = 0.10	2.23	Z = -1.99; p = 0.05	1.41	Z = -2.05; p = 0.04	1.43	Z = -0.64; p = 0.52			1.31	Z = 1.17; p = 0.24
<i>Dama dama</i> absent	1.28		2.40		1.50		1.45		1.19			
<i>Cervus elaphus</i> present			2.36	Z = 1.02; p = 0.31			1.43	Z = -0.19; p = 0.85				
<i>Cervus elaphus</i> absent			2.28				1.44					
<i>Bos primigenius</i> present	1.24	Z = 1.19; p = 0.24	2.33	Z = -0.81; p = 0.42			1.43	Z = -0.28; p = 0.78	1.12	Z = -0.52; p = 0.60	1.30	Z = 0.49; p = 0.62
<i>Bos primigenius</i> absent	1.14		2.42			1.43	1.17		1.25			
<i>S. hemitoechus</i> present	1.11	Z = -0.72; p = 0.47	2.24	Z = -1.89; p = 0.06	1.45	Z = -0.59; p = 0.55	1.43	Z = -0.64; p = 0.52				
<i>S. hemitoechus</i> absent	1.19		2.41		1.50		1.45					
<i>M. giganteus</i> present	1.15	Z = -1.57; p = 0.12	2.37	Z = 1.32; p = 0.19	1.46	Z = 0.24; p = 0.81	1.43	Z = -0.19; p = 0.85			1.30	Z = 0.78; p = 0.44
<i>M. giganteus</i> absent	1.32		2.28		1.44		1.44		1.20			
<i>R. tarandus</i> present	1.19	Z = 0.29; p = 0.67	2.41	Z = 0.88; p = 0.38	1.50	Z = 0.58; p = 0.57	1.44	Z = 0.30; p = 0.77				
<i>R. tarandus</i> absent	1.18		2.32		1.45		1.43					
<i>B. priscus</i> present	1.15	Z = -1.32; p = 0.19	2.40	Z = 2.93; p = 0.003	1.48	Z = 1.00; p = 0.32			1.19	Z = 1.79; p = 0.07		
<i>B. priscus</i> absent	1.27		2.19		1.44		1.06					
<i>E. ferus</i> present	1.19	Z = 0.35; p = 0.72			1.46	Z = 0.24; p = 0.81	1.41	Z = -0.46; p = 0.64	1.13	Z = -0.22; p = 0.83	1.25	Z = -1.00; p = 0.32
<i>E. ferus</i> absent	1.20				1.44		1.46		1.14		1.33	
<i>C. antiquitatis</i> present	1.2	Z = 1.02; p = 0.31	2.41	Z = 2.18; p = 0.03	1.50	Z = -0.56; p = 0.57	1.45	Z = 0.64; p = 0.52				
<i>C. antiquitatis</i> absent	1.12		2.23		1.44		1.43					

larger than those of Clacton and Grays, but the deer from the overlying MIS 10 glacial assemblage of Grube Sammet are larger still. The particularly large mean body masses of *C. elaphus* in the last glacial populations at Villa Seckendorff (considered early Weichselian, possibly MIS 5d-a), Kent's Cav-

ern (the cave earth fauna, considered MIS 3 in age) and Gough's Cave (Bølling interstadial) are significantly higher than those of the preceding (last interglacial) and succeeding (Holocene) populations, which are generally associated within more temperate, low NAP environments. The largest

TABLE 5. Pairwise correlations (correlation coefficients from pairwise comparisons) of mean body mass between species, and (bottom three rows) correlation coefficients of species' mean body mass with minimum, maximum and mean NAP percentages in localities. Correlations based on comparisons of three or more pairs are shown. The pairwise correlations and their p-values are given in Appendix 5. Statistically significant ($p < 0.05$) correlations are emboldened.

	<i>B. priscus</i>	<i>B. scho.</i>	<i>B. prim.</i>	<i>E. ferus</i>	<i>A. alces</i>	<i>C. latifrons</i>	<i>C. elaphus</i>	<i>D. dama</i>	<i>M. giganteus</i>	<i>C. capreolus</i>	<i>R. tarandus</i>	<i>S. kirch.</i>	<i>S. hem.</i>	<i>S. hund.</i>	<i>C. antiq.</i>
<i>Bison priscus</i>			0.65	-0.67			0.3	-0.71	0.52		-0.99		0.99		
<i>Bison schoet.</i>						-0.78	-0.35							0.37	
<i>Bos primigenius</i>	0.65			0.62			-0.08	0.18		-0.4			0.89		
<i>Equus ferus</i>	-0.67		0.62				-0.64	0.22	-0.21						
<i>Alces alces</i>															
<i>Cervalces latifrons</i>		-0.78					0.76								
<i>Cervus elaphus</i>		-0.35	-0.08	-0.64		0.76		-0.07	-0.91	-0.98			-0.75	-0.41	
<i>Dama dama</i>	-0.71			0.22			-0.07						-0.93		
<i>Meg. giganteus</i>	0.52			-0.21			-0.91								
<i>Capreolus capreolus</i>			-0.4				-0.98								
<i>Rangifer tarandus</i>	-0.99														
<i>Steph. kirch.</i>															
<i>Steph. hemit.</i>	0.99		0.89				-0.75	-0.93							
<i>Steph. hund.</i>		0.37					-0.41								
<i>Coelodonta antiquitatis</i>															
Minimum NAP %	-0.06	-0.64	0.1	-0.89			0.55	-0.91	1				0.56	-0.88	
Maximum NAP %	-0.22	-0.58	0.17	-0.52			0.46	-0.63	0.81				0.66	-0.06	
Mean NAP %	-0.11	-0.82	0.18	-0.78			0.61	-0.82	0.92				0.66	0.07	

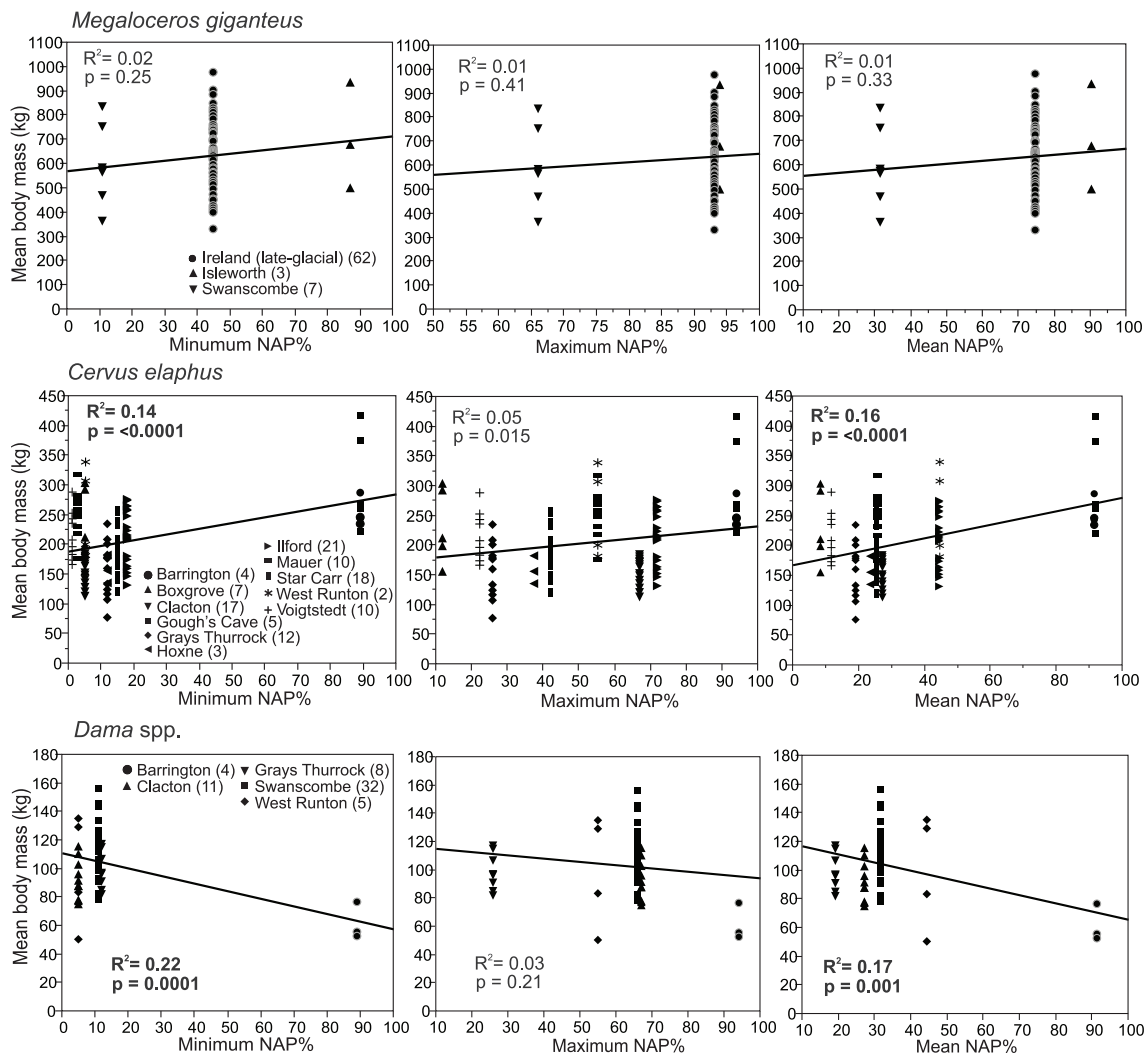


FIGURE 5. Linear regressions of body mass (kg) of deer (Cervidae) from localities with pollen records, and minimum, maximum and mean NAP % in the pollen records of the localities. Each point represents an individual specimen. Numbers of specimens per locality are given in brackets after the locality names.

mean size of this species occurs at Gough's Cave, which pertains to a warm interstadial but with open environment. These observations contribute to the positive correlation of mean body mass with NAP % of the localities, indicating that habitat openness is associated with larger size in this species.

The negative correlation of the mean body mass of *Dama dama* with the NAP % of localities (Figure 5 and Table 5) is due to the small size of this species in the very high NAP locality of Barrington, England. When Barrington (where the NAP may be locally biased) is excluded from the analyses, any significant correlation is lost (mean NAP %: $R^2 = 0.13$, $p = 0.56$; min. NAP %: $R^2 = 0.53$, $p = 0.17$; max. NAP %: $R^2 = 0.04$, $p = 0.73$). There is a taxonomic difference linked to geological age, how-

ever: The stage MIS 11 populations (*D. d. clactoni-ana*) have significantly larger mean body mass than the later *D. d. dama* populations (Appendix 7).

Sample sizes of *Capreolus sp.* are small and no reliable analysis of the correlation of body mass with environmental proxies could be made. Two specimens from the MIS 16 cool-climate assemblage of Süssenborn are relatively large, but sample sizes are too small for conclusive comparison with the other populations (Figure 6). There is little statistical significance in the spatial and temporal body size variation of this species (Appendix 8).

There is no significant relationship of body mass with vegetation openness in *Megaloceros giganteus* (Figure 5), but it does have slightly larger mean body masses in the probably more open

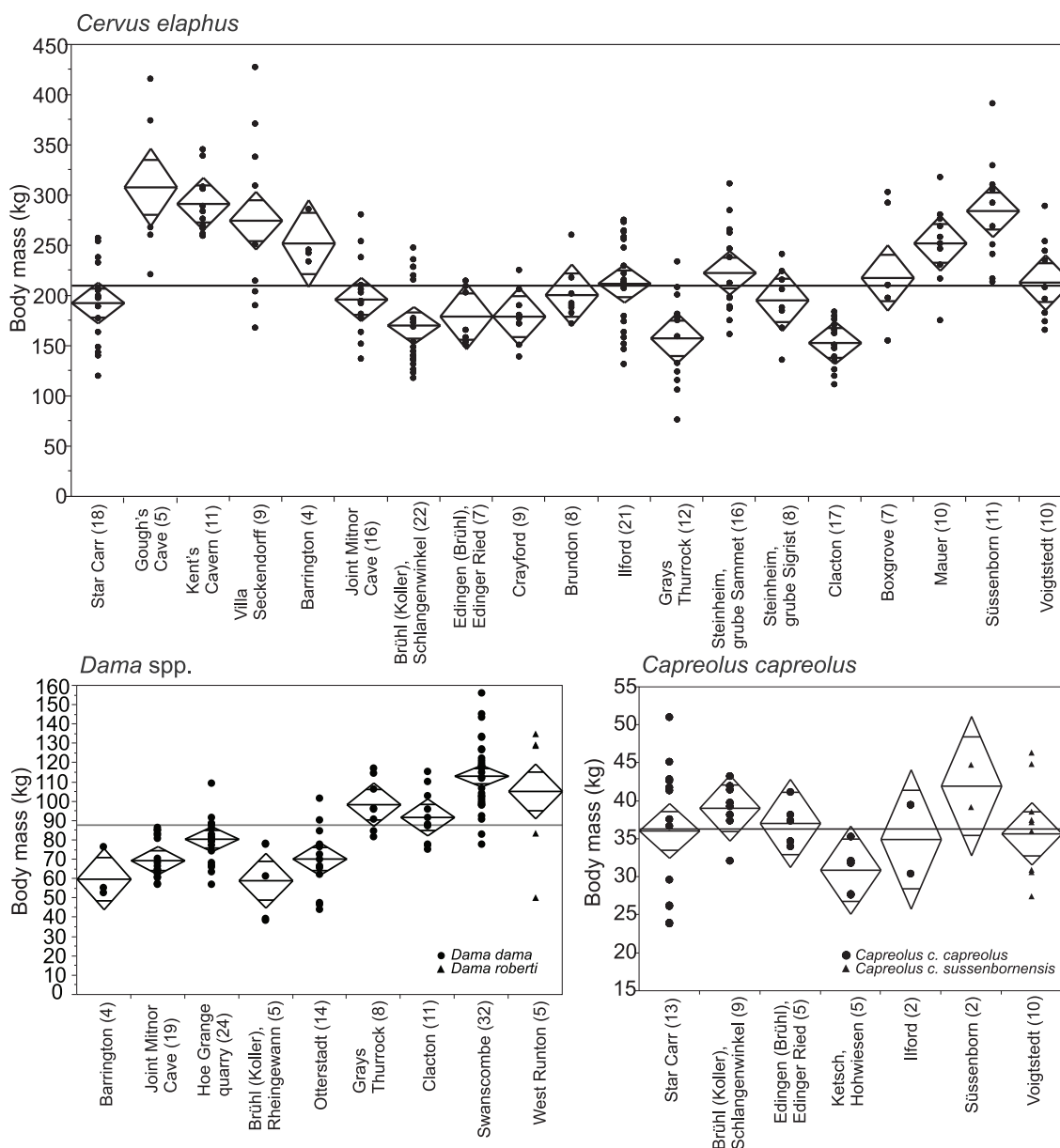


FIGURE 6. Body mass of *Cervus elaphus*, *Dama* spp. and *Capreolus capreolus* in Middle and Late Pleistocene localities in Britain and Germany. The localities are arranged from oldest (right) to youngest (left) estimated age. The middle line in the diamonds marks the mean body mass and the upper and lower lines mark the 95% confidence limits of the mean. Diamonds that do not overlap at the 95% lines indicate statistically significant difference between populations. The central line in the figures indicates the combined mean body mass of all the populations. The individual body mass estimates of each specimen are shown as data points. Sample sizes are given in brackets for each locality.

environments of Isleworth and late glacial Ireland than at Swanscombe (Figure 7). More significantly, continental animals appear to be larger than those of the British Isles: the MIS 11 interglacial population from Swanscombe, of comparable age to Steinheim, has a relatively small mean body mass for *M. giganteus* (Lister, 1986, 1994), while German last-glacial samples show larger mean sizes

than those of Britain and Ireland (Figure 7). These differences are statistically significant (Appendix 9).

Rangifer tarandus has similar mean body mass in the early Devensian glacial (MIS 5a-d) localities of Isleworth and Wretton, and a significantly smaller mean body mass in the middle Devensian glacial (MIS 3) locality of Kent's Cavern (Figure 7, see Appendix 10 for pairwise Wilcoxon test comparisons).

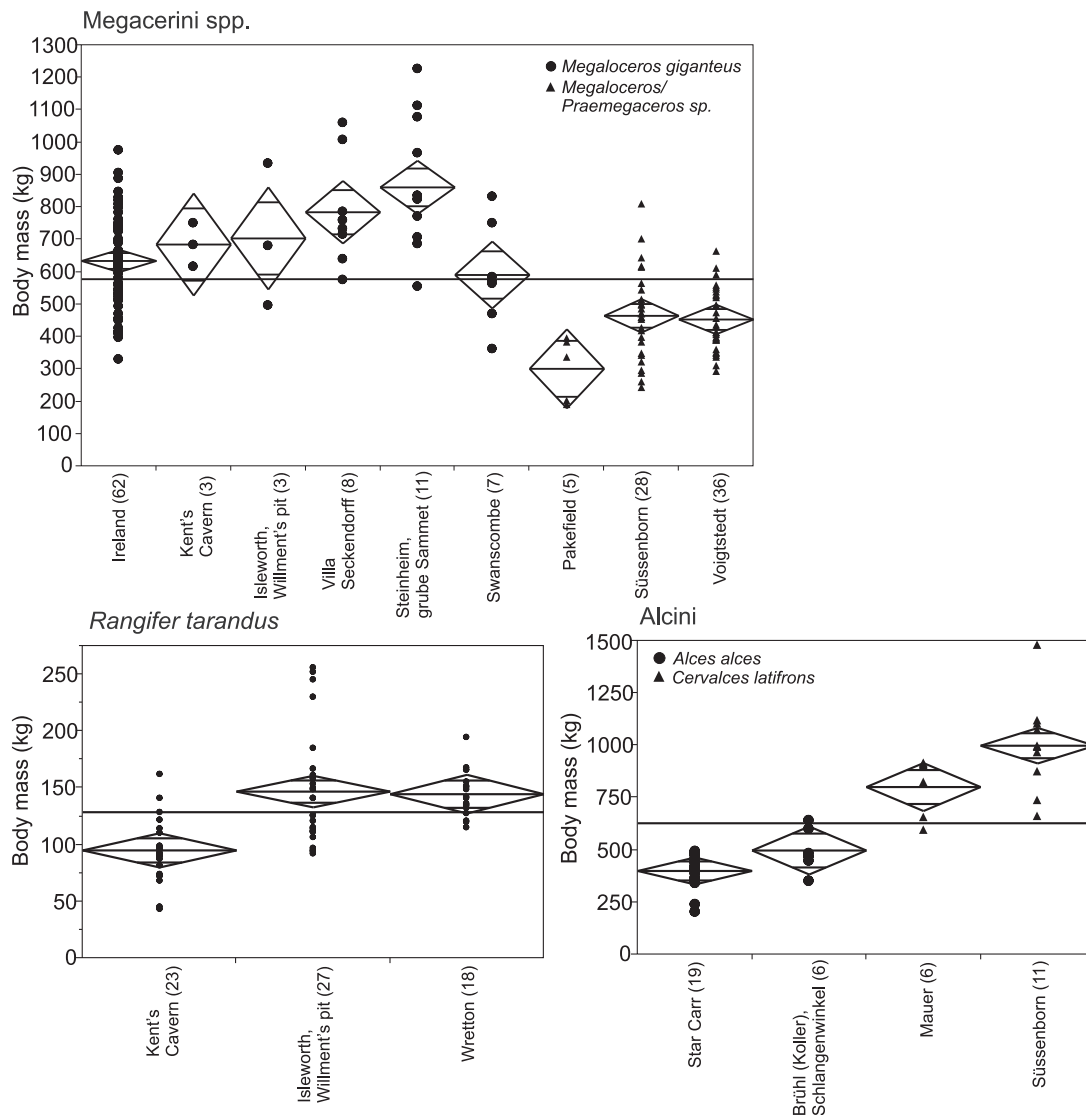


FIGURE 7. Body mass of Megacerini, *Rangifer tarandus* and Alcini in Middle and Pleistocene localities from Britain and Germany. For explanation of graph, see Figure 6.

There are insufficient data to show any correlation of *Alces alces* body size with environmental openness. As is well known (e.g., Lister, 1993), the Late Pleistocene and Holocene *Alces alces* is significantly smaller than its Middle Pleistocene relative *Cervalces latifrons* (Figure 7, Appendix 11). In the early Middle Pleistocene of Germany, *Cervalces latifrons* had a significantly larger mean body mass in the apparently more open, probably MIS 16 locality of Süssenborn than in the MIS 15 interglacial locality of Mauer.

Rhinocerotidae. The body mass of the four rhino species, *Stephanorhinus hundsheimensis*, *S. kirchbergensis*, *S. hemitoechus* and *Coelodonta antiquitatis*, is shown in Figure 8. There are no sig-

nificant intraspecific differences in the mean body mass of populations of these species (Appendices 12-14). Because of this, and the shortage of environmental proxy data from the localities, intraspecific connections of body mass and environmental proxies did not yield any conclusive results. Mainly because of the larger size of the open-adapted *C. antiquitatis* than *Stephanorhinus spp.*, the Rhinocerotidae as a whole show statistically significant positive correlation of mean body mass with mean NAP % of the localities ($R^2 = 0.52$, $p = 0.03$).

Bovidae, Bovini. The large bovids do not show any clear pattern of body mass in relation to vegetation openness of the localities. *Bison priscus* and *Bos primigenius* do not show significant correlation

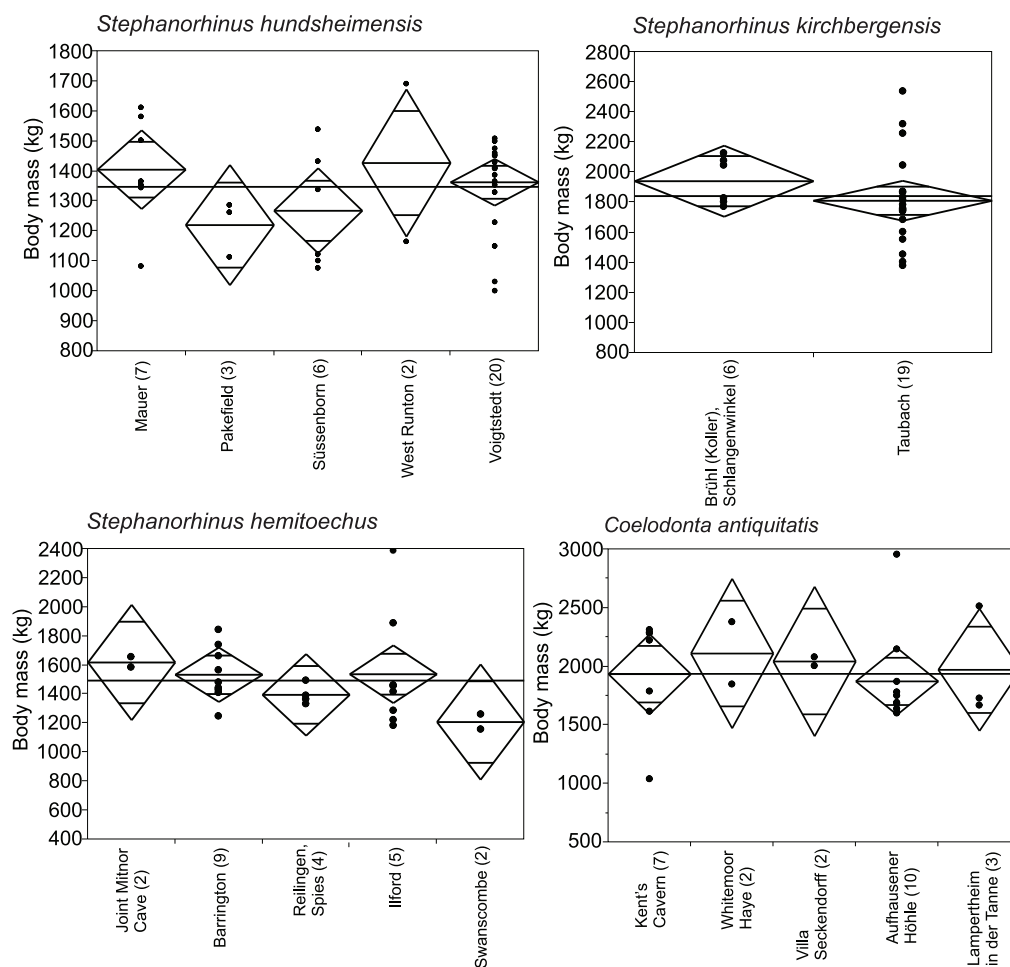


FIGURE 8. Body mass of Rhinocerotidae from Pleistocene localities of Britain and Germany. For explanation of graph, see Figure 6.

of mean body mass with the NAP % of the localities. *Bison schoetensacki*, however, shows a negative correlation, although is significant for minimum NAP % only (Figure 9 and Table 5).

Body mass of *Bison priscus* and *B. schoetensacki* in Middle and Late Pleistocene localities from Britain and Germany, ranked from oldest (right) to youngest (left) are shown in Figure 10. There is considerable variation in the body mass of *Bison* between populations. The earliest populations analysed here (*Bison schoetensacki*), from West Runton (MIS 17), Süssenborn (? MIS 16) and Pakefield (? MIS 15), have slightly but not significantly smaller mean body mass than the average of all the populations. The *Bison priscus* populations from Steinheim an der Murr (Grube Sammet, MIS 10), Taubach (MIS 5e) and Kent's Cavern (MIS 3) have significantly larger than average mean body masses, whereas the two early Devensian (MIS 5a-d) British populations, from Wretton and Isle-

worth, have significantly smaller than average mean body masses (Appendix 15).

Bos primigenius has relatively similar mean body mass through the record, without any obvious pattern in relation to environmental conditions (Figures 9-10). The only significant difference is between the largest mean body masses in some of the Middle Pleistocene localities (Grays Thurrock and Ilford) and the smallest, in the Early Holocene population from Star Carr (Appendix 16).

Equidae. The horse data are concentrated on the Middle and Late Pleistocene caballine horses, primarily the wild horse *Equus ferus*. They show significant negative correlation of mean body mass with minimum and mean NAP % of localities (Figure 9, Table 5). However, the negative correlation is mostly caused by the small size of this species in the open environment of Gough's Cave, so the pattern should be interpreted with caution.

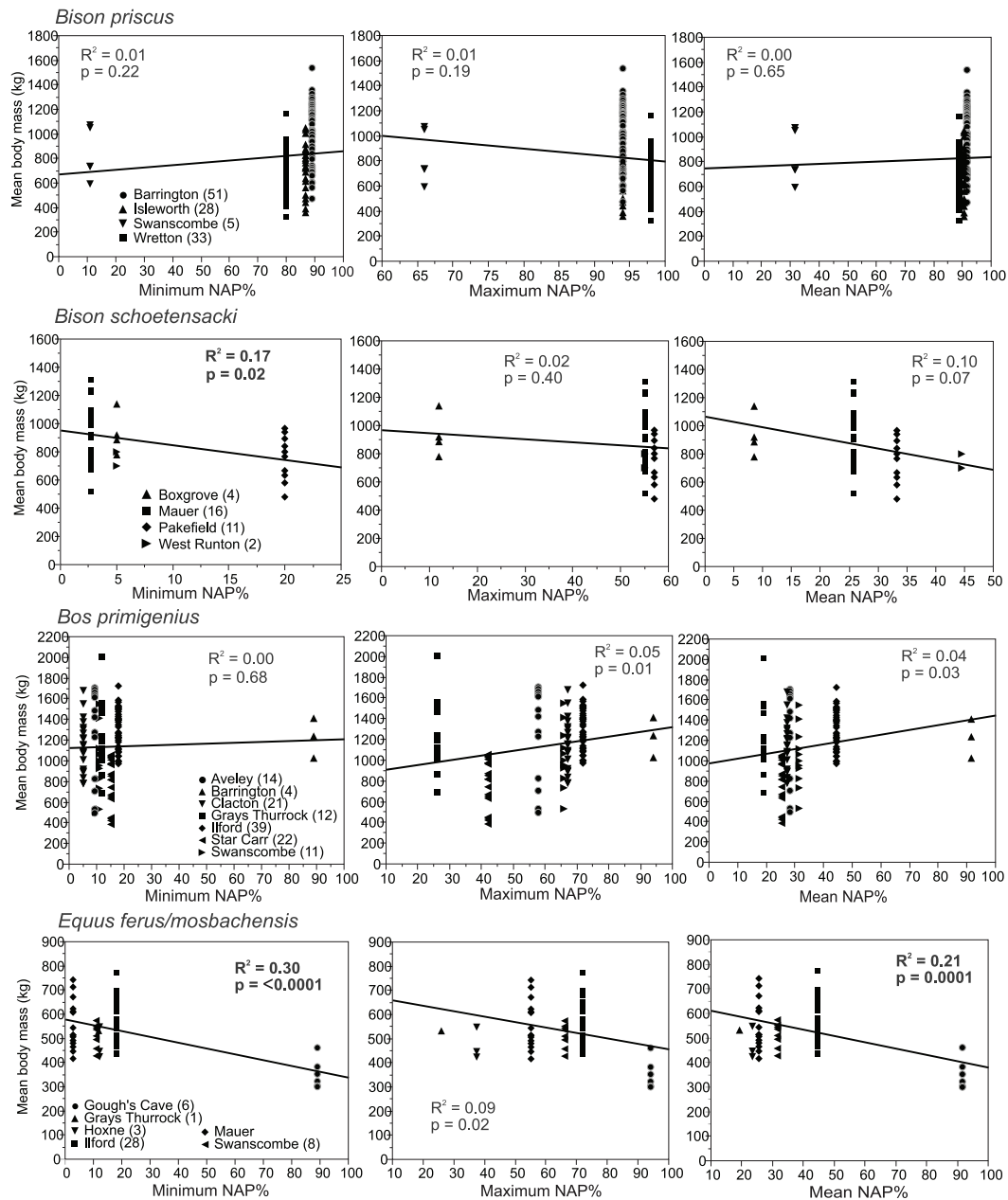


FIGURE 9. Linear regressions of body mass (kg) of Bovidae and *Equus ferus/mosbachensis* from localities with pollen records, and minimum, maximum and mean NAP % in the pollen records of the localities. Each point represents an individual specimen. Numbers of specimens per each locality are given in brackets after the locality names.

Significantly larger than average mean body mass of *E. ferus* occurs in the interglacial locality of Ilford (MIS 7), but most of the interglacial assemblages show remarkably consistent mean body masses (Figure 11, Appendix 17). Significantly smaller than average body mass of *E. ferus* occurs at Steinheim an der Murr (Grube Sammet, MIS 10), Aufhausener Höhle (last glacial), Kent's Cavern

(MIS 3) and especially Gough's Cave (MIS 2) (Appendix 17). All these localities are correlated with glacial stages, and their faunas indicate open environmental conditions. These findings give support to the negative correlation between the mean body mass of *E. ferus* and NAP percentages, indicating that the species was on average smaller in open than in closed environments.

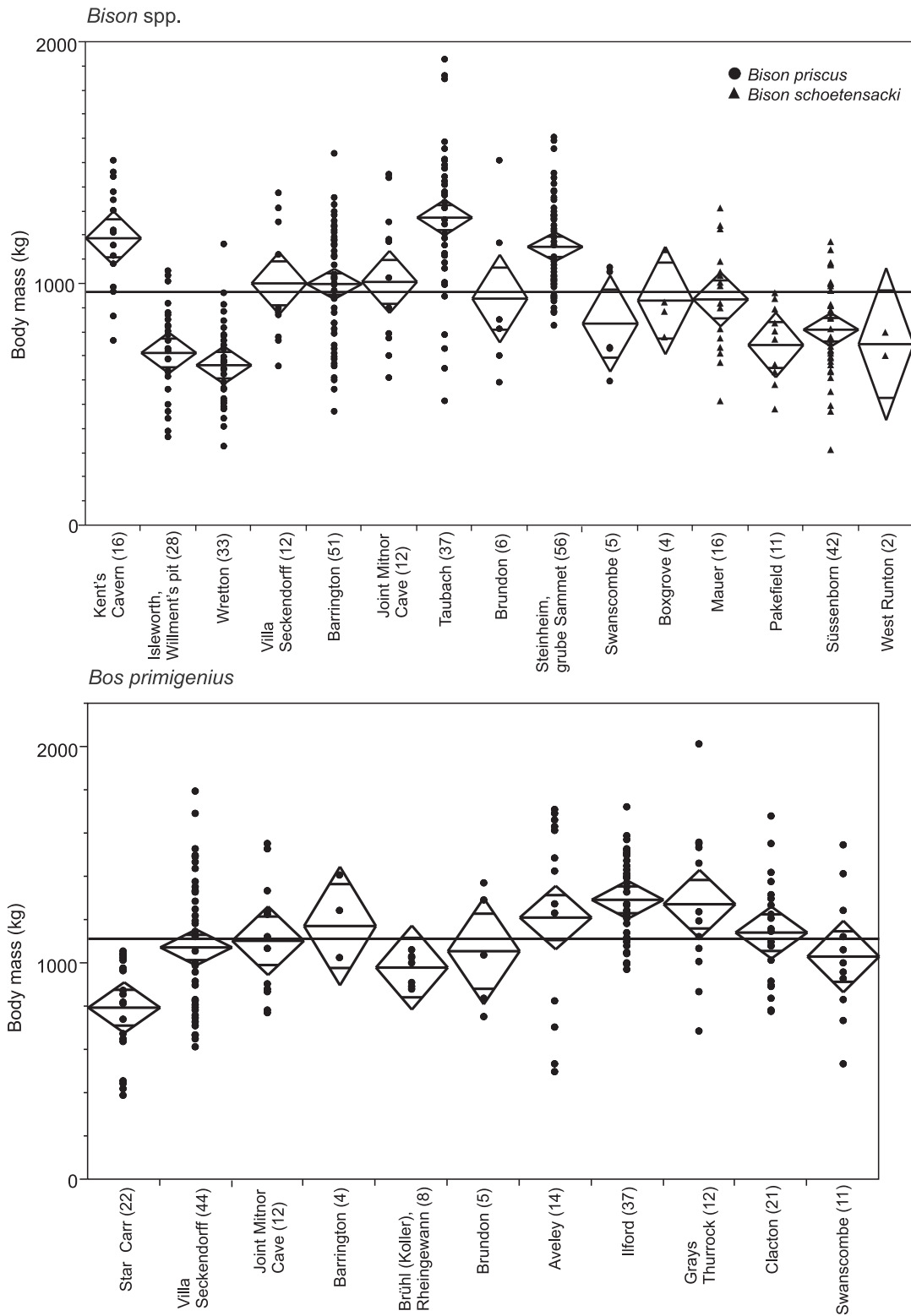


FIGURE 10. Body mass of bovine Bovidae (*Bison priscus* and *Bos primigenius*) from Middle and Late Pleistocene localities of Britain and Germany. For explanation of graph, see Figure 6.

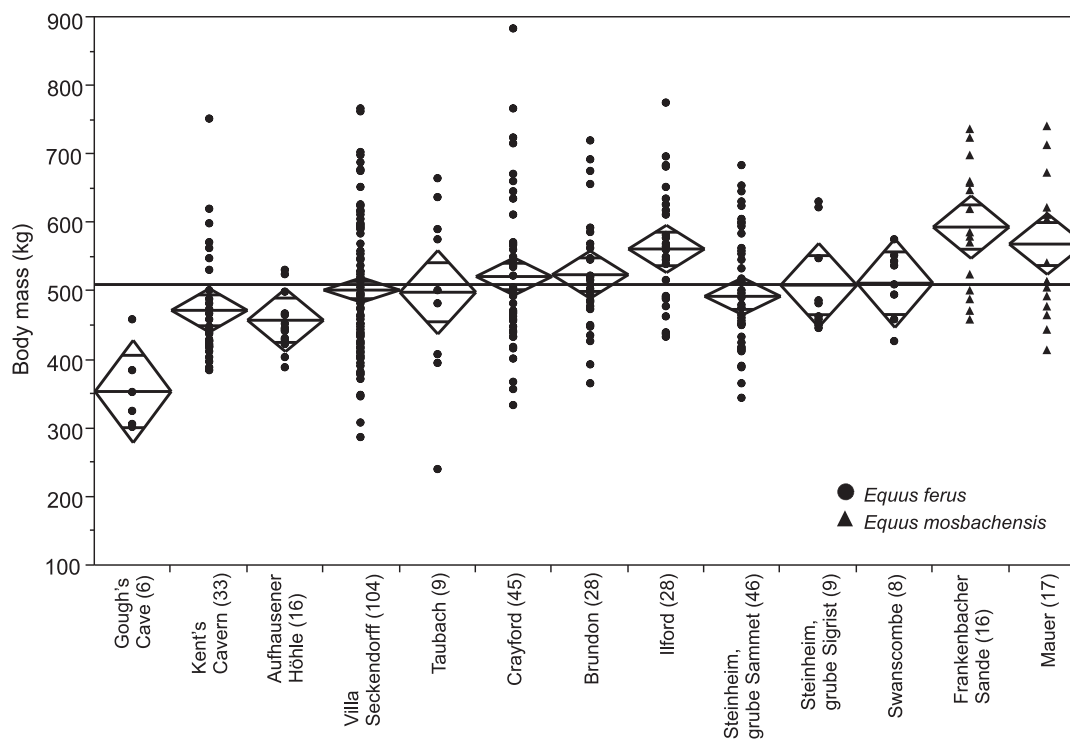


FIGURE 11. Body mass of caballine Equidae (*Equus ferus* and *E. mosbachensis*) in Middle and Late Pleistocene localities from Britain and Germany. For explanation of graph, see Figure 6.

DISCUSSION

The results indicate that the diets of local ungulate faunas reflect their environments: the average mesowear signal of the whole ungulate faunas is positively correlated with NAP % of the localities. When ungulate species are studied separately, it is evident that there are significant differences in the correlations between habitat, diet and body size of different species. This is likely to reflect basic differences in the ecological strategies and physiology of the species as well as competition effects between them.

Diet and Habitat

Community-level correlations. Mean mesowear signal of complete ungulate communities shows remarkably high and significant positive correlation with minimum, maximum and mean non-arboreal (NAP) pollen percentages recorded from the mammal bearing sediments or at least closely associated strata from the Middle and Late Pleistocene localities studied here. This would suggest that the result is not overly affected by the accuracy of the stratigraphical association of the mammal and pollen samples, possibly because both are almost always somewhat time-averaged. In reality, the

correlations may be even stronger, because of biases in the mesowear signal of some communities. For example, Barrington shows anomalously high NAP % compared to other contemporaneous localities, which is higher than would be expected from the mean mesowear signal of the ungulates and may be partly due to bias in the pollen assemblage itself (see above), but *Hippopotamus amphibius* could not be included in the mesowear data (see above), and as a grazer it would be likely to affect the total dietary signal significantly. We suggest that studies attempting to reconstruct palaeoenvironmental conditions from mesowear signal of ungulates should ideally be based on as complete ungulate communities as possible. Even better would be to extend the analysis to all herbivorous mammals. This is underlined by the different mesowear patterns of different species, so that the mesowear of a single species is likely to misrepresent the overall community signal. Species differences in the correlation of mesowear signal and vegetation openness are clearly related to different ecological strategies. For example, the reindeer (*Rangifer tarandus*) is absent from low NAP localities which indicate a closed forest environment, yet it has low mean mesowear value, and together

these indicate specialised open-habitat browsing diet.

Family-level correlations. At family-level, Cervidae, Rhinocerotidae and Bovidae (*Bos* and *Bison*) show significant positive correlations of mesowear with the NAP percentages of the localities. These correlations manifest themselves at the level of both taxic composition of the assemblage, and for some species, intra-species flexibility. Equidae as a family (*Equus ferus*, *E. mosbachensis*, *E. suessenbornensis* and *E. altidens*), however, does not show such correlations. This indicates that Pleistocene palaeoenvironmental inferences could to a certain degree be made from the tooth wear signal of cervids, bovids or especially rhinos, but not from equids alone.

Species-level correlations. Equine horses are highly adapted to grazing, and the key to their success may well be their ability to avoid competition with other ungulates by selecting the most abrasive and digestively challenging plants (grasses) in a variety of environments (Janis et al., 1994). Observations of extant feral horses and cattle in Europe have shown that horses tend to select highly productive low-growing grasses, whereas cattle include more browse, such as shrubs and forbs, in their diet (Menard et al., 2002). It is therefore remarkable that the Middle and Late Pleistocene wild horse, *Equus ferus*, occurs in a wide range of environments, from relatively low NAP % (e.g., Grays Thurrock) to very high NAP % (e.g., Gough's Cave). There is also some local variation in its always strongly abrasion-dominated mesowear signal, indicating a small browse component at some localities, which is positively (but not significantly so) related to NAP%. These findings indicate that *Equus ferus* was an ecologically flexible species of equid which was able to thrive in various environments despite its general adaptation to grazing and usually very abrasion-dominated mesowear signal. The remarkable recent discovery of browse-dominated feeding in a Middle Pleistocene horse population from Schöningen, Germany (Rivals et al., 2015b) supports this conclusion, although in the light of the data presented here it must be considered exceptional. Nonetheless, this discovery further indicates that Pleistocene horses were more variable in their habitat and feeding than has usually been expected from their ecomorphological adaptations to grazing.

Bison priscus, which occurs mostly in open environments but some more closed ones as well, has much more variation in mean mesowear values than *Bos primigenius* or *Bison schoetensacki*,

both of which are associated predominately with closed environments (Table 2, mesowear SD and NAP%). Nonetheless, both species of bison show significant positive correlation of mesowear signal and NAP%, whereas *Bos primigenius* does not. This indicates that bison were more flexible than *Bos primigenius* in their diets, shifting to more abrasive diets in open environments, and *B. priscus* was also more catholic in its choice of habitat. *Bos primigenius* has both a limited environmental range and a very similar mesowear signal in all localities, indicating a quite stable mixed-feeding dietary preference. This finding is in agreement with earlier studies that suggest, based on pollen, insects, historical descriptions and landscape analysis, that *B. primigenius* mostly utilised particular kinds of marshy woodland environments (such as sedge marshes in riverine floodplains), which would have provided relatively constant resources (van Vuure, 2005; Hall, 2008).

The mixed-feeding species *Stephanorhinus hundsheimensis* shows significant correlations of mean mesowear to NAP%, but *S. hemitoechus* does not. The lack of correlation in *S. hemitoechus* is largely driven by its very abrasion-dominated mean mesowear value in Swanscombe. However, the validity of the Swanscombe pollen record has been challenged (Turner, 1985), so this result should be interpreted with caution. For the browser *S. kirchbergensis* and the grazer *Coelodonta antiquitatis* the correlation of mesowear and vegetation could unfortunately not be analysed because of the shortage of associated pollen data. *S. kirchbergensis* shows marginally, but not significantly, more abrasive mesowear signal in the more open environment of Ilford than in the closed environment of Grays Thurrock. Van Asperen and Kahlke (2015) analysed the mesowear signals of rhinoceroses of the genus *Stephanorhinus* from Britain and Germany, and concluded that all the species were mostly flexible mixed-feeders and only *S. hundsheimensis* from Voigtstedt was a browser. Our results largely support this but indicate more browse-dominated diets for *S. kirchbergensis*. In this respect our results are closer to those of Hernesniemi et al. (2011). The woolly rhino (*C. antiquitatis*) shows surprisingly low mean mesowear value in the German last glacial locality of Aufhausener Höhle, indicating browse-dominated mixed-feeding, which differs drastically from the usual abrasion-dominated, grazing mesowear signal of this species. This could indicate an atypical environment and potentially sub-optimal feeding opportunities for the species, such as browsing

on herbs or even forest vegetation, but unfortunately this cannot be investigated because pollen data is lacking from this locality.

Alces alces, *Capreolus capreolus* and *Rangifer tarandus* have on average very attrition-dominated mesowear values and little variation, which indicates specialized browsing diets, as in their extant populations (e.g., Geist, 1998; Latham, 1999). *Alces alces* and *Capreolus capreolus* have very low mean mesowear values, corresponding to specialist browsers, as in their extant populations. The values show very little variation between localities, but sample sizes are too small for statistical robustness. *Rangifer tarandus* tends to be an open-landscape browser (Geist, 1998), and this is well recorded by the low mesowear values but high environmental NAP for this species in our data. *Dama dama* and *Cervus elaphus* have on average higher and more variable mesowear values indicating browse-dominated mixed-feeding, as in their extant populations (e.g., Geist, 1998; Gebert and Verheyden-Tixier, 2001). There are intriguing differences in the correlation of mesowear and NAP between the species of Cervidae. The abundant and ecologically flexible *Cervus elaphus* does not show significant correlation of mesowear and NAP of the localities, especially because of its very attrition-dominated mesowear signal in the relatively closed environment of Star Carr. The mesowear signal of *Megaloceros giganteus* has only two data points, but Megacerini as a whole shows one of the best correlations in this study. *Dama dama* shows positive relation between mesowear signal and NAP percentages, although the sample sizes are so low that this result must be considered highly tentative.

In sum, although some species do show dietary variation in keeping with environmental vegetation, correlations between mesowear and vegetation openness are likely to be more pronounced across the larger taxonomic groupings because of the varied feeding specializations among the species.

Competition effects. It is likely that competition with other species does affect the diets of at least the ecologically more flexible ungulate species. This can be investigated by examining dietary (mesowear) variation of a species in comparison with the presence or absence of potential competitor species (Table 4). Most of the ungulate species, most significantly *Equus ferus* and *Bos primigenius*, have mesowear values indicating a larger component of browse in their diet in the presence of species associated with closed environments

(mostly browsers such as *Alces alces* and *Capreolus capreolus*), than in the presence of species associated with open environments (such as *Bison priscus*, *Megaloceros giganteus* and *Coelodonta antiquitatis*), which reflects the relationship between diet and vegetational environment rather than any effect of competitive displacement. However, *Cervus elaphus*, the only species which does not show even tentative correlation of mesowear signal and NAP percentages, shows significantly more attrition-dominated mesowear values at localities where forest-adapted browsers, especially *Alces*, and less significantly *Capreolus*, are present than where they are absent. This probably indicates resource competition, which could have driven the ecologically flexible *C. elaphus* to utilize more abrasive plants than when competing browsers are absent. Several observations support this interpretation. Gebert and Verheyden-Tixier (2001) suggest, based on dietary analysis of extant *C. elaphus* populations in Europe, that the roe deer (*Capreolus capreolus*) is the most important potential competitor of *C. elaphus*. The mean mesowear value of *C. elaphus* is remarkably high in the localities where *Capreolus* is present (Süssenborn, West Runton, Taubach, Grays Thurrock and Star Carr). The large and well sampled population of *C. elaphus* from the Early Holocene locality of Star Carr shows the most abrasive mesowear signal of this species, whereas the other species of deer, *Alces alces* and *C. capreolus*, show totally attrition dominated mesowear signals. *Alces* is absent from almost all other studied localities, and *Capreolus* is rare in most of the Pleistocene localities. Star Carr is therefore an intriguing case where competition over food resources could have driven the dietarily more flexible *Cervus elaphus* to utilize more of the abrasive plants like grasses and sedges along the lakeshore environment.

Body Size and Synthesis

Differences in mean body mass of ungulate species between localities, and their correlations with NAP percentages, indicate that vegetation structure, resource availability and interspecific relationships all affected the body size patterns. However, in some cases the analyses did not provide statistically robust results, due to the sometimes very restricted sample sizes (in roe deer and the rhinoceroses in particular).

Among the deer (Cervidae), *Cervus elaphus* shows positive correlation of body mass with NAP of localities. This trend appears not to be correlated

to diet, as there is no significant relationship between mesowear signal and either body size or NAP in this species, even though the species shows considerable dietary flexibility across localities (see above). Nor does it appear to be driven by temperature, as *C. elaphus* of large size occurs not only in cold, but also in open but warm, contexts (corroborated by Commonality Analysis in Lister et al., in prep.). The best example of this is Gough's Cave, dated to the warmest part of the Bølling interstadial (GI-1e) (Jacobi and Higham, 2009), where palynological investigations indicate a very open environment (mean NAP % = 92). The mean body mass of *C. elaphus* from Gough's Cave is significantly larger than in any other locality analysed here. This suggests that although deer tend to be larger in "glacial" localities, this is not because of the benefits of larger size for maintaining body temperature in colder climates, but because of the benefits of large size in open habitats. This finding supports results from earlier studies. For example, in a study of MIS 11 red deer, Lister (1996) found small body sizes at Clacton, and also at Swanscombe, but the population from Hoxne, probably from a later, less forested phase of MIS 11 (Ashton et al., 2008), was of more typical size. Langvatn and Albon (1986) showed that there is negative correlation of body size with temperature and precipitation in the extant populations of *C. elaphus* in Norway (i.e., following "Bergmann's Rule"), but they suggest this is not because of physiological benefits in heat conservation, but rather because of the positive effect of decrease in temperature and precipitation on nutritional quality and digestibility of plants in that region. The large size of *C. elaphus* in open environments of the Pleistocene may have been enabled by seasonally high productivity, providing plenty of good quality food for herbivores because of fertile soils produced by glacial erosion and reduced defence mechanisms of the plants (see e.g., Zimov et al., 1995; Geist, 1998). There are many suggested benefits of large size in open environments, such as energy-efficient locomotion over large distances, improved ability to escape predators and benefits of large size for reproductive success in larger groups (Peters, 1983; Geist, 1971).

Our results on body size variation in *Megaloceros giganteus* correspond well with those of Lister (1994), whose data came largely from the same localities. There is no significant correlation with NAP, but the smallest mean size of this species occurred at Swanscombe, which had more closed vegetation than the other *Megaloceros* localities

analysed here. However, the differences in mean size between localities are small, and the validity of the pollen record from Swanscombe has been challenged (Turner, 1985). Other populations from Middle and Late Pleistocene Britain are similar in size to each other, including the late-glacial (Allerød interstadial) population from Ireland. Samples from Germany are noticeably larger but we lack sufficient environmental proxy data to interpret this. To summarise the evidence, *M. giganteus* occupied various environments from relatively closed (e.g., Grays Thurrock) to very open (Irish Late Glacial sites), was slightly but not significantly larger in more open environments and had a mixed-feeding diet with more abrasive plant material (grass) in open than in closed environments. Like *Cervus elaphus*, therefore, it follows the prediction of large size being advantageous in open environments, but unlike *C. elaphus* it also clearly follows the prediction of a more abrasion-dominated (grazing) diet in open environments. The size variation, however, does not appear to be determined by diet per se.

The lack of consistent body mass-NAP correlation for *Dama dama* could simply reflect the fact that it only occurs in warm, relatively wooded (low NAP) environments. Instead, there is a temporal trend in *Dama dama*, with larger body size in the MIS 11 and MIS 9 population of Swanscombe, Clacton and Grays than in the MIS 5e populations of Brühl (Koller), Hoe Grange Quarry, Barrington and Joint Mitnor Cave, reflecting the transition from the larger *D. d. clactoniana* to the smaller *D. d. dama* (Lister, 1986). To summarise, *D. dama* occupied various, but always at least partly wooded, environments during the warm stages of the Pleistocene, and does not show any clear connection between body size and environment or diet, but it did have a more abrasion-dominated diet in more open environments, similar to *Megaloceros*.

The rhinoceroses show little intraspecific variation in mean body mass between the localities. For some species this is probably due to adaptation to particular kinds of environments where the conditions were roughly similar. The browser *Stephanorhinus kirchbergensis* is mostly associated with closed environments, whereas the specialized grazer *Coelodonta antiquitatis* is associated with open environments and is absent from forested (low NAP) localities. The ecologically more flexible species *S. hundsheimensis* and especially *S. hemitoechus*, which had mixed-feeding diets and more variable habitats (wider range of NAP %), show somewhat more variation in body

size, but still there are no significant differences between localities. The open-adapted *C. antiquitatis* is the largest species but the closed-adapted *S. kirchbergensis* is almost as big, so even interspecifically a connection of body size and environmental conditions is elusive in the Rhinocerotidae. Lacombat (2006) suggested that climatic variations played a significant role in the body size variation in Mediterranean and French Pleistocene rhinoceroses, especially *Stephanorhinus hemitoechus*. However, he also notes a temporal trend of increasing size in most of the rhinoceros species (Lacombat, 2006, 2009), and the variation superimposed on those size trends does not seem to closely correspond with climatic fluctuations. In our data the mean body mass of *Stephanorhinus hemitoechus* is larger in the MIS 5e locality of Joint Mitnor Cave than in the MIS 11 locality of Swanscombe, but the sample sizes are small, and the difference is not statistically significant.

Bison priscus does not show significant correlation of mean body mass with NAP, but *B. schoetensacki* shows a negative correlation only with minimum NAP %, providing some indication of larger size in the most densely forested environments. It is also the only species that shows a correlation of body size with mesowear, indicating that it was larger when it consumed more browse. However, because both mesowear and NAP are negatively correlated with size in this species, this would suggest that it was larger in more closed environments where it ate more browse, rather than indicating that browsing diet as such enabled the species to grow larger.

The remarkably small-sized *Bison priscus* from the Early Devensian of Wretton (Norfolk) and Isleworth (Thames basin) are interesting because while both are open habitats, the Isleworth remains are considered to come from a temperate episode (Kerney et al., 1982) and the Wretton ones from a cooler one (West et al., 1974), again suggesting that temperature is not the deciding factor in determining body size. Among last-glacial samples, the smaller body size of *Bison* in the flat, open habitats of these localities than at Kent's Cavern (Devon) potentially fits this pattern, since its hilly, possibly partly wooded environment could have imposed different selective pressures. In summary, smaller body size appears likely to be associated with open environments in *Bison*.

Bos primigenius shows a relatively small size in the Early Holocene population of Star Carr compared with Pleistocene populations of that species. This finding remains unexplained in our analyses.

The caballine horses (*Equus ferus sensu lato*) are significantly smaller in high NAP localities, although not necessarily in colder climates. The smallest body size occurs in the open but warm environment of Gough's Cave. The tendency of horses to have relatively small body size in steppe-like, open vegetated environments during the Pleistocene has been noted by several authors. Sickenberg (1962) noted that the large forms were connected with warm climatic phases and the small forms with cold phases, which contradicts any assumption of thermoregulation based on 'Bergmann's rule'. In addition, several authors (Forstén, 1991; Forstén, 1993; Alberdi et al., 1995; Guthrie 2003) have noted a generally decreasing size trend in Eurasian *Equus* through the Late Pleistocene. Guthrie (2003) suggested the Pleistocene-Holocene climatic warming to be the cause of the size decrease, but as Forstén (1993) notes, the diminishing trend in the body size of the caballine horses started long before the beginning of Holocene, with small-sized animals in cold and open environmental conditions during the glacial phases of the Late Pleistocene. Moreover, horses from previous cold stages (such as MIS 6) have been noted to be small in size (Bates et al., 2000; van Asperen, 2010). Correlation of small body size with open environments seems to be a more general phenomenon among horses, as it can be observed in Miocene equids, especially hipparionines, as well (Saarinen, 2009).

In the Pleistocene, *E. ferus* ranged from temperate localities with largely forested vegetation (e.g., Grays Thurrock) to open but warm environments (e.g., Gough's Cave) and cold environments (e.g., Kent's Cavern). Nonetheless, the dietary signal of *E. ferus* has low variation and indicates mostly very abrasion-dominated (grazing) diets, which would suggest that even in partly closed environments it usually inhabited its preferred, open habitat patches. Therefore the area occupied by this species (and presumably total population size) was smaller in more closed environments. Higher population densities, possibly related to larger group sizes (e.g., Khan et al., 1996; Borkowski, 2000) in open environments may have selected for reduced body size of *E. ferus*, because resources available for an individual were limited by intraspecific competition. We suggest that this combination of open-adaptedness and gregarious behaviour leading to large population densities in favourable conditions (open environments), is the most plausible explanation for the observed body size pattern of horses. Similar factors may explain

the reduced body size observed in *Bison* in this study.

Van Asperen (2010) made a thorough analysis of variation in body size and proportions of European caballine horses from Middle to Late Pleistocene. Middle Pleistocene interglacial horses were found to be large and occurring in relatively closed, high-productivity environments, which would be in concert with our interpretation. The particularly small size of the glacial horses was noted in that study as well, but low productivity of those environments rather than high population density was suggested to be the explanation. However, the “mammoth steppes” of the cold stages were, at least seasonally, high productivity environments and able to sustain diverse assemblages of large-sized mammals, many with prominent luxury organs (Zimov, 1995; Geist, 1998). Moreover, as we demonstrate, other species, such as *Cervus elaphus*, were particularly large in those environments, which does not support the interpretation of low productivity. Some interglacial horse populations, such as those from Swanscombe and Steinheim, have been suggested to comprise small and slender animals because of warm climate and forested vegetation (Forsten, 1999; Van Asperen, 2010, 2013). However, despite the slightly smaller size, we did not find significant differences in the mean body mass estimates in these horse populations compared to other interglacial populations, such as the one with a large mean body size from Ilford. Instead, the horses from open, glacial environments are significantly smaller than the ones from interglacial assemblages. We therefore suggest as an alternative explanation that the small sizes of the horses in open environments could be due to the limiting effect of large group sizes (high density) and increased intraspecific competition.

Resource availability, often limited by high population density, has been shown to be the major driver behind body size variation in several extant mammal species, such as reindeer (Skogland, 1983), feral donkeys (Choquenot, 1991) and roe deer (Toïgo et al., 2006). Wolverton et al. (2009) were able to show that there is a negative correlation between individual body size and population density in the extant white-tailed deer (*Odocoileus virginianus*) in North America, and that body size variation in that species is better explained by geographic differences in food availability than by thermoregulatory benefits suggested by “Bergmann’s Rule”. The effect of population density on individual body size is most evident in gregarious species which form large herds in open

environments. Studies of modern reindeer populations (*Rangifer tarandus*) are a good example. Skogland (1983) noted that average body size in local Norwegian reindeer populations (with population sizes ranging from 500 to 26 000 individuals in areas ranging from 445 to 8000 km²) was negatively correlated with population density. In Finland, forest reindeer (*R. t. fennicus*) have on average a larger body size than wild and semi-domestic tundra reindeer (*R. t. tarandus*) from Lapland (Nieminen and Helle, 1980). Of these subspecies, the tundra reindeer, which inhabits open environments, is more gregarious and regularly forms groups of up to several hundred individuals, whereas the forest reindeer lives most of the year in small groups of 2 to 20 animals (Rankama and Ukkonen, 2001). High population density and low lichen availability cause increased tooth wear rates and smaller body size in reindeer (Kojola et al., 1998). A similar case is the extant North American bison (*Bison bison*). According to Meagher (1986) the woodland subspecies (*B. b. athabascae*) is on average larger and moves in smaller groups than the plains subspecies (*B. b. bison*) which tends to form larger herds (probably increasing population density and intraspecific resource competition [see Khan et al., 1996; Borkowski, 2000]). Moreover, tests on the North American wapiti (*Cervus elaphus canadensis*) have shown that in a controlled situation where two populations, one with high density and one with low density, were compared yearly between 1998 and 2001, mean body mass was always reduced in the high-density population (Stewart et al., 2005).

In our study bison, like horses, tend to have smaller body sizes in open environments, which conforms to the hypothesis of reduced size because of large group size and density, as in modern North American bison (Meagher, 1986). However, the larger body size in the Early Devensian British reindeer (*Rangifer tarandus*) compared with that of the MIS 3 population from Kent’s Cavern is exactly opposite to the pattern in bison. This suggests that other factors are influencing body size in this species, but this cannot be explored further with our dataset because of the shortage of localities with data and the absence of reliable pollen from Kent’s Cavern. Other species, which in contrast to horses and bison, have larger size in open environments (most notably *Cervus elaphus*), must also have been influenced by other selective pressures; they probably retained significantly smaller group sizes and population densities under open conditions, so that food limitation due

to intraspecific competition was less likely the determining factor.

Finally, in all of the species for which the correlation of body size and NAP could be analysed, the significant correlations of mean body mass are with minimum or, in the case of *C. elaphus*, with mean NAP % of the localities. This would suggest that a transition from moderate to high tree cover (low to moderate NAP cover) has stronger selective force on body size than a transition from low to moderate tree cover (moderate to high NAP cover). For species that are significantly larger in open environments (e.g., *Megaloceros giganteus* and *Cervus elaphus*) this would mean that the spread of dense forest vegetation would have favoured a smaller and more compact body size, as suggested by Bro-Jørgensen (2008) on grounds of maneuverability and Geist (1974) on grounds of reduced group size and inter-male competition. Conversely, it implies that for the gregarious species that tend to be smaller in open environments (especially *Equus ferus*), even moderate closing of the open environment reduces group size and hence intraspecific competition, leading to a larger body size.

CONCLUSIONS

The mesowear (dietary) signals of the most abundant ungulate species in the Middle and Late Pleistocene of Western Europe indicate habitat and dietary adaptations. Overall, there is a positive correlation between local vegetation and diet, both for ungulate assemblages as a whole, and their constituent species. The response of mesowear signal to habitat openness, however, varies considerably between the species, reflecting different ecological strategies and probably also competition relationships between the species.

Our data show different, species-specific patterns of body size response to environmental conditions. Population densities and social structures, together with vegetation and climate, affect the resource availability for each individual of a species, and are thus likely to be the key factors contributing to the different body mass patterns seen across the ungulate groups. We did not, however, find evidence that dietary shifts in accordance with environment have a direct effect on body size.

In some cases, most clearly shown by red deer, larger size is seen in open vegetated environments, which we suggest is not based on physiological benefits for heat conservation, but rather on other ecological factors, primarily the ecological benefits of larger size in open habitats.

Horses, conversely, are smaller at more open sites, and this, to some extent, is true of *Bison* as well. Both horse and bison are grazing-adapted herbivores with the tendency to occur in large numbers in open environments. We suggest the main factor driving their body mass smaller in open environments is high population density and gregarious behaviour, leading to increased intraspecific resource competition.

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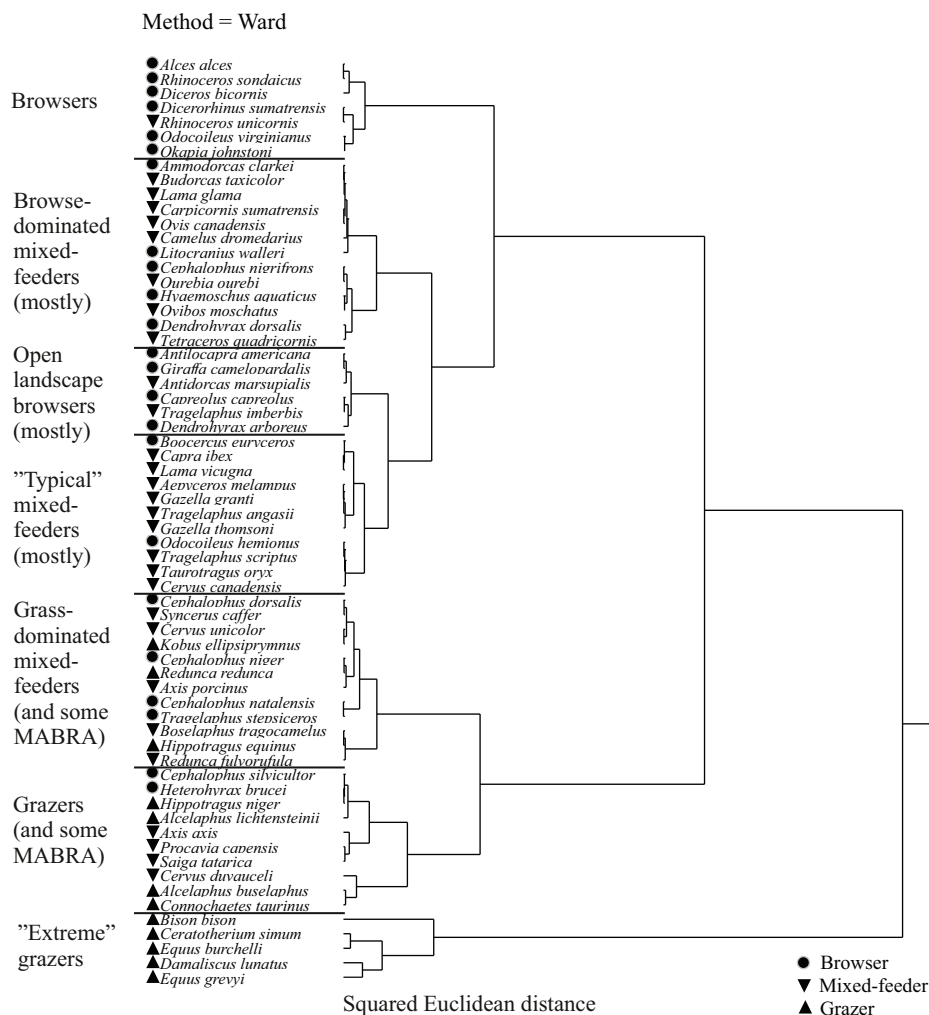
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APPENDIX 1.

Statistical tests of univariate mesowear values calculated by our method on the original mesowear data for modern ungulate species (Fortelius and Solounias, 2000). The hierarchical clustering analysis (A 1.1) yielded similar results to the ones shown by Fortelius and Solounias (2000), clustering the species in relatively consistent and biologically meaningful dietary groups, with extreme browsers at one end and extreme grazers at the other. Typical diets in each cluster are named according to those of the dominant species in each cluster. MABRA = "minute abraded brachydonts"; a special case of small ungulates which feed on fruit seeds and acquire a more abrasion-dominated mesowear signal than other browsers because of cusp tip-crushing wear (none of these were present in the Pleistocene of Europe). Discriminant analysis (A 1.2), following the methodology of Fortelius and Solounias (2000) showed that our univariate mesowear values still classify ca. 65 % of all extant ungulate species (excluding MABRA) and 85 % of extant ungulate species "typical of their dietary class" (see Fortelius and Solounias, 2000) correctly into the broad "traditional" dietary classes of "browsers", "mixed-feeders" and "grazers".

A 1.1



A 1.2

	Without MABRA	Typical
	64.81	85.19

APPENDIX 2.

Mean mesowear values of species in localities, with standard errors.

Locality	<i>B. pri.</i>	<i>B. scho.</i>	<i>Bo. prim.</i>	<i>E. fer.</i>	<i>E. mosb.</i>	<i>A. alces</i>	<i>C. lat.</i>	<i>Ce. elap.</i>	<i>Dama sp.</i>	<i>Meg. gig.</i>	<i>Meg. sp.</i>	<i>Cap. sp.</i>	<i>R. tar.</i>	<i>S. kir.</i>	<i>S. hem.</i>	<i>S. hun.</i>	<i>Co. ant.</i>
Star Carr						1±0		1.38±0.13				1±0					
Ireland (late-glacial)										1.69±0.25							
Gough's Cave				2.39±0.15				1.17±0.1									
Kent's Cavern	1.38±0.1			2.43±0.08				1.29±0.1		1.44±0.06			1.03±0.04				2.53±0.15
Isleworth																	
Wretton	1.44±0.06																
Barrington	1.43±0.1														1.37±0.06		
Joint Mitnor Cave	1.43±0.06							1.1±0.04	1.17±0.08						1.25±0.08		
Kirkdale Cave			1.5±0														
Hoe Grange Quarry			1.44±0.06						1.1±0.1								
Brundon				2.4±0.2													
Ilford			1.45±0.05	2.08±0.21									1.17±0.17	1.19±0.09			
Crayford			1.5±0	2.31±0.19									1±0				2.33±0.28
Aveley			1.5±0	2.55±0.14													
Grays Thurrock			1.35±0.08	2.21±0.15				1.13±0.08	1.04±0.04	1.17±0.17			1.07±0.07				
Clacton			1.44±0.06	2.3±0.2											1.2±0.12		
Swanscombe	1.42±0.06			2.29±0.21					1.17±0.09						1.44±0.06		
Hoxne				2.0±0.15													
Boxgrove								1.03±0.03	1±0		1.3±0.12						1±0
Pakefield																	1.17±0.11
West Runton		1.5±0						1.13±0.08	1.1±0.1		1.2±0.12	1±0					
Aufhausener Höhle				2.28±0.12													1.33±0.1
Villa Seckendorff	1.83±0.33		1.5±0	2.44±0.1				1±0									
Taubach				2.25±0.25				1.20±0.07				1.17±0.1					
Steinheim (Sammet)	1.5±0		1.44±0.06	2.45±0.1						1.1±0.1							
Frankenbacher Sande					2.57±0.07												
Mauer		1.42±0.08			2.07±0.23		1±0	1.07±0.07									1.14±0.06
Süssenborn		1.46±0.04					1.23±0.08	1.19±0.06			1.41±0.1						1.22±0.06
Voigtstedt											1.11±0.06	1±0					1±0
Brühl (Koller), Upper Rhine														1.13±0.13			

APPENDIX 3.

Mean body mass (kg) of all species in localities, with standard errors.

Locality	<i>B. pri.</i>	<i>B. scho.</i>	<i>Bo. prim.</i>	<i>E. fer.</i>	<i>E. mosb.</i>	<i>A. alces</i>	<i>C. lat.</i>	<i>Ce. ela.</i>	<i>Dama sp.</i>	<i>Meg. gig.</i>	<i>Meg. sp.</i>	<i>Cap. sp.</i>	<i>R. tar.</i>	<i>S. kir.</i>	<i>S. hem.</i>	<i>S. hun.</i>	<i>Co. ant.</i>
Star Carr			795.9 ±48.5			400 ±18		193 ±12.8				36.1 ±2.5					
Ireland (late-glacial)										634 ±17.8							
Gough's Cave				354.3 ±24.5				308.3 ±37.1									
Kent's Cavern	1168.6 ±57.6			472.7 ±14.5				291.8 ±9		684.7 ±38.7			95 ±5.7				1934.8 ±182.8
Isleworth	714.9 ±35.5									703.7 ±126			146.8 ±9.4				
Wretton	664.3 ±30.8												144.5 ±4.8				
Barrington	1000.3 ±34		1173.3 ±93.9					252.4 ±11.7	59.9 ±5.6						1534 ±61.6		
Joint Mitnor Cave	1008.8 ±82.8							196.6 ±9.2	69.5 ±2.5						1618.6 ±36.2		
Kirkdale cave			1226.1 ±30.6														
Hoe Grange quarry	1100 ±65.5		1114.2 ±45						80.6 ±2.4								
Brundon	939.6 ±61.6		1056.8 ±121.6	524.8 ±16.3				201 ±9.7									
Ilford			1294.4 ±30.9	562.3 ±16.5				212.3 ±9.9				35 ±4.5			1537.9 ±143.7		
Crayford			1351.9 ±119.8	522.1 ±16.6				179.6 ±8.7									
Aveley			1212.3 ±123.4														
Grays Thurrock			1274.1 ±105.2	530.6 ±0				157.9 ±13.6	98.5 ±4.7								
Clacton			1142.8 ±54.1					153.3 ±5.2	91.9 ±4								
Swanscombe	836.2 ±94		1032.2 ±88.3	512.3 ±17.4					113.2 ±3.1	590.7 ±60.3					1208.5 ±49.1		
Hoxne				472.8 ±38.3				157.4 ±13.6									
Boxgrove		931.6 ±75.3						218 ±22.4									
Pakefield		747.7 ±46.6							120.7 ±12.5		301 ±43.8					1220.4 ±54	
West Runton		751.3 ±48.9						254.7 ±53.6	105.3 ±16.6		440 ±61.8					1427.3 ±264	
Aufhausener Höhle				458.3 ±10.7													1873.2 ±130.7
Villa Seckendorff	1003 ±70.6		1074.2 ±45.5	502.4 ±9.6				275.1 ±30.2		784.4 ±59.4							2043.2 ±26.7
Taubach	1274.8 ±49.6			499.2 ±45.2									1811.4 ±69.9				
Steinheim (Sammet)	1155.1 ±26			493.2 ±13				201.5 ±11		861.1 ±63.1							
Frankenbacher Sande		865.6 ±78.2			594.2 ±22.3		784.4 ±63.7	169.8 ±14.4									
Mauer		936.5 ±56			569.5 ±25.2		801.4 ±58	252.5 ±12.3									1405.2 ±68
Süssenborn		811.1 ±29.7					999 ±64.8	284.7 ±15.9			464.5 ±25.5	42 ±2.8				1268.2 ±79.5	
Voigtstedt								244.2 ±25.2			453.3 ±14.7	35.7 ±2.1				1363.1 ±33.2	
Brühl (Koller), Upper Rhine			981.1 ±27.1			497.8 ±43.5		170.7 ±8.8	59.1 ±8.8			39.1 ±1.1		1941.6 ±64.6			

APPENDIX 4.

Pairwise correlation analyses of mean body mass (kg) and mean mesowear of species in localities. Indications of correlation in brackets refer to R^2 values, which do not have significant p-values, and ones without brackets refer to significant correlations. + = positive, - = negative, none = no correlation.

Genus	species	Correlation	DF	R^2	p
<i>Equus</i>	<i>ferus</i>	none	11	0.001	0.91
<i>Stephanorhinus</i>	<i>hemitoechus</i>	(-)	3	0.58	0.23
<i>Stephanorhinus</i>	<i>hundsheimensis</i>	(-)	4	0.32	0.32
<i>Megaloceros</i>	<i>giganteus</i>	(-)	2	0.96	0.13
<i>Dama</i>	<i>dama</i>	none	3	0.001	0.9
<i>Coelodonta</i>	<i>antiquitatis</i>	(+)	2	0.99	0.07
<i>Cervus</i>	<i>elaphus</i>	none	8	0.05	0.54
<i>Bos</i>	<i>primigenius</i>	none	7	0.01	0.81
<i>Bison</i>	<i>schoetensacki</i>	-	3	0.98	0.001
<i>Bison</i>	<i>priscus</i>	none	5	0.01	0.85

APPENDIX 5.

Pairwise correlation analyses of mean body mass (kg) between the species (upper rows) and with minimum, maximum and mean NAP % (lower rows) across localities. Count = number of pairs compared. Statistically significant p-values are emboldened.

Variable	by Variable	Correlation coefficient	Count	p
<i>Alces alces</i>	<i>Bos primigenius</i>	1	2	
<i>Bos primigenius</i>	<i>Bison priscus</i>	0.65	5	0.24
<i>Capreolus capreolus</i>	<i>Alces alces</i>	1	2	
<i>Capreolus capreolus</i>	<i>Bos primigenius</i>	-0.40	3	0.74
<i>Capreolus capreolus</i>	<i>Cervus elaphus</i>	-0.98	3	0.14
<i>Capreolus capreolus</i>	<i>Equus ferus</i>	-1	2	
<i>Cervalces latifrons</i>	<i>Bison schoetensacki</i>	-0.78	3	0.43
<i>Cervus elaphus</i>	<i>Alces alces</i>	-1	2	
<i>Cervus elaphus</i>	<i>Bison priscus</i>	0.30	6	0.57
<i>Cervus elaphus</i>	<i>Bison schoetensacki</i>	-0.35	5	0.57
<i>Cervus elaphus</i>	<i>Bos primigenius</i>	-0.08	9	0.84
<i>Cervus elaphus</i>	<i>Cervalces latifrons</i>	0.76	3	0.45
<i>Cervus elaphus</i>	<i>Equus ferus</i>	-0.64	11	0.03
<i>Coelodonta antiquitatis</i>	<i>Bison priscus</i>	-1	2	
<i>Coelodonta antiquitatis</i>	<i>Cervus elaphus</i>	-1	2	
<i>Coelodonta antiquitatis</i>	<i>Equus ferus</i>	1.00	3	0.02
<i>Coelodonta antiquitatis</i>	<i>Megaloceros giganteus</i>	1	2	
<i>Dama dama</i>	<i>Bison priscus</i>	-0.71	4	0.29
<i>Dama dama</i>	<i>Bos primigenius</i>	0.18	6	0.73
<i>Dama dama</i>	<i>Cervus elaphus</i>	-0.07	6	0.89
<i>Dama dama</i>	<i>Equus ferus</i>	0.22	3	0.86
<i>Equus ferus</i>	<i>Bison priscus</i>	-0.67	6	0.15
<i>Equus ferus</i>	<i>Bos primigenius</i>	0.62	7	0.14
<i>Megaloceros giganteus</i>	<i>Bison priscus</i>	0.52	5	0.37
<i>Megaloceros giganteus</i>	<i>Bos primigenius</i>	1	2	
<i>Megaloceros giganteus</i>	<i>Cervus elaphus</i>	-0.91	3	0.27
<i>Megaloceros giganteus</i>	<i>Equus ferus</i>	-0.21	4	0.79
<i>Rangifer tarandus</i>	<i>Bison priscus</i>	-0.99	3	0.08
<i>Rangifer tarandus</i>	<i>Megaloceros giganteus</i>	1	2	
<i>Stephanorhinus hemitoechus</i>	<i>Bison priscus</i>	0.99	3	0.10
<i>Stephanorhinus hemitoechus</i>	<i>Bos primigenius</i>	0.89	3	0.30
<i>Stephanorhinus hemitoechus</i>	<i>Cervus elaphus</i>	-0.75	3	0.46
<i>Stephanorhinus hemitoechus</i>	<i>Dama dama</i>	-0.93	3	0.23
<i>Stephanorhinus hemitoechus</i>	<i>Equus ferus</i>	1	2	
<i>Stephanorhinus hundsheimensis</i>	<i>Bison schoetensacki</i>	0.37	5	0.53
<i>Stephanorhinus hundsheimensis</i>	<i>Cervalces latifrons</i>	-1	2	
<i>Stephanorhinus hundsheimensis</i>	<i>Cervus elaphus</i>	-0.41	5	0.49

Variable	by Variable	Correlation coefficient	Count	p
<i>Stephanorhinus kirchbergensis</i>	<i>Equus ferus</i>	1	2	
Minimum NAP %	<i>Bison priscus</i>	-0.06	4	0.94
Minimum NAP %	<i>Bison schoetensacki</i>	-0.64	4	0.36
Minimum NAP %	<i>Bos primigenius</i>	0.10	7	0.84
Minimum NAP %	<i>Capreolus capreolus</i>	-1	2	
Minimum NAP %	<i>Cervus elaphus</i>	0.55	11	0.08
Minimum NAP %	<i>Dama dama</i>	-0.91	5	0.03
Minimum NAP %	<i>Equus ferus</i>	-0.89	5	0.04
Minimum NAP %	<i>Megaloceros giganteus</i>	1.00	3	0.05
Minimum NAP %	<i>Rangifer tarandus</i>	1	2	
Minimum NAP %	<i>Stephanorhinus hemitoechus</i>	0.56	3	0.62
Minimum NAP %	<i>Stephanorhinus hundsheimensis</i>	-0.88	5	0.05
Maximum NAP %	<i>Bison priscus</i>	-0.22	4	0.78
Maximum NAP %	<i>Bison schoetensacki</i>	-0.58	4	0.42
Maximum NAP %	<i>Bos primigenius</i>	0.17	7	0.71
Maximum NAP %	<i>Capreolus capreolus</i>	-1	2	
Maximum NAP %	<i>Cervus elaphus</i>	0.46	11	0.16
Maximum NAP %	<i>Dama dama</i>	-0.63	5	0.26
Maximum NAP %	<i>Equus ferus</i>	-0.52	5	0.37
Maximum NAP %	<i>Megaloceros giganteus</i>	0.81	3	0.40
Maximum NAP %	Minimum NAP %	0.80	17	0.0001
Maximum NAP %	<i>Rangifer tarandus</i>	-1	2	
Maximum NAP %	<i>Stephanorhinus hemitoechus</i>	0.66	3	0.54
Maximum NAP %	<i>Stephanorhinus hundsheimensis</i>	-0.06	5	0.92
Mean NAP %	<i>Bison priscus</i>	-0.11	4	0.89
Mean NAP %	<i>Bison schoetensacki</i>	-0.82	4	0.18
Mean NAP %	<i>Bos primigenius</i>	0.18	7	0.70
Mean NAP %	<i>Capreolus capreolus</i>	-1	2	
Mean NAP %	<i>Cervus elaphus</i>	0.61	11	0.05
Mean NAP %	<i>Dama dama</i>	-0.82	5	0.09
Mean NAP %	<i>Equus ferus</i>	-0.78	5	0.12
Mean NAP %	Maximum NAP %	0.92	17	<0.0001
Mean NAP %	<i>Megaloceros giganteus</i>	0.92	3	0.25
Mean NAP %	Minimum NAP %	0.95	17	<0.0001
Mean NAP %	<i>Rangifer tarandus</i>	1	2	
Mean NAP %	<i>Stephanorhinus hemitoechus</i>	0.66	3	0.54
Mean NAP %	<i>Stephanorhinus hundsheimensis</i>	0.07	5	0.91

APPENDIX 6.

Pairwise comparison by Wilcoxon tests of mean body mass of *Cervus elaphus* in localities. Negative Z values indicate smaller body size and positive values larger body size in the population marked in the first column compared to the one in the second column. Statistically significant p-values are emboldened.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Star Carr	Grays Thurrock	6.04	3.28	1.84	0.07
Star Carr	Brühl (Koller), Schlangenwinkel	6.77	3.71	1.82	0.07
Star Carr	Ilford	-5.93	3.66	-1.62	0.11
Star Carr	Boxgrove	-3.67	3.27	-1.12	0.26
Star Carr	Crayford	3.42	3.24	1.06	0.29
Star Carr	Edingen (Brühl), Edinger Ried	1.09	3.28	0.33	0.74
Star Carr	Brundon	-0.45	3.25	-0.14	0.89
Star Carr	Joint Mitnor Cave	0.35	3.42	0.10	0.92
Star Carr	Kent's Cavern	-14.43	3.26	-4.43	<0.0001
Star Carr	Clacton	10.92	3.46	3.15	0.0016
Star Carr	Mauer	-10.03	3.24	-3.09	0.0020
Star Carr	Gough's Cave	-10.35	3.43	-3.02	0.0025
Star Carr	Barrington	-8.71	3.59	-2.43	0.015
Gough's Cave	Boxgrove	3.77	2.10	1.79	0.07
Gough's Cave	Barrington	1.58	1.84	0.86	0.39
Gough's Cave	Clacton	10.87	3.30	3.29	0.0010
Gough's Cave	Brühl (Koller), Schlangenwinkel	12.40	3.93	3.15	0.0016
Gough's Cave	Crayford	6.53	2.33	2.80	0.0051
Gough's Cave	Edingen (Brühl), Edinger Ried	5.83	2.11	2.76	0.0058
Gough's Cave	Brundon	5.69	2.22	2.56	0.010
Kent's Cavern	Gough's Cave	0.29	2.57	0.11	0.91
Kent's Cavern	Brühl (Koller), Schlangenwinkel	16.43	3.57	4.60	<0.0001
Kent's Cavern	Clacton	13.93	3.18	4.38	<0.0001
Kent's Cavern	Grays Thurrock	11.41	2.83	4.03	<0.0001
Kent's Cavern	Ilford	14.27	3.49	4.09	<0.0001
Kent's Cavern	Joint Mitnor Cave	12.66	3.11	4.07	<0.0001
Kent's Cavern	Crayford	9.90	2.66	3.72	0.0002
Kent's Cavern	Brundon	9.18	2.61	3.51	0.0004
Kent's Cavern	Edingen (Brühl), Edinger Ried	8.88	2.58	3.44	0.0006
Kent's Cavern	Boxgrove	5.61	2.58	2.18	0.030
Kent's Cavern	Barrington	5.28	2.61	2.02	0.043
Villa Seckendorff	Brundon	4.13	2.45	1.68	0.09
Villa Seckendorff	Steinheim a.d. Murr, grube Sigrist	4.13	2.45	1.68	0.09
Villa Seckendorff	Ilford	5.40	3.51	1.54	0.12
Villa Seckendorff	Steinheim a.d. Murr, grube Sammet	4.43	3.07	1.44	0.15
Villa Seckendorff	Boxgrove	3.30	2.40	1.38	0.17
Villa Seckendorff	Gough's Cave	-2.18	2.33	-0.93	0.35

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Villa Seckendorff	Kent's Cavern	-1.82	2.66	-0.68	0.49
Villa Seckendorff	Süssenborn	-1.01	2.66	-0.38	0.70
Villa Seckendorff	Barrington	0.18	2.34	0.08	0.94
Villa Seckendorff	Mauer	0.11	2.59	0.04	0.97
Villa Seckendorff	Clacton	12.07	3.15	3.83	0.0001
Villa Seckendorff	Brühl (Koller), Schlangenwinkel	10.88	3.60	3.03	0.0025
Villa Seckendorff	Grays Thurrock	8.07	2.74	2.95	0.0032
Villa Seckendorff	Crayford	6.22	2.52	2.47	0.013
Villa Seckendorff	Edingen (Brühl), Edinger Ried	5.84	2.40	2.43	0.015
Villa Seckendorff	Star Carr	7.42	3.24	2.29	0.022
Villa Seckendorff	Joint Mitnor Cave	6.86	3.07	2.24	0.025
Joint Mitnor Cave	Crayford	3.73	3.07	1.22	0.2234
Joint Mitnor Cave	Ilford	-4.35	3.59	-1.21	0.2259
Joint Mitnor Cave	Boxgrove	-2.77	3.07	-0.90	0.3667
Joint Mitnor Cave	Edingen (Brühl), Edinger Ried	2.36	3.07	0.77	0.4422
Joint Mitnor Cave	Brundon	-1.03	3.06	-0.34	0.7362
Joint Mitnor Cave	Clacton	12.31	3.37	3.66	0.0003
Joint Mitnor Cave	Gough's Cave	-9.06	3.18	-2.85	0.0044
Joint Mitnor Cave	Barrington	-7.66	3.31	-2.32	0.021
Joint Mitnor Cave	Brühl (Koller), Schlangenwinkel	7.99	3.65	2.19	0.029
Joint Mitnor Cave	Grays Thurrock	6.27	3.14	2.00	0.046
Brühl (Koller), Schlangenwinkel	Boxgrove	-6.87	3.69	-1.86	0.0627
Brühl (Koller), Schlangenwinkel	Barrington	-11.67	4.16	-2.81	0.0050
Brühl (Koller), Schlangenwinkel	Brundon	-7.24	3.63	-1.99	0.046
Edingen (Brühl), Edinger Ried	Clacton	5.65	3.17	1.78	0.0753
Edingen (Brühl), Edinger Ried	Boxgrove	-2.57	2.23	-1.15	0.2491
Edingen (Brühl), Edinger Ried	Brundon	-2.54	2.31	-1.10	0.2716
Edingen (Brühl), Edinger Ried	Brühl (Koller), Schlangenwinkel	2.45	3.69	0.66	0.5075
Edingen (Brühl), Edinger Ried	Crayford	-0.25	2.40	-0.11	0.9157
Edingen (Brühl), Edinger Ried	Barrington	-5.30	2.08	-2.55	0.011
Crayford	Brundon	-4.13	2.45	-1.68	0.0922
Crayford	Boxgrove	-3.30	2.40	-1.38	0.1682
Crayford	Brühl (Koller), Schlangenwinkel	3.52	3.60	0.98	0.3274
Crayford	Barrington	-6.32	2.34	-2.70	0.0069
Crayford	Clacton	7.82	3.15	2.48	0.013
Brundon	Boxgrove	-1.21	2.31	-0.52	0.60
Brundon	Barrington	-4.69	2.21	-2.12	0.034
Ilford	Crayford	6.51	3.51	1.86	0.06

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Ilford	Edingen (Brühl), Edinger Ried	6.29	3.59	1.75	0.08
Ilford	Barrington	-6.10	4.02	-1.52	0.13
Ilford	Brundon	2.50	3.54	0.71	0.48
Ilford	Boxgrove	0.00	3.59	0.00	1
Ilford	Clacton	13.31	3.63	3.67	0.0002
Ilford	Brühl (Koller), Schlangenwinkel	10.52	3.83	2.75	0.0060
Ilford	Grays Thurrock	9.49	3.50	2.71	0.0067
Ilford	Gough's Cave	-9.16	3.81	-2.41	0.016
Grays Thurrock	Boxgrove	-5.09	2.67	-1.90	0.06
Grays Thurrock	Crayford	-2.43	2.74	-0.89	0.37
Grays Thurrock	Edingen (Brühl), Edinger Ried	-2.38	2.68	-0.89	0.37
Grays Thurrock	Brühl (Koller), Schlangenwinkel	-2.25	3.57	-0.63	0.53
Grays Thurrock	Clacton	1.21	3.21	0.38	0.71
Grays Thurrock	Gough's Cave	-8.08	2.69	-3.00	0.0027
Grays Thurrock	Barrington	-7.50	2.75	-2.73	0.0064
Grays Thurrock	Brundon	-5.52	2.70	-2.04	0.041
Steinheim a.d. Murr, grube Sammet	Mauer	-5.12	3.08	-1.66	0.10
Steinheim a.d. Murr, grube Sammet	Joint Mitnor Cave	5.44	3.32	1.64	0.10
Steinheim a.d. Murr, grube Sammet	Star Carr	5.55	3.42	1.62	0.10
Steinheim a.d. Murr, grube Sammet	Brundon	3.38	3.06	1.10	0.27
Steinheim a.d. Murr, grube Sammet	Barrington	-3.59	3.31	-1.09	0.28
Steinheim a.d. Murr, grube Sammet	Ilford	1.49	3.59	0.41	0.68
Steinheim a.d. Murr, grube Sammet	Boxgrove	0.82	3.07	0.27	0.79
Steinheim a.d. Murr, grube Sammet	Clacton	15.10	3.37	4.49	<0.0001
Steinheim a.d. Murr, grube Sammet	Kent's Cavern	-10.51	3.11	-3.38	0.0007
Steinheim a.d. Murr, grube Sammet	Brühl (Koller), Schlangenwinkel	11.93	3.65	3.27	0.0011
Steinheim a.d. Murr, grube Sammet	Grays Thurrock	9.41	3.14	2.99	0.0028
Steinheim a.d. Murr, grube Sammet	Crayford	7.55	3.07	2.46	0.014
Steinheim a.d. Murr, grube Sammet	Gough's Cave	-6.96	3.18	-2.19	0.029
Steinheim a.d. Murr, grube Sammet	Edingen (Brühl), Edinger Ried	6.06	3.07	1.97	0.049
Steinheim a.d. Murr, grube Sigrist	Grays Thurrock	5.10	2.70	1.89	0.06
Steinheim a.d. Murr, grube Sigrist	Brühl (Koller), Schlangenwinkel	5.20	3.63	1.43	0.15
Steinheim a.d. Murr, grube Sigrist	Steinheim a.d. Murr, grube Sammet	-3.84	3.06	-1.26	0.21

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Steinheim a.d. Murr, grube Sigris	Edingen (Brühl), Edinger Ried	2.54	2.31	1.10	0.27
Steinheim a.d. Murr, grube Sigris	Crayford	2.48	2.45	1.01	0.31
Steinheim a.d. Murr, grube Sigris	Ilford	-3.11	3.54	-0.88	0.38
Steinheim a.d. Murr, grube Sigris	Boxgrove	-0.94	2.31	-0.41	0.68
Steinheim a.d. Murr, grube Sigris	Joint Mitnor Cave	0.66	3.06	0.21	0.83
Steinheim a.d. Murr, grube Sigris	Star Carr	0.45	3.25	0.14	0.89
Steinheim a.d. Murr, grube Sigris	Brundon	-0.13	2.38	-0.05	0.96
Steinheim a.d. Murr, grube Sigris	Kent's Cavern	-9.39	2.61	-3.59	0.0003
Steinheim a.d. Murr, grube Sigris	Clacton	9.10	3.15	2.88	0.0039
Steinheim a.d. Murr, grube Sigris	Mauer	-6.86	2.53	-2.71	0.0067
Steinheim a.d. Murr, grube Sigris	Gough's Cave	-5.69	2.22	-2.56	0.010
Steinheim a.d. Murr, grube Sigris	Barrington	-5.44	2.21	-2.46	0.014
Clacton	Brühl (Koller), Schlangenwinkel	-3.18	3.68	-0.86	0.39
Clacton	Brundon	-11.67	3.15	-3.70	0.0002
Clacton	Barrington	-10.35	3.45	-3.00	0.0027
Clacton	Boxgrove	-8.67	3.17	-2.73	0.0063
Boxgrove	Barrington	-2.16	2.07	-1.04	0.30
Mauer	Boxgrove	3.28	2.49	1.32	0.19
Mauer	Gough's Cave	-2.55	2.45	-1.04	0.30
Mauer	Barrington	0.53	2.47	0.21	0.83
Mauer	Clacton	12.94	3.16	4.09	<0.0001
Mauer	Brühl (Koller), Schlangenwinkel	13.45	3.58	3.76	0.0002
Mauer	Grays Thurrock	9.63	2.78	3.46	0.0005
Mauer	Crayford	8.13	2.59	3.14	0.0017
Mauer	Edingen (Brühl), Edinger Ried	7.65	2.49	3.07	0.0021
Mauer	Joint Mitnor Cave	8.53	3.08	2.77	0.0056
Mauer	Kent's Cavern	-6.40	2.71	-2.36	0.018
Mauer	Brundon	5.96	2.53	2.35	0.019
Mauer	Ilford	7.90	3.49	2.26	0.024
Süssenborn	Mauer	3.25	2.71	1.20	0.23
Süssenborn	Barrington	2.90	2.61	1.11	0.27
Süssenborn	Kent's Cavern	-1.09	2.77	-0.39	0.69
Süssenborn	Gough's Cave	-0.87	2.57	-0.34	0.73
Süssenborn	Brühl (Koller), Schlangenwinkel	14.80	3.57	4.14	<0.0001
Süssenborn	Clacton	13.93	3.18	4.38	<0.0001
Süssenborn	Grays Thurrock	11.06	2.83	3.91	<0.0001

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Süssenborn	Star Carr	12.67	3.26	3.89	0.0001
Süssenborn	Joint Mitnor Cave	11.74	3.11	3.78	0.0002
Süssenborn	Crayford	9.49	2.66	3.57	0.0004
Süssenborn	Edingen (Brühl), Edinger Ried	8.65	2.58	3.35	0.0008
Süssenborn	Ilford	11.22	3.49	3.21	0.0013
Süssenborn	Steinheim a.d. Murr, grube Sigrist	8.31	2.61	3.18	0.0015
Süssenborn	Brundon	8.10	2.61	3.10	0.0020
Süssenborn	Steinheim a.d. Murr, grube Sammet	8.82	3.11	2.84	0.0045
Süssenborn	Boxgrove	6.31	2.58	2.45	0.014
Voigtstedt	Mauer	-5.10	2.65	-1.93	0.05
Voigtstedt	Crayford	4.96	2.59	1.92	0.06
Voigtstedt	Edingen (Brühl), Edinger Ried	4.25	2.49	1.71	0.09
Voigtstedt	Villa Seckendorff	-3.91	2.59	-1.51	0.13
Voigtstedt	Barrington	-3.33	2.47	-1.34	0.18
Voigtstedt	Joint Mitnor Cave	3.01	3.08	0.98	0.33
Voigtstedt	Star Carr	2.72	3.24	0.84	0.40
Voigtstedt	Steinheim a.d. Murr, grube Sammet	-2.36	3.08	-0.76	0.44
Voigtstedt	Steinheim a.d. Murr, grube Sigrist	1.46	2.53	0.58	0.56
Voigtstedt	Brundon	0.79	2.53	0.31	0.76
Voigtstedt	Boxgrove	-0.36	2.49	-0.15	0.88
Voigtstedt	Ilford	-0.07	3.49	-0.02	0.98
Voigtstedt	Clacton	11.75	3.16	3.72	0.0002
Voigtstedt	Kent's Cavern	-9.16	2.71	-3.38	0.0007
Voigtstedt	Süssenborn	-7.73	2.71	-2.85	0.0043
Voigtstedt	Brühl (Koller), Schlangenwinkel	9.09	3.58	2.54	0.011
Voigtstedt	Grays Thurrock	6.69	2.78	2.41	0.016
Voigtstedt	Gough's Cave	-5.55	2.45	-2.27	0.024

APPENDIX 7.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Dama dama* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif	Z	p
Joint Mitnor Cave	Brühl (Koller), Rheingewann	4.04	3.55	1.14	0.26
Joint Mitnor Cave	Clacton	-12.34	3.33	-3.70	0.0002
Joint Mitnor Cave	Grays Thurrock	-11.99	3.35	-3.58	0.0003
Joint Mitnor Cave	Hoe Grange quarry	-11.17	3.85	-2.90	0.0037
Joint Mitnor Cave	Barrington	7.41	3.73	1.99	0.047
Hoe Grange quarry	Grays Thurrock	-11.17	3.83	-2.92	0.0035
Hoe Grange quarry	Barrington	11.81	4.44	2.66	0.0078
Hoe Grange quarry	Brühl (Koller), Rheingewann	10.27	4.18	2.45	0.014
Hoe Grange quarry	Clacton	-7.89	3.73	-2.11	0.034
Brühl (Koller), Rheingewann	Barrington	0.23	1.84	0.12	0.90
Otterstadt	Brühl (Koller), Rheingewann	3.12	2.93	1.06	0.29
Otterstadt	Barrington	3.05	3.03	1.01	0.31
Otterstadt	Joint Mitnor Cave	1.24	3.41	0.36	0.72
Otterstadt	Grays Thurrock	-9.23	2.88	-3.21	0.0013
Otterstadt	Clacton	-8.77	2.96	-2.96	0.0031
Otterstadt	Hoe Grange quarry	-7.86	3.74	-2.10	0.035
Grays Thurrock	Clacton	2.70	2.61	1.03	0.30
Grays Thurrock	Brühl (Koller), Rheingewann	6.34	2.22	2.85	0.0043
Grays Thurrock	Barrington	5.81	2.21	2.63	0.0085
Swanscombe	Hoe Grange quarry	24.97	4.40	5.67	<0.0001
Swanscombe	Joint Mitnor Cave	24.62	4.31	5.72	<0.0001
Swanscombe	Otterstadt	21.56	4.30	5.01	<0.0001
Swanscombe	Brühl (Koller), Rheingewann	18.15	5.21	3.49	0.0005
Swanscombe	Clacton	14.78	4.39	3.37	0.0008
Swanscombe	Barrington	17.86	5.59	3.20	0.0014
Swanscombe	Grays Thurrock	10.31	4.62	2.23	0.026
West Runton	Otterstadt. Otterstadler Altrhein (Oberrhein)	5.56	2.93	1.90	0.06
West Runton	Brühl (Koller), Rheingewann (Oberrhein)	3.60	1.91	1.88	0.06
West Runton	Joint Mitnor Cave	6.06	3.55	1.71	0.09
West Runton	Hoe Grange quarry	6.16	4.18	1.47	0.14
West Runton	Barrington	2.48	1.84	1.35	0.18
West Runton	Clacton	2.33	2.57	0.91	0.36

West Runton	Grays Thurrock	1.46	2.22	0.66	0.51
West Runton	Swanscombe	1.04	5.21	0.20	0.84

APPENDIX 8.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Capreolus sp.* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Star Carr	Ketsch, Hohwiesen	2.49	2.81	0.89	0.38
Star Carr	Brühl (Koller), Schlangenwinkel	-1.50	2.82	-0.53	0.59
Star Carr	Edingen (Brühl), Edinger Ried	0.55	2.81	0.20	0.84
Star Carr	Ilford	0.29	3.40	0.08	0.93
Edingen (Brühl), Edinger Ried	Brühl (Koller), Schlangenwinkel	-2.96	2.33	-1.27	0.20
Ketsch, Hohwiesen	Ilford	-1.05	1.81	-0.58	0.56
Ketsch, Hohwiesen	Brühl (Koller), Schlangenwinkel	-6.22	2.33	-2.67	0.0077
Ketsch, Hohwiesen	Edingen (Brühl), Edinger Ried	-4.00	1.91	-2.09	0.037
Ilford	Brühl (Koller), Schlangenwinkel	-2.14	2.59	-0.82	0.41
Ilford	Edingen (Brühl), Edinger Ried	-0.35	1.81	-0.19	0.85
Süssenborn	Ketsch, Hohwiesen	3.15	1.81	1.74	0.08
Süssenborn	Edingen (Brühl), Edinger Ried	2.45	1.81	1.36	0.18
Süssenborn	Brühl (Koller), Schlangenwinkel	2.14	2.59	0.82	0.41
Süssenborn	Star Carr	2.60	3.40	0.76	0.44
Süssenborn	Ilford	0.50	1.29	0.39	0.70
<i>Voigtstedt</i>	<i>Brühl (Koller), Schlangenwinkel</i>	-3.91	2.58	-1.51	0.13
<i>Voigtstedt</i>	<i>Süssenborn</i>	-3.30	2.79	-1.18	0.24
<i>Voigtstedt</i>	<i>Ketsch, Hohwiesen</i>	2.55	2.45	1.04	0.30
<i>Voigtstedt</i>	<i>Edingen (Brühl), Edinger Ried</i>	-1.05	2.45	-0.43	0.67
<i>Voigtstedt</i>	<i>Ilford</i>	0.00	2.79	0.00	1.00
<i>Voigtstedt</i>	<i>Star Carr</i>	0.00	2.85	0.00	1.00

APPENDIX 9.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of Megacerini spp. in localities. The significant differences are mostly due to the smaller size of early Middle Pleistocene *Praemegaceros* and *Megaloceros* species compared to late Middle and Late Pleistocene *Megaloceros giganteus*.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Kent's Cavern	Ireland	7.86	11.18	0.70	0.48
Kent's Cavern	Isleworth, Willment's pit	0.00	1.53	0.00	1.00
Isleworth, Willment's pit	Ireland	5.77	11.18	0.52	0.61
Villa Seckendorff	Swanscombe	4.42	2.31	1.91	0.06
Villa Seckendorff	Kent's Cavern	2.06	2.25	0.92	0.36
Villa Seckendorff	Isleworth, Willment's pit	1.60	2.25	0.71	0.48
Villa Seckendorff	Steinheim, grube Sammet	-1.84	2.61	-0.70	0.48
Villa Seckendorff	Süssenborn	15.99	4.22	3.79	0.0002
Villa Seckendorff	Pakefield	6.34	2.22	2.85	0.0043
Villa Seckendorff	Ireland	17.01	7.65	2.22	0.026
Steinheim, grube Sammet	Kent's Cavern	4.24	2.72	1.56	0.12
Steinheim, grube Sammet	Isleworth, Willment's pit	3.39	2.72	1.25	0.21
Steinheim, grube Sammet	Ireland	22.85	6.94	3.29	0.0010
Steinheim, grube Sammet	Pakefield	7.85	2.57	3.06	0.0022
Swanscombe	Kent's Cavern	-2.38	2.09	-1.14	0.25
Swanscombe	Isleworth, Willment's pit	-1.43	2.09	-0.68	0.49
Swanscombe	Ireland	-5.17	8.00	-0.65	0.52
Swanscombe	Pakefield	5.14	2.11	2.44	0.015
Swanscombe	Steinheim, grube Sammet	-5.84	2.58	-2.26	0.024
Pakefield	Ireland	-32.74	9.06	-3.61	0.0003
Pakefield	Isleworth, Willment's pit	-3.73	1.79	-2.09	0.037
Pakefield	Kent's Cavern	-3.73	1.79	-2.09	0.037
Süssenborn	Swanscombe	-8.48	4.33	-1.96	0.05
Süssenborn	Ireland	-27.68	5.95	-4.65	<0.0001
Süssenborn	Steinheim, grube Sammet	-18.04	4.06	-4.45	<0.0001
Süssenborn	Pakefield	11.67	4.69	2.49	0.013
Süssenborn	Kent's Cavern	-13.10	5.52	-2.37	0.018
Süssenborn	Isleworth, Willment's pit	-11.26	5.52	-2.04	0.042
Voigtstedt	Süssenborn	-0.79	4.69	-0.17	0.87
Voigtstedt	Ireland	-34.80	5.96	-5.84	<0.0001
Voigtstedt	Steinheim, grube Sammet	-22.85	4.72	-4.84	<0.0001
Voigtstedt	Villa Seckendorff	-21.16	5.02	-4.21	<0.0001
Voigtstedt	Kent's Cavern	-18.96	6.85	-2.77	0.0057
Voigtstedt	Pakefield	15.15	5.72	2.65	0.0081
Voigtstedt	Swanscombe	-11.86	5.19	-2.29	0.022
Voigtstedt	Isleworth, Willment's pit	-14.63	6.85	-2.13	0.033

APPENDIX 10.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Rangifer tarandus* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Kent's Cavern	Isleworth, Willment's pit	-17.67	4.14	-4.27	<0.0001
Wretton	Kent's Cavern	17.53	3.77	4.65	<0.0001
Wretton	Isleworth, Willment's pit	3.06	4.00	0.76	0.44

APPENDIX 11.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Alcini* in localities. The significant differences are mostly due to the larger size of early Middle Pleistocene *Cervalces latifrons* compared to Late Pleistocene and Holocene *Alces alces*.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Star Carr	Mauer	-12.39	3.45	-3.60	0.0003
Star Carr	Brühl (Koller), Schlangenwinkel	-6.47	3.45	-1.88	0.061
Mauer	Brühl (Koller), Schlangenwinkel	5.17	2.08	2.48	0.013
Süssenborn	Star Carr	14.93	3.34	4.48	<0.0001
Süssenborn	Brühl (Koller), Schlangenwinkel	8.37	2.56	3.27	0.0011
Süssenborn	Mauer	5.54	2.56	2.16	0.031

APPENDIX 12.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Stephanorhinus hundsheimensis* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Pakefield	Mauer	-3.33	2.09	-1.60	0.11
Süssenborn	Mauer	-2.63	2.17	-1.21	0.22
Süssenborn	Pakefield	0.25	1.94	0.13	0.90
West Runton	Süssenborn	1.67	2.00	0.83	0.40
West Runton	Pakefield	0.42	1.44	0.29	0.77
West Runton	Mauer	0.32	2.20	0.15	0.88
Voigtstedt	Pakefield	7.48	4.20	1.78	0.08
Voigtstedt	Süssenborn	3.36	3.56	0.94	0.35
Voigtstedt	Mauer	-1.06	3.49	-0.30	0.76
Voigtstedt	West Runton	-1.38	4.82	-0.29	0.78

APPENDIX 13.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Stephanorhinus hemitoechus* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Joint Mitnor Cave	Ilford	2.19	2.39	0.91	0.36
Joint Mitnor Cave	Barrington	1.53	2.59	0.59	0.56
Reilingen, Spies	Joint Mitnor Cave	-2.63	1.62	-1.62	0.11
Reilingen, Spies	Barrington	-3.43	2.34	-1.47	0.14
Reilingen, Spies	Ilford	-0.19	2.21	-0.08	0.93
Ilford	Barrington	-1.53	2.45	-0.63	0.53
Swanscombe	Barrington	-4.58	2.59	-1.77	0.08
Swanscombe	Reilingen, Spies	-2.63	1.62	-1.62	0.11
Swanscombe	Ilford	-3.44	2.39	-1.44	0.15
Swanscombe	Joint Mitnor Cave	-1.50	1.29	-1.16	0.25

APPENDIX 14.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Coelodonta antiquitatis* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Kent's Cavern	Aufhausener höhle	2.31	2.49	0.93	0.35
Whitemoor Haye	Aufhausener höhle	3.30	2.79	1.18	0.24
Whitemoor Haye	Kent's Cavern	1.61	2.20	0.73	0.46
Whitemoor Haye	Lampertheim in der Tanne	0.42	1.44	0.29	0.77
Villa Seckendorff	Aufhausener höhle	3.30	2.79	1.18	0.24
Villa Seckendorff	Lampertheim in der Tanne	0.42	1.44	0.29	0.77
Villa Seckendorff	Kent's Cavern	-0.32	2.20	-0.15	0.88
Villa Seckendorff	Whitemoor Haye	0.00	1.29	0.00	1.00
Lampertheim in der Tanne	Aufhausener höhle	0.65	2.56	0.25	0.80
Lampertheim in der Tanne	Kent's Cavern	0.00	2.09	0.00	1.00

APPENDIX 15.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Bison priscus/schoetensacki* in localities. Some of the significant differences are due to the smaller size of early Middle Pleistocene *Bison schoetensacki* compared to Late Pleistocene *B. priscus*.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Kent's Cavern	Boxgrove	6.41	3.31	1.94	0.053
Kent's Cavern	Brundon	5.16	3.11	1.66	0.097
Kent's Cavern	Joint Mitnor Cave	5.18	3.14	1.65	0.099
Kent's Cavern	Isleworth, Willment's pit	19.59	4.03	4.87	<0.0001
Kent's Cavern	Barrington	14.33	5.58	2.57	0.010
Isleworth, Willment's pit	Brundon	-6.38	4.48	-1.42	0.16
Isleworth, Willment's pit	Barrington	-24.42	5.40	-4.53	<0.0001
Isleworth, Willment's pit	Boxgrove	-10.71	5.01	-2.14	0.033
Wretton	Swanscombe	-8.52	5.33	-1.60	0.11
Wretton	Pakefield	-6.67	4.47	-1.49	0.14
Wretton	Isleworth, Willment's pit	-5.31	4.56	-1.17	0.24
Wretton	West Runton	-7.69	7.46	-1.03	0.303
Wretton	Barrington	-30.00	5.45	-5.50	<0.0001
Wretton	Kent's Cavern	-22.78	4.35	-5.23	<0.0001
Wretton	Steinheim, grube Sammet	-42.07	5.67	-7.42	<0.0001
Wretton	Taubach	-31.07	4.87	-6.38	<0.0001
Wretton	Villa Seckendorff	-16.88	4.43	-3.81	0.0001
Wretton	Mauer	-16.33	4.35	-3.75	0.0002
Wretton	Joint Mitnor Cave	-15.97	4.43	-3.61	0.0003
Wretton	Süssenborn	-16.45	5.07	-3.24	0.0012
Wretton	Boxgrove	-14.44	5.73	-2.52	0.012
Wretton	Brundon	-10.93	5.06	-2.16	0.031
Villa Seckendorff	Kent's Cavern	-5.32	3.14	-1.69	0.09
Villa Seckendorff	Swanscombe	3.83	2.69	1.42	0.16
Villa Seckendorff	West Runton	4.38	3.20	1.37	0.17
Villa Seckendorff	Brundon	2.13	2.67	0.80	0.43
Villa Seckendorff	Mauer	1.82	3.14	0.58	0.56
Villa Seckendorff	Barrington	0.41	5.88	0.07	0.94
Villa Seckendorff	Boxgrove	0.17	2.75	0.06	0.95
Villa Seckendorff	Joint Mitnor Cave	-0.08	2.89	-0.03	0.98
Villa Seckendorff	Isleworth, Willment's pit	13.04	4.03	3.23	0.0012
Villa Seckendorff	Taubach	-12.25	4.75	-2.58	0.0099
Villa Seckendorff	Pakefield	6.19	2.83	2.18	0.029
Villa Seckendorff	Süssenborn	11.20	5.15	2.17	0.030
Villa Seckendorff	Steinheim, grube Sammet	-13.56	6.29	-2.16	0.031
Joint Mitnor Cave	Brundon	1.38	2.67	0.52	0.61
Joint Mitnor Cave	Boxgrove	0.83	2.75	0.30	0.76
Joint Mitnor Cave	Barrington	-0.15	5.88	-0.03	0.98
Joint Mitnor Cave	Isleworth, Willment's pit	11.13	4.03	2.76	0.0058
Taubach	Kent's Cavern	5.28	4.62	1.14	0.25
Taubach	Barrington	23.39	5.52	4.24	<0.0001
Taubach	Isleworth, Willment's pit	27.89	4.74	5.89	<0.0001
Taubach	Pakefield	20.40	4.81	4.24	<0.0001
Taubach	Süssenborn	31.34	5.17	6.06	<0.0001
Taubach	Mauer	16.79	4.62	3.63	0.0003
Taubach	Swanscombe	15.89	5.85	2.72	0.0066
Taubach	Steinheim, grube Sammet	14.07	5.72	2.46	0.014

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Taubach	Joint Mitnor Cave	11.31	4.75	2.38	0.017
Taubach	Boxgrove	14.27	6.30	2.26	0.024
Taubach	Brundon	10.94	5.53	1.98	0.048
Brundon	Barrington	-5.31	7.16	-0.74	0.46
Brundon	Boxgrove	-0.63	1.95	-0.32	0.75
Steinheim, grube Sammet	Joint Mitnor Cave	10.98	6.29	1.75	0.081
Steinheim, grube Sammet	Kent's Cavern	-4.58	5.93	-0.77	0.44
Steinheim, grube Sammet	Isleworth, Willment's pit	38.46	5.65	6.81	<0.0001
Steinheim, grube Sammet	Pakefield	31.05	6.43	4.83	<0.0001
Steinheim, grube Sammet	Brundon	15.22	7.75	1.96	0.050
Steinheim, grube Sammet	Mauer	18.48	5.93	3.12	0.0018
Steinheim, grube Sammet	Barrington	17.63	6.01	2.93	0.0033
Steinheim, grube Sammet	Boxgrove	20.49	9.04	2.27	0.023
Swanscombe	Barrington	-10.76	7.64	-1.41	0.16
Swanscombe	Joint Mitnor Cave	-3.26	2.69	-1.21	0.23
Swanscombe	Isleworth, Willment's pit	5.30	4.69	1.13	0.26
Swanscombe	Boxgrove	-1.58	1.84	-0.86	0.39
Swanscombe	Mauer	-2.23	3.18	-0.70	0.48
Swanscombe	Pakefield	1.75	2.57	0.68	0.50
Swanscombe	Brundon	-0.55	2.01	-0.27	0.78
Swanscombe	Kent's Cavern	-8.27	3.18	-2.60	0.0093
Swanscombe	Steinheim, grube Sammet	-20.70	8.29	-2.50	0.013
Boxgrove	Barrington	-6.07	8.32	-0.73	0.47
Mauer	Barrington	-4.89	5.58	-0.88	0.38
Mauer	Joint Mitnor Cave	-1.68	3.14	-0.53	0.59
Mauer	Brundon	1.03	3.11	0.33	0.74
Mauer	Boxgrove	0.00	3.31	0.00	1.000
Mauer	Isleworth, Willment's pit	11.83	4.03	2.94	0.0033
Mauer	Kent's Cavern	-8.69	3.32	-2.62	0.0088
Pakefield	Boxgrove	-3.92	2.61	-1.50	0.133
Pakefield	Brundon	-2.70	2.56	-1.06	0.29
Pakefield	Isleworth, Willment's pit	1.84	4.06	0.45	0.65
Pakefield	Kent's Cavern	-12.04	3.11	-3.87	0.0001
Pakefield	Barrington	-18.57	6.00	-3.10	0.0020
Pakefield	Mauer	-7.13	3.11	-2.29	0.022
Pakefield	Joint Mitnor Cave	-5.84	2.83	-2.06	0.039
Süssenborn	Mauer	-9.49	4.96	-1.91	0.056
Süssenborn	Isleworth, Willment's pit	9.02	4.97	1.82	0.069
Süssenborn	Boxgrove	-8.90	7.02	-1.27	0.21
Süssenborn	Pakefield	5.79	5.23	1.11	0.27
Süssenborn	Brundon	-3.33	6.11	-0.55	0.59
Süssenborn	Swanscombe	-1.01	6.49	-0.16	0.88
Süssenborn	Kent's Cavern	-23.00	4.96	-4.64	<0.0001
Süssenborn	Steinheim, grube Sammet	-38.83	5.80	-6.69	<0.0001
Süssenborn	Barrington	-20.84	5.62	-3.71	0.0002
Süssenborn	Joint Mitnor Cave	-10.98	5.15	-2.13	0.033
West Runton	Taubach	-16.07	8.28	-1.94	0.05
West Runton	Barrington	-15.85	11.13	-1.42	0.16
West Runton	Mauer	-4.78	4.00	-1.19	0.23
West Runton	Boxgrove	-1.88	1.62	-1.16	0.25
West Runton	Joint Mitnor Cave	-3.21	3.20	-1.00	0.32
West Runton	Brundon	-1.00	2.00	-0.50	0.62

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
West Runton	Süssenborn	-3.93	9.30	-0.42	0.67
West Runton	Swanscombe	-0.35	1.81	-0.19	0.85
West Runton	Isleworth, Willment's pit	0.80	6.44	0.12	0.90
West Runton	Pakefield	0.00	2.99	0.00	1.000
West Runton	Steinheim, grube Sammet	-28.74	12.15	-2.37	0.018
West Runton	Kent's Cavern	-8.16	4.00	-2.04	0.042

APPENDIX 16.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Bos primigenius* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Star Carr	Brundon	-6.63	3.93	-1.69	0.092
Star Carr	Clacton	-15.03	3.83	-3.92	<0.0001
Star Carr	Ilford	-28.83	4.73	-6.09	<0.0001
Star Carr	Grays Thurrock	-13.07	3.57	-3.66	0.0003
Star Carr	Joint Mitnor Cave	-9.98	3.57	-2.79	0.0052
Star Carr	Aveley	-9.18	3.60	-2.55	0.011
Star Carr	Barrington	-10.19	4.16	-2.45	0.014
Star Carr	Brühl (Koller), Rheingewann	-7.93	3.63	-2.18	0.029
Villa Seckendorff	Grays Thurrock	-9.60	5.31	-1.81	0.071
Villa Seckendorff	Aveley	-5.98	5.18	-1.15	0.25
Villa Seckendorff	Clacton	-4.99	5.01	-1.00	0.32
Villa Seckendorff	Barrington	-5.86	7.31	-0.80	0.42
Villa Seckendorff	Brühl (Koller), Rheingewann	3.62	5.82	0.62	0.53
Villa Seckendorff	Joint Mitnor Cave	-2.28	5.31	-0.43	0.67
Villa Seckendorff	Swanscombe	1.25	5.40	0.23	0.82
Villa Seckendorff	Brundon	-0.11	6.74	-0.02	0.99
Villa Seckendorff	Ilford	-18.79	5.30	-3.54	0.0004
Villa Seckendorff	Star Carr	16.13	5.01	3.22	0.0013
Joint Mitnor Cave	Grays Thurrock	-3.00	2.89	-1.04	0.30
Joint Mitnor Cave	Brühl (Koller), Rheingewann	2.19	2.70	0.81	0.42
Joint Mitnor Cave	Aveley	-2.24	3.01	-0.75	0.46
Joint Mitnor Cave	Barrington	-1.50	2.75	-0.55	0.59
Joint Mitnor Cave	Clacton	-1.51	3.50	-0.43	0.67
Joint Mitnor Cave	Brundon	0.99	2.69	0.37	0.71
Joint Mitnor Cave	Ilford	-10.13	4.91	-2.07	0.040
Barrington	Aveley	-1.45	3.03	-0.48	0.63
Brühl (Koller), Rheingewann	Barrington	-2.81	2.21	-1.27	0.20
Brühl (Koller), Rheingewann	Aveley	-3.04	2.88	-1.06	0.29
Brühl (Koller), Rheingewann	Brundon	-0.49	2.22	-0.22	0.83
Brundon	Aveley	-1.76	2.93	-0.60	0.55
Brundon	Barrington	-0.68	1.84	-0.37	0.71
Ilford	Brundon	11.73	6.10	1.92	0.055
Ilford	Barrington	7.58	6.59	1.15	0.25
Ilford	Aveley	-1.02	4.81	-0.21	0.83
Ilford	Grays Thurrock	0.82	4.91	0.17	0.87
Ilford	Brühl (Koller), Rheingewann	20.71	5.32	3.89	<0.0001
Ilford	Clacton	11.06	4.73	2.34	0.019
Grays Thurrock	Brundon	2.98	2.69	1.11	0.27
Grays Thurrock	Clacton	3.08	3.50	0.88	0.38
Grays Thurrock	Barrington	1.17	2.75	0.42	0.67
Grays Thurrock	Aveley	-0.23	3.01	-0.08	0.94
Grays Thurrock	Brühl (Koller), Rheingewann	5.73	2.70	2.12	0.034
Clacton	Brühl (Koller), Rheingewann	6.47	3.54	1.83	0.067
Clacton	Aveley	-2.80	3.54	-0.79	0.43

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Clacton	Brundon	2.60	3.81	0.68	0.49
Clacton	Barrington	-1.04	4.02	-0.26	0.80
Swanscombe	Grays Thurrock	-4.79	2.83	-1.69	0.091
Swanscombe	Clacton	-3.74	3.49	-1.07	0.28
Swanscombe	Aveley	-3.00	2.97	-1.01	0.31
Swanscombe	Barrington	-2.39	2.61	-0.91	0.36
Swanscombe	Joint Mitnor Cave	-1.31	2.83	-0.46	0.64
Swanscombe	Brühl (Koller), Rheingewann	0.65	2.61	0.25	0.80
Swanscombe	Brundon	-0.29	2.57	-0.11	0.91
Swanscombe	Ilford	-13.46	4.98	-2.71	0.0068
Swanscombe	Star Carr	7.30	3.57	2.04	0.041

APPENDIX 17.

Pairwise comparison by Wilcoxon tests of mean body mass (kg) of *Equus ferus/mosbachensis* in localities.

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Gough's Cave	Brundon	-15.48	4.48	-3.46	0.0005
Gough's Cave	Frankenbacher Sande	-10.66	3.11	-3.43	0.0006
Gough's Cave	Crayford	-22.01	6.46	-3.41	0.0007
Gough's Cave	Aufhausener Höhle	-8.82	3.11	-2.84	0.0045
Kent's Cavern	Aufhausener Höhle	-1.07	4.35	-0.25	0.81
Kent's Cavern	Frankenbacher Sande	-17.31	4.35	-3.98	<0.0001
Kent's Cavern	Ilford	-18.35	4.56	-4.02	<0.0001
Kent's Cavern	Gough's Cave	15.46	5.06	3.06	0.0022
Kent's Cavern	Brundon	-12.25	4.56	-2.68	0.0073
Kent's Cavern	Crayford	-12.74	5.19	-2.45	0.014
Villa Seckendorff	Kent's Cavern	13.71	7.93	1.73	0.08
Villa Seckendorff	Aufhausener Höhle	15.14	9.34	1.62	0.11
Villa Seckendorff	Brundon	-10.02	8.14	-1.23	0.22
Villa Seckendorff	Crayford	-6.78	7.70	-0.88	0.38
Villa Seckendorff	Swanscombe	-7.67	11.91	-0.64	0.52
Villa Seckendorff	Steinheim, grube Sigrist	-5.43	11.38	-0.48	0.63
Villa Seckendorff	Steinheim, grube Sammet	2.68	7.69	0.35	0.73
Villa Seckendorff	Taubach	-1.75	11.38	-0.15	0.88
Villa Seckendorff	Gough's Cave	44.69	13.39	3.34	0.0008
Villa Seckendorff	Frankenbacher Sande	-30.58	9.34	-3.27	0.0011
Villa Seckendorff	Ilford	-24.48	8.14	-3.01	0.0026
Villa Seckendorff	Mauer	-21.87	9.18	-2.38	0.017
Taubach	Frankenbacher Sande	-4.77	3.07	-1.56	0.12
Taubach	Mauer	-3.91	3.15	-1.24	0.22
Taubach	Aufhausener Höhle	3.39	3.07	1.10	0.27
Taubach	Ilford	-4.04	4.15	-0.97	0.33
Taubach	Kent's Cavern	3.89	4.61	0.84	0.40
Taubach	Steinheim, grube Sammet	2.19	5.84	0.38	0.71
Taubach	Brundon	-1.10	4.15	-0.27	0.79
Taubach	Steinheim, grube Sigrist	0.22	2.52	0.09	0.93
Taubach	Crayford	-0.40	5.74	-0.07	0.94
Taubach	Swanscombe	0.12	2.45	0.05	0.96
Taubach	Gough's Cave	5.14	2.36	2.18	0.029
Crayford	Brundon	-3.07	5.11	-0.60	0.55
Crayford	Aufhausener Höhle	12.28	5.17	2.38	0.017
Brundon	Aufhausener Höhle	11.15	4.03	2.77	0.0056
Ilford	Brundon	6.68	4.36	1.53	0.13
Ilford	Frankenbacher Sande	-5.16	4.03	-1.28	0.20
Ilford	Aufhausener Höhle	15.76	4.03	3.92	<0.0001
Ilford	Gough's Cave	16.29	4.48	3.64	0.0003

Fossil population	by Fossil population	Score Mean Difference	Std. Err. Dif.	Z	p
Ilford	Crayford	10.60	5.11	2.08	0.038
Steinheim, grube Sammet	Brundon	-7.53	5.15	-1.46	0.14
Steinheim, grube Sammet	Kent's Cavern	7.42	5.24	1.42	0.16
Steinheim, grube Sammet	Aufhausener Höhle	7.08	5.24	1.35	0.18
Steinheim, grube Sammet	Crayford	-6.22	5.54	-1.12	0.26
Steinheim, grube Sammet	Frankenbacher Sande	-17.73	5.24	-3.39	0.0007
Steinheim, grube Sammet	Gough's Cave	21.01	6.58	3.19	0.0014
Steinheim, grube Sammet	Ilford	-15.31	5.15	-2.97	0.0030
Steinheim, grube Sammet	Mauer	-13.01	5.20	-2.50	0.012
Steinheim, grube Sigrist	Kent's Cavern	8.98	4.61	1.95	0.05
Steinheim, grube Sigrist	Aufhausener Höhle	5.82	3.07	1.90	0.06
Steinheim, grube Sigrist	Ilford	-6.68	4.15	-1.61	0.11
Steinheim, grube Sigrist	Mauer	-4.33	3.15	-1.37	0.17
Steinheim, grube Sigrist	Brundon	-2.72	4.15	-0.65	0.51
Steinheim, grube Sigrist	Steinheim, grube Sammet	2.86	5.84	0.49	0.62
Steinheim, grube Sigrist	Crayford	-0.80	5.74	-0.14	0.89
Steinheim, grube Sigrist	Gough's Cave	6.53	2.36	2.77	0.0056
Steinheim, grube Sigrist	Frankenbacher Sande	-7.12	3.07	-2.32	0.020
Swanscombe	Kent's Cavern	8.85	4.72	1.88	0.06
Swanscombe	Ilford	-6.35	4.22	-1.50	0.13
Swanscombe	Mauer	-3.40	3.15	-1.08	0.28
Swanscombe	Steinheim, grube Sammet	4.92	6.03	0.82	0.41
Swanscombe	Steinheim, grube Sigrist	1.06	2.45	0.43	0.67
Swanscombe	Crayford	1.99	5.93	0.34	0.74
Swanscombe	Brundon	-0.40	4.22	-0.10	0.92
Swanscombe	Gough's Cave	6.27	2.26	2.78	0.0055
Swanscombe	Aufhausener Höhle	6.84	3.06	2.24	0.025
Swanscombe	Frankenbacher Sande	-6.47	3.06	-2.11	0.035
Frankenbacher Sande	Aufhausener Höhle	13.44	3.32	4.05	<0.0001
Frankenbacher Sande	Crayford	14.11	5.17	2.73	0.0063
Frankenbacher Sande	Brundon	9.48	4.03	2.35	0.019
Mauer	Crayford	8.55	5.14	1.66	0.10
Mauer	Brundon	5.06	4.04	1.25	0.21
Mauer	Frankenbacher Sande	-2.00	3.37	-0.59	0.55
Mauer	Ilford	0.43	4.04	0.11	0.92
Mauer	Gough's Cave	10.94	3.22	3.40	0.0007
Mauer	Kent's Cavern	14.62	4.35	3.36	0.0008
Mauer	Aufhausener Höhle	10.74	3.37	3.19	0.0014