Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity

You'll have to take pot luck!

(proverb)

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Abstract

To trace the dietary evolution of the two abundant Middle to Late Pleistocene rhinoceros species *Stephanorhinus kirchbergensis* and *S. hemitoechus* in Europe over several climatic cycles, we examined comprehensive material of stratigraphically well-defined palaeopopulations from different regions and interglacials. Using morphometrics and

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mesowear analysis, these reconstructions of *Stephanorhinus* diets indicate that habitat diversity and interspecific competition with closely related rhinoceros species induced variation in feeding behaviour. Although anatomical features of both species suggest significantly higher dietary specializations compared to the Early to early Middle Pleistocene *S. hundsheimensis*, their mesowear signals are characteristic of a mixed feeder diet, similar to that of extant mammal species in relatively open habitats. Both species retained a degree of dietary flexibility, enabling them to survive in a range of environments. Although each of these rhinoceroses preferred different habitats, species identity alone is not sufficient to establish the real dietary traits of a *Stephanorhinus* palaeopopulation. As a consequence, their occurrence in a faunal assemblage alone cannot be taken to indicate a specific habitat.

S. kirchbergensis and *S. hemitoechus* were embedded in a dynamic process of temporo-spatial replacements and interspecific differentiation of rhinoceroses in the western Palaearctic. However, dietary specialization in these Middle to Late Pleistocene European rhinoceroses was not the result of a directed time-transgressive evolution. Rather, within the range of each species' ecological tolerance, it was controlled by environmental parameters, with habitat variability as the main factor.

1. Introduction

The reconstruction of fossil faunal assemblages can significantly contribute to our understanding of the natural variability and evolution of past ecosystems and climates. In particular, assessments of dietary requirements for each species and inferences to their corresponding subsistence strategies have proved to be valuable methods for reconstructing palaeoenvironmental parameters. In the case of herbivores, reconstructions of the vegetational character of associated palaeoenvironments based on dietary signals may provide detailed insights into the behaviour of different species, when corresponding palaeobotanical records are not available.

Pleistocene herbivore communities clearly reflect fluctuations in global climate and resulting environmental changes (e.g. Lister, 2004; Kahlke et al., 2011). Rhinocerotids in particular are among the most significant ecological trace species of the Palaearctic (Zeuner, 1934; Loose, 1975; Guérin, 1980; Fortelius, 1982; Fortelius et al., 1993; Lacombat, 2006; Hernesniemi et al., 2011; Kahlke, 2014). Recent investigations have revealed that Pleistocene rhinoceroses show an individualistic response to changes in the periodicity of environmental variation (Raymo and Nisancioglu, 2003, Figure 1; Lisiecki and Raymo, 2005, Figure 4), resulting in different evolutionary patterns between species. Thus, the subsistence strategy of *Stephanorhinus hundsheimensis*, as the only rhinocerotid species of western Palaearctic mammal faunas between 1.4/1.2 and 0.6/0.5 Ma BP, was that of a generalist. Its lifestyle evolved under the influence of the relatively stable 41 ka climatic periodicity and proved to be very successful also during the more unsteady climate course of the transitional interval linking with the following 100 ka regime (Kahlke et al., 2011, p. 1388). The dietary variability of *S. hundsheimensis* ranged from grazing regimes to predominantly browsing ones, characterising the species as the ecologically most tolerant rhinoceros of the Palaearctic Plio-Pleistocene (Kahlke and Kaiser, 2011).

A different path of evolution can be traced in the genus *Coelodonta*. From the Late Pliocene onwards (Deng et al., 2011), its range was for more than three million years restricted to open landscapes in Central Asia. Strictly progressive adaptation to efficient grazing enabled woolly rhinoceroses to inhabit the pan-Eurasian tundra-steppe for the first time around 460 ka BP (Kahlke and Lacombat, 2008). This new type of biome originated during marine isotope stage (MIS) 12, a long-lasting and pronounced cold interval within the 100 ka periodicity span. During most of the subsequent warm and humid stages *Coelodonta* populations retreated from western Palaearctic areas, only to re-occupy extended Eurasian territories as increasingly more specialized grazers during the succeeding cold and continental periods (Kahlke, 2014).

Over substantial periods of the Pleistocene *Stephanorhinus hundsheimensis* and *Coelodonta* species occupied huge territories of the Palaearctic. Members of both groups predominantly occurred as the only rhinoceros species of corresponding faunas, and their subsistence strategies were principally different. However, at present it is not well understood whether a co-occurrence of two species of Pleistocene rhinoceros might have affected their dietary specialization, and whether rhinoceros dietary flexibility interacts with environmental conditions. Sympatries of closely related species are not uncommon in mammalian communities (e.g. Jacoby et al., 1999; Hayward and Kerley, 2008; Li et al., 2008; Dammhahn et al., 2013). Such co-occurrences of closely related species are durable only if intraspecific competition is stronger than interspecific competition (Elton, 1927). Sympatric species tend to reduce competition through differences in their use of resources, whether by focusing on different resources, by using these resources at different times or at different intensities, or by exploiting different habitats within the same landscape (e.g. Chase and Leibold, 2003). Several extant rhinoceros species occur sympatrically. Specialised grazer *Ceratotherium simum* and the co-occurring browsing species *Diceros bicornis* have little overlap in diet (Groves, 1972; Owen-Smith, 1988; Hillman-Smith and Groves, 1994; Codron et al., 2007; Steuer et al., 2010). The browsing species *Dicerorhinus sumatrensis* and *Rhinoceros sondaicus*, whose ranges overlapped in the past, avoided competitive interactions by using upland resp. lowland habitats (Groves and Kurt, 1972; Groves and Leslie, 2011).

Here we investigate the subsistence strategy of two closely related rhinoceros species, *Stephanorhinus kirchbergensis* (Jäger, 1839), the so-called forest rhinoceros, and *S. hemitoechus* (Falconer, 1868), the slightly smaller-bodied steppe rhinoceros. Both species occurred in most regions of the western Palaearctic during temperate periods of the Middle and Late Pleistocene, sometimes allopatrically, at other times sympatrically. To trace their dietary evolution in Europe over several climatic cycles we examined *Stephanorhinus* material from palaeopopulations of different regions and interglacials.

2. Appearance and spread of *Stephanorhinus kirchbergensis* and *S. hemitoechus* in Europe

During the early Middle Pleistocene two new rhinoceros species, *S. kirchbergensis* and *S. hemitoechus*, with different and more specialised feeding strategies, appeared in Europe to compete with the previously unchallenged generalist *Stephanorhinus hundsheimensis*. After a period of sympatry between 0.7 and 0.6 Ma BP, documented in the faunal assemblages of several early Middle Pleistocene sites, such as Kolkotova Balka and Sukleya near Tiraspol (Moldova), Mauer and Mosbach 2 (Germany), as well as Soleilhac (France), *S. kirchbergensis* started to replace *S. hundsheimensis* in temperate faunas (Beljaeva and David, 1975; Guérin, 1980; Fortelius et al., 1993; Schreiber, 2005). *S. kirchbergensis*, an immigrant of Asian origin (Guérin, 1980; Van der Made, 2000), was a very large animal with long legs, a high head posture, and moderately hypsodont molars (Fortelius et al., 1993), indicating a diet with significant portions of browsing.

Between 0.6 and 0.5 Ma, a second rhinoceros species, *S. hemitoechus*, appeared in Europe, as recorded in the Mosbach 2 gravels (Fortelius et al., 1993; Hemmer et al., 2003). Its anatomy, especially its relatively short limbs, the low-slung cranium, more hypsodont molars and reduced premolar segment of the tooth rows compared to those of *S. kirchbergensis*, indicate affinities to less forested landscapes or open grasslands (Guérin, 1980; Janis, 1990; Mazza, 1993; Fortelius et al., 1993). This is corroborated by the fact that it was especially widespread in Europe under dryer and/or moderate to cooler conditions. The origins of both rhinoceroses, *S. kirchbergensis* and *S. hemitoechus*, seem to ultimately derive from the development of the 100 ka periodicity in the global climatic record, which led to a longer lasting environmental continuity in the resulting biomes compared to the preceding 41 ka span of time (Kahlke et al., 2011).

Alternating stages of prolonged colder and temperate climatic conditions resulted in mutual alternations of *Coelodonta tologoijensis* / *C. antiquitatis* and *S. hemitoechus* populations from the Middle Pleistocene onwards. When *C. tologoijensis* spread into Eastern and Central Europe during MIS 12, *S. hemitoechus* retreated to Western Europe and survived there, as it is recorded e.g. from Tautavel (Ensemble III) in France (Moigne et al., 2006). Both species co-occurred at the sites of La Fage (layer 5) in France during MIS 10 or 8 (Guérin, 1973) and Weimar-Ehringsdorf (Upper Travertines) in Germany during MIS 7 and/or 5 (Kahlke, 1975; Kahlke et al., 2002). Stratigraphic sequences at the latter site indicate that *S. hemitoechus* was replaced successively by *Coelodonta*. A similar alternation has been observed in areas of Great Britain (Schreve, 2001a) and in the northern part of the Iberian Peninsula (Álvarez-Lao and García, 2011). During interstadials and especially during periods of interglacial warming the opposite happened: *S. hemitoechus* prevailed and *Coelodonta* disappeared from large areas of Europe. However, under optimal interglacial conditions with extensive afforestation, the steppe rhino was successively replaced by the ecologically more demanding *S. kirchbergensis*, as far as the latter had access to corresponding areas.

During the Last Glacial *Stephanorhinus* withdrew from most areas of Europe to - probably several - southern refugia. Both *S. kirchbergensis* and *S. hemitoechus* became extinct in the Western Palaearctic well before the Last Glacial Maximum (LGM). Youngest finds of *S. kirchbergensis* from the Grotte des Enfants and the Grotte du Prince (Grimaldi Caves) in Italy are assigned to MIS 4 to 3 (Lacombat, 2005, 2006). The latest occurrence of *S. hemitoechus* reported so far, from the Bulgarian Bacho Kiro Cave, approximately 42.542 ± 1.068 cal. ka in age (Stuart and Lister, 2007), may correlate with Greenland Interstadial (GI) 10 of MIS 3 (Van Meerbeeck et al., 2011). Supposedly younger *Stephanorhinus* finds of Azilian or Neolithic age from Spain are dubious (Cerdeño, 1990; Sánchez et al., 2005; D.J. Álvarez-Lao, pers. comm.).

3. Material and methods

3.1. Material

To achieve a reliable dataset documenting the history of dietary specialization of *S. kirchbergensis* and *S. hemitoechus*, rhinoceros palaeopopulations from two European regions of different biogeographic location were selected. The inclusion of fossil rhino remains from different geographic areas provides control over the effect that regional differences, such as a reported geographic gradient in body size (Lacombat, 2009), may have on the results. We chose Central Germany and the British Isles representing Central and Northwest Europe respectively, because in both of these regions extensive fossil material of the two species from a range of more or less well-dated faunal assemblages is available (Figure 1; Table 1). Moreover, the dietary signals obtained here should not have been overprinted by the influence of competing species, because all assemblages considered here have a similar fauna of co-occurring herbivores feeding on the same levels of vegetation as the two rhinoceroses, often even at similar abundances (see references below). While episodes of co-occurrence of the two *Stephanorhinus* species have been documented for earlier interglacials (MIS 11, 7), during some parts of the Last Interglacial (MIS 5e) the species had a largely disjunct distribution in the studied area.

In Central Germany, the rhinoceros remains from Bilzingsleben, Weimar-Ehringsdorf and Weimar-Taubach (all in Thüringen; Table 1), were included in our study. The rhinoceros remains of these sites originate from travertine layers. Bilzingsleben II (hominin site) is related to one of the warm stages of the late Middle Pleistocene “Holstein-Komplex” (Mania, 1997, 2006; Heinrich, 2003), assigned by most authors to MIS 11 (Nitychoruk et al., 2006). Schreve and Bridgland (2002) correlate Bilzingsleben II with the younger of two temperate warm substages documented in the MIS 11 sequence of the Thames valley (UK). The fossil layer of Bilzingsleben II formed within a very short and hence biostratigraphically instantaneous time span, and produced a considerable number of individuals of both *S.*

kirchbergensis and *S. hemitoechus* (Figures 2a-b and 3a-b; Table 1; Van der Made, 2000), so that sympatry has to be concluded.

The very complex Pleistocene sequence of Weimar-Ehringsdorf contains remains of at least 12 biochronologically distinguishable mammal faunas (Kahlke et al., 2002 and references therein). The abundant *S. kirchbergensis* finds of Weimar-Ehringsdorf were recovered exclusively from the lower and middle parts of the Lower Travertin (hominin layers, Mammal Fauna 2), which reflect fully developed interglacial conditions (Kahlke, 1975: p. 385). The stratigraphic distribution of Ehringsdorf's rhinoceros fossils (Figures 2c-d and 3c-d), as far as accurate data on their discovery horizons are available (Kahlke, 1975: Figure 32), clearly indicate the co-occurrence of *S. kirchbergensis* and *S. hemitoechus* during the accumulation of the middle part of the Lower Travertine (Fauna 2). Such sympatry is not repeated during the later part of the Ehringsdorf faunal sequence. With the deposition of the upper part of the Lower Travertine (Mammal Fauna 3) the *kirchbergensis*-population has been completely replaced by *hemitoechus*-rhinos. Low numbers of *S. hemitoechus* fossils were also recorded in Ehringsdorf's Pariser horizon above the Lower Travertine (Mammal Fauna 5) and more frequently in the Upper Travertines (Mammal Faunas 7-8), here either as the only rhinoceros species or jointly with *Coelodonta antiquitatis* (Kahlke, 1975: p. 383). The stratigraphic classification of the individual fossiliferous horizons of Weimar-Ehringsdorf is still debated. The majority of biostratigraphic arguments (compiled in Kahlke et al., 2002; Katzschmann, 2007) assign the Lower Travertine with its Mammal Faunas 2 und 3 to MIS 7, without, however, ultimate clarity. The correlation of the *S. hemitoechus* bearing Upper Travertines either with MIS 7 or with 5e is also uncertain (Kahlke et al., 2002; Katzschmann, 2007).

The travertines of Weimar-Taubach inclusive of the Lower Travertine Sands, which produced the extended series of *S. kirchbergensis* finds (Table 1, Figure 2e-f), are confidently assigned to the Eemian, i.e. to the MIS 5e interglacial (Kahlke, 1977; Heinrich, 2003). Since the majority of Weimar-Taubach's rhinoceros remains are the result of Middle Palaeolithic killing and butchering activities (Bratlund, 1999 and references therein), they represent not just the immediate vicinity of the site within the water-rich floodplain of the river Ilm, but the more extended range of the human hunters. *S. kirchbergensis* therefore appears to have been the only rhino species present fully developed interglacial conditions in the Taubach area. The origin of a single *hemitoechus*-p4 from Weimar-Taubach is unclear; it probably derives from younger layers (Kahlke, 1977).

A range of rhinoceros fossils from the British Isles dated to MIS 7 and MIS 5e were studied (Table 1). Three rhinoceros species are recorded from the temperate deposits at Ilford (Uphall Pit; West et al., 1964) in the Lower Thames Valley: *S. hemitoechus*, *S. kirchbergensis* and a few specimens of *C. antiquitatis* (Schreve, 1997). The faunal material was collected from the Taplow-Mucking Formation in specific brickearth pits during the 19th century, although their exact provenance is largely unknown.

The sequence at Crayford (Scott, 2009), also in the Lower Thames Valley, shows great similarities to the Ilford sequence and has a similar research history (Bridgland, 1994; Gibbard, 1994). As at Ilford, the exact provenance of most specimens is unclear. The fauna from the Crayford Gravel underlying the brickearth includes *S. hemitoechus* and *C. antiquitatis*. The Lower Brickearth contained specimens of *S. kirchbergensis* and *C. antiquitatis* (Schreve, 1997). Amino acid ratios are indicative of an MIS 7 age for the temperate sediments at both sites (Penkman et al., 2008).

A temperate fauna, including a virtually complete skeleton of *S. hemitoechus*, was recovered from Bed 2 of the Lifeboat Station channel near Selsey, West Sussex (West et al., 1960). The channel is dated to MIS 7 based mainly on the composition of the mammalian fauna (Parfitt, 1998).

All three faunas are correlated with the late MIS 7 Sandy Lane Mammal Assemblage Zone (MAZ), which is thought to reflect relatively continental climatic conditions (Schreve, 2001a, b). Co-occurrence of *S. hemitoechus* and *S. kirchbergensis* can only tentatively be asserted for

Ilford, whilst at Crayford and Selsey only a single *Stephanorhinus* species is documented in each assemblage. However, these sites date from the same temperate stage, and both species have been found co-occurring at other Sandy Lane MAZ sites (e.g. West Thurrock, Pontnewydd; Green, 1984; Schreve et al., 2006). Both species were therefore present during MIS 7 and may have interacted. Below, these samples are collectively referred to as the 'British MIS 7 *S. hemitoechus*' or 'British MIS 7 *S. kirchbergensis*' sample.

For MIS 5e, six sites were chosen based on the reported presence of rhinoceros material in good condition. The Last Interglacial faunal assemblage from Victoria Cave was collected from the Hyaena Bone Bed within the Lower Cave Earth (Lord et al., 2007). Inside the cave, it is overlain by a thin flowstone, which started forming relatively late in the interglacial (Lundberg et al., 2010). The flowstone and calcite encasing a red deer antler from the Hyaena Bone Bed was dated directly by U-series and TIMS to the Last Interglacial (Gascoyne et al., 1981: p. 654; Gilmour et al., 2007: p. 795; Lundberg et al., 2010). In Kirkdale Cave the fossiliferous deposit is reported to have been of homogeneous character, with a depth of about 30 cm (Dawkins, 1874; Boylan, 1981). A flowstone on top of this bone bed was dated by U-series to the Last Interglacial (McFarlane and Ford, 1998). A number of specimens that are labelled as coming from Kirkdale Cave have very different preservation characteristics from the main collections. These specimens are excluded here. Based on faunal composition, the site is correlated with the climatic optimum of the Ipswichian (MIS 5e). The fossiliferous layer at Raygill Fissure (Davis, 1880) was correlated with *Hippopotamus*-bearing Ipswichian clay in the Leeds area (Earp, 1961). The fossiliferous deposit in Joint Mitnor Cave (Figure 3e-f) is dated to the Ipswichian based on faunal content (Sutcliffe, 1960). The Great Bone Bed in Tornewton Cave can be correlated to the Hyaena Stratum of later excavations (Sutcliffe and Zeuner, 1962; Currant, 1998). The age of the Hyaena Stratum is bracketed by two TIMS dates of ca. 134 and 98 ka BP on stalagmite, although some authors regard the fauna as dating from a later part of MIS 5 based on pollen and faunal composition (Gilmour et al., 2007).

A single fluvial site, Barrington, was included (Figure 3g-h). Channel infills, known as the Barrington Beds, were exposed in quarries, and produced mammalian remains (Sparks, 1952). Based on the composition of the mammal fauna, the Barrington Beds are ascribed to the Ipswichian (Gibbard and Stuart, 1975).

All six Ipswichian sites considered produced remains of a single rhinoceros species, *Stephanorhinus hemitoechus*. No *S. kirchbergensis* remains have been recovered from any Last Interglacial sites in the British Isles even though rich faunal assemblages are available from a range of depositional contexts dated to different phases of the interglacial. We therefore here assume that *S. kirchbergensis* was absent from or extremely rare in the British Isles during MIS 5e (Van Asperen, in prep.). Since all the above-mentioned British MIS 5e sites, except for the lowland site of Barrington, come from upland areas, they are collectively referred to as the 'British MIS 5e upland' sample in the DFA. The lowland sample from Barrington is analyzed separately. In all other analyses, all British MIS 5e sites are collated into a single sample.

[Insert here: Figure 1. Sites with remains of late Middle to Late Pleistocene *Stephanorhinus* palaeopopulations studied for dietary signature (in the order of appearance in the text, see section 3.1.): 1 - Bilzingsleben II; 2 - Weimar-Ehringsdorf; 3 - Weimar-Taubach; 4 - Ilford; 5 – Crayford; 6 - Selsey; 7 - Victoria Cave; 8 - Kirkdale Cave; 9 - Raygill Fissure; 10 - Joint Mitnor Cave; 11 - Tornewton Cave; 12 - Barrington.

Figure 2. Tooth rows of *Stephanorhinus kirchbergensis*, occlusal and buccal views; a and b. Bilzingsleben (no. 388-163, P2-M3 sin); c and d. Weimar-Ehringsdorf (IQW 1965-3440 (Ehr. 4089) and IQW 1965-3377 (Ehr. 10072), P2-M2 dex); e and f. Taubach (IQW 1968-10692 (Taub. 2632…2639), P3-M3 dex).

Figure 3. Teeth of *Stephanorhinus hemitoechus*, occlusal and buccal views; a and b. Bilzingsleben (no. 663-4; M2 sin); c-d. Weimar-Ehringsdorf (IQW 1965-318 (Ehr. 3410), M2

dex); e-f. Joint Mitnor Cave (P36774, M1 sin; courtesy of Torquay Museum); g-h. Barrington (BGS GSM779, M2 sin; courtesy of the Geological Survey Museum, Keyworth).]

[Insert here: Table 1. Minimum number of individuals (MNI) represented by the material of *Stephanorhinus* studied; abbreviations in [] used in Figures]

3.2. Morphometrics

Due to differences in size and morphology, it is usually relatively straightforward to distinguish skeletal elements of *S. kirchbergensis* and *S. hemitoechus*, although a degree of overlap occurs (Staesche, 1941; Fortelius et al., 1993; Mazza, 1993; Van der Made, 2000; Lacombat, 2005, 2009). Measurements were taken and qualitative characteristics were recorded for the upper and lower teeth following Lacombat (2009), who provides a system of measurements that is modified and expanded from the work of Guérin (1980), Mazza (1988) and Fortelius et al. (1993).

Overall levels of sexual dimorphism appear to be low in extant rhinoceroses (Loose, 1975). Dimorphism in cranial measurements has been documented in free-ranging *Ceratotherium simum* (Owen-Smith, 1988; Berger, 1994; Rachlow and Berger, 1997). Although several cranial measurements are significantly different between the sexes in *Rhinoceros unicornis*, and to a lesser degree in *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis,* dental measurements are not (Groves, 1982; Dinerstein, 1991). To assess the impact of sexual dimorphism on dental characters in Pleistocene *Stephanorhinus*, coefficients of variation (CVs, standard deviation/mean*100) were calculated for the different samples, as well as overall CVs for the two species. These were compared with CVs for the same measurements on extant rhinoceros teeth. CVs provide a means of comparing the degree of variation between measurements of different absolute sizes. CVs for the same measurements for closely related extant species gives some indication of how much variability can be expected to occur in fossil species (Cope and Lacy, 1995). Although CVs should be used with caution as indicators of biologically meaningful variables such as number of species and sexual dimorphism (Carrasco, 1998, 2004), some trends can be discerned. Linear measurements of mammalian dentitions tend to show little sexual dimorphism and have CVs between 5 and 10 (Gingerich, 1974; Yablokov, 1974; Gingerich and Schoeninger, 1979; Gingerich and Winkler, 1979). Sexually dimorphic variables tend to have coefficients of variation greater than 10 (Mihlbachler, 2007). Summary statistics for extant species and the Pleistocene samples can be found in the Supplementary Data.

To examine the extent of the size differentiation between the two species, t-tests were carried out for lengths and widths of the teeth. Results for the tests were considered significant if $p \leq 0.05$. Only samples where $n \geq 10$ were included in the tests since these tests are relatively sensitive to small sample size.

3.3. Mesowear analysis

Mesowear analysis is a well-validated method that indicates wear patterns over a large part of the lifespan of an individual animal (Fortelius and Solounias, 2000; Rivals et al., 2007). Tooth wear in browsers, which consume mainly low-abrasive foodstuffs, is dominated by sharp cusps and high relief. In contrast, grazers consume more grasses, often with a higher amount of grit, both of which contribute to an abrasion-dominated wear pattern with round or blunt cusps with low relief (Williams and Kay, 2001). Relatively small samples ($n>10$) give reliable and significant results (Fortelius and Solounias, 2000).

The upper first and second molars were scored for mesowear on the buccal side of the tooth (Franz-Odendaal and Kaiser, 2003). The occlusal relief was scored as either high or low. Cusp shape was scored on the sharpest cusp as sharp, round or blunt. Teeth of very young (more sharp cusps) and very old (more blunt cusps) individuals were excluded to prevent any influence extreme wear stages may have on the classification (Fortelius and Solounias, 2000; Rivals et al., 2007). The rhinoceros assemblage from Weimar-Taubach reflects selective hunting of young individuals (Bratlund, 1999), leading to a reduced MNI for mesowear analysis compared to total MNI (Table 1).

Scores for relief and cusp shape were combined into an overall mesowear score (0 = high and sharp, 1 = high and round, 2 = low and sharp, 3 = low and round, 4 = low and blunt; Louys et al., 2012). The Kruskal-Wallis test was used to analyse differences in mesowear scores between the samples. For those analyses where the Kruskal-Wallis test showed a significant difference, Mann-Whitney U-tests were used to investigate which samples had significantly different mesowear scores. An overall Mann-Whitney U-test between the scores for *S. hemitoechus* and *S. kirchbergensis* was also carried out.

Using the comparative dataset for 64 extant ungulates, compiled by Fortelius & Solounias (2000), as a training set, a stepwise discriminant function analysis using Wilk's lambda was carried out with the Pleistocene rhinoceros samples as ungrouped specimens. Mesowear data for M1/2 of the *Stephanorhinus hundsheimensis* samples from the Central German sites of Süßenborn [SUE] and Voigtstedt [VOI] (Kaiser and Kahlke, 2005; Kahlke and Kaiser, 2011) were also included as ungrouped specimens. Mesowear scores for the fossil assemblages can be found in Table 2. Because the mesowear scores are not independent (teeth with blunt cusps have low relief), variables entered in the analysis were % of teeth with high relief, % of teeth with sharp cusps and % of teeth with round cusps. Species with problematic dietary data (the 'mabra' species of Fortelius and Solounias, 2000) were left out of further analyses (cf. Kaiser and Solounias, 2003), and the conservative dietary classification of Fortelius and Solounias (2000) was used. The accuracy and robusticity of the differentiation between the dietary categories was investigated with jackknifed cross-validation models, using a single species as ungrouped case while using the other species in the original dataset as a generator set for calculating discriminant functions. Hierarchical cluster analysis with complete linkage (furthest neighbour, squared Euclidean distance) was carried out on the same dataset to investigate which extant species are the most similar in their mesowear signature to the

Pleistocene rhinoceroses. All statistical analyses were performed with the Statistical Package for the Social Sciences (SPSS) version 21.

[Insert here: Table 2. Mesowear scores for the fossil assemblages.]

Recently, there has been considerable discussion about the value of mesowear in determining diets of past herbivore populations. The question has been raised whether mesowear provides a dietary signal or whether environmental factors, in particular the amount of dust or grit on the foodstuffs consumed, influence the mesowear value. Kaiser et al. (2013) suggested that mesowear is primarily related to diet, whilst the presence of dust particles on the food may contribute to overall wear of the tooth (and thus exerts selective pressure towards hypsodonty), but does not impact on the morphology of tooth wear facets due to the small size of the particles and the relatively uniform distribution of this wear. Kaiser et al. (2013) also showed that mesowear is not related to habitat. Loffredo and DeSantis (2014) found that teeth with similar mesowear values can display a wide range of δ^{13}C values. Therefore they state that mesowear values should not be taken as indicative of individual diets, although they regard the method as moderately reliable for assessing diet at population level. Like Loffredo and DeSantis (2014), Ecker et al. (2013) found that there was no correlation between mesowear, microwear (Rivals et al., 2009) and δ^{13}C values for a range of herbivore species from the site of Payre in southeast France, dated to MIS 8-5. However, Ecker et al. (2013) inferred that these herbivore species maintain their browsing or grazing diet across different habitats, with δ^{13}C values reflecting differences in vegetation openness between e.g. river valley and plateau. Differences between mesowear and microwear signatures can be explained by the different timescales recorded by these two methods: while mesowear reflects diet over a longer period of time (months to years), microwear records the diet over the last days to weeks of an animal’s life (Fortelius and Solounias, 2000; Rivals et al., 2007). In the light of this discussion and the clear correlation of mesowear with diet in extant species (Fortelius and Solounias, 2000), we here conclude that mesowear provides valid information on a species' diet, especially at population level.

The diet of extant rhinoceros species varies from grazing via mixed feeding to browsing (Owen-Smith, 1988). The diet of Pleistocene rhinoceroses was equally diverse. Hernesniemi et al. (2011) compared mesowear scores for the extant species *Diceros bicornis, Ceratotherium simum, Dicerorhinus sumatrensis, Rhinoceros sondaicus* and *R. unicornis* with scores for the Pleistocene species *Stephanorhinus kirchbergensis, S. hemitoechus, S. hundsheimensis* and *Coelodonta antiquitatis* from the British Isles. Cluster analysis for the scores on M1 and M2 grouped *Stephanorhinus kirchbergensis* with *Dicerorhinus sumatrensis* and *S. hundsheimensis* with *Rhinoceros sondaicus*. Together with the somewhat more distant *Stephanorhinus hemitoechus,* these browsing species were clearly distinct from the mixed feeder *Rhinoceros unicornis*, which grouped closely with British *Coelodonta antiquitatis* in a cluster which also contains the grazer *Ceratotherium simum*. Within-species variation can be almost equally large. Mesowear analysis of two samples of early Middle Pleistocene *S. hundsheimensis* from the Central German sites of Süßenborn and Voigtstedt showed this species had a wide dietary range (Kaiser and Kahlke, 2005; Kahlke and Kaiser, 2011) varying from moderate grazing to non-specialised browsing with a high diversity of food items.

4. Results

4.1. Absolute size

The teeth of the two *Stephanorhinus* species are similar in shape but differ in size. T-tests are significant for all upper and lower lengths and widths (Table 3). Scatterplots of width versus length show two clusters, with varying but small degrees of overlap (Figure 4). Overall, the metric characteristics are congruent with qualitative traits; teeth with traits characteristic for *S. kirchbergensis* are mostly larger than teeth with *S. hemitoechus* traits. The teeth of *S.*

kirchbergensis from Bilzingsleben II are relatively small and overlap in size with the *S. hemitoechus* teeth from the same location, although qualitative characteristics of the teeth, as well as qualitative and quantitative data for the postcranial remains, clearly indicate the presence of two species.

Van der Made (2000) documented a linear size increase of the lower third molars within the *kirchbergensis*-group from Bilzingsleben II via Weimar-Ehringsdorf to Weimar-Taubach. Our data, which includes the British MIS 7 *S. kirchbergensis* teeth and larger samples for the German sites, confirm this trend (Figure 5).

[Insert here: Table 3. Table 3. Results of t-tests for dental measurements of *S. hemitoechus* and *S. kirchbergensis*.

Figure 4. Scatterplots of width (L10/L9) vs. length (L2) for a. M2; b. m2; abbreviations: see Table 1.

Figure 5. Mean values for the width of the posterior lobe of m1, m2 and m3 of *S. kirchbergensis* from German late Middle Pleistocene sites.]

4.2. Coefficient of variation

73% of measurements of the upper and lower dentition of both extant and Pleistocene rhinoceroses have CVs below 10. In the upper dentitions, some measurements for extant *Ceratotherium simum* are relatively high, particularly on M2. The maximum length of the crochet (L6) in the upper teeth is a highly variable qualitative characteristic, which is also small in absolute size. Similarly, the two measurements in the lower teeth that are small in absolute size (minimum height of the anterior and posterior valleys, L6 and L5) range widely, more than half having a CV higher than 15. It is a well-known phenomenon for measurements of small absolute size to have relatively high coefficients of variation (Yablokov, 1974; MacFadden, 1989). Partly this is caused by the stronger impact of measurement error on smaller variables, although in the case of L6 in the upper dentition it reflects a high level of natural variation in this characteristic. CVs for measurements with small sample sizes are somewhat higher than those for larger samples.

4.3. Mesowear

An overall Mann-Whitney U-test for differences between the mesowear scores for the two *Stephanorhinus* species is significant (U=3184, p=0.035). A Kruskal-Wallis test for all samples is significant (χ^2=13.023, p=0.011). Mann-Whitney U-tests reveal that the Weimar-Ehringsdorf *S. kirchbergensis* sample is significantly different from the British MIS 5e *S. hemitoechus* sample (U=879, p=0.016) and the Bilzingsleben II *S. kirchbergensis* sample (*U=1012,* p=0.005), whilst the Weimar-Taubach *S. kirchbergensis* sample is also different from these two samples (British MIS 5e *S. hemitoechus*: U=256.5, p=0.050; Bilzingsleben II *S. kirchbergensis*: U= 296.5, p=0.027).

The DFA has an overall correct reclassification rate of 72.2% (cross-validation: 64.8%). 7 out of the 11 studied Pleistocene rhinoceros samples are classified as mixed feeders (Table 4). The *S. hemitoechus* samples from the British MIS 7 sites and the MIS 5e lowland site fall along the grazer axis (Figure 6). The other samples fall along a straight line, with the Weimar-Ehringsdorf *S. hemitoechus* identified as a grazer and with early Middle Pleistocene *S. hundsheimensis* from Voigtstedt located at the extreme browser end of the spectrum. The *S. kirchbergensis* samples align more closely with the browsers and mixed feeders, and the *S. hemitoechus* samples cluster toward the mixed feeder-grazer end of the spectrum.

[Insert here: Table 4. Dietary classification of Pleistocene *Stephanorhinus* samples using DFA]

The patterns found in the DFA are born out in the cluster analysis (Figure 7). The main distinction is between a browser cluster, a number of mixed feeder clusters and a grazer cluster. The three browsing and one mixed feeding extant rhinoceros species are included in a browser-dominated cluster, while the grazing *Ceratotherium simum* falls within the cluster of the extreme grazers.

The British MIS 7 *S. hemitoechus* sample is the only fossil assemblage that clusters with the extreme grazers. The remaining *S. hemitoechus* samples, as well as the *S. kirchbergensis* samples from Bilzingsleben II and early Middle Pleistocene *S. hundsheimensis* from Süßenborn, are linked most closely with a mixed feeder-grazer group of Artiodactyla with a mesowear signature is characterised by a high percentage of teeth with high relief and round cusps. The mixed feeder cluster that includes the *S. kirchbergensis* samples from the British MIS 7 sites, Weimar-Ehringsdorf and Weimar-Taubach consists of cervids, bovids and camelids with a high percentage of teeth with high relief, while a higher percentage of teeth with sharp cusps is present than in the *S. hemitoechus* cluster. The Voigtstedt *S. hundsheimensis* remains are in the same group as the browsing extant rhinoceros species (cf. Kahlke and Kaiser, 2011).

[Insert here: Figure 6. Plot of scores on DF2 vs. DF1 for a range of extant herbivore species and Pleistocene rhinoceros assemblages; abbreviations: see Table 1.

Figure 7. Cluster diagram using mesowear variables for extant herbivores and European Pleistocene rhinoceros assemblages; dots: extant rhinoceros species; arrows: Pleistocene samples.]

5. Discussion

The overall mesowear signature of the studied samples of European Pleistocene *Stephanorhinus* indicates a predominantly mixed feeder diet (Table 4). Interestingly, the only fossil sample that clusters closely with any of the extant rhinoceros species, at the browser end of the spectrum, is the Voigtstedt *S. hundsheimensis* sample (see Kahlke and Kaiser, 2011). In comparison with the extant Asian and African rhinoceroses, most European late Middle Pleistocene *Stephanorhinus* had a diet that was shifted more towards the mixed feeder-grazer end of the dietary spectrum (Figure 6). Extant rhinoceros species therefore do not provide the most suitable dietary analogues for European Pleistocene rhinoceroses (compare Hernesniemi et al., 2011; Taylor et al., 2013). The British MIS 7 *S. hemitoechus* sample falls in the same group of grazers as *Ceratotherium simum*, characterised by a high percentage of teeth with low relief. These grazers feed primarily on grasses, particularly short grasses, in open environments, apart from *Saiga tatarica*, a mixed feeder that today lives in the Central Asian dry steppe and semi-desert (Bannikow, 1963; Bekenov et al., 1998; Sokolov and Zhirnov, 1998).

The remaining *S. hemitoechus* samples from Central Europe, as well as the *S. kirchbergensis* sample from Bilzingsleben II and the *S. hundsheimensis* sample from Süßenborn, align with the extant bovids *Alcelaphus lichtensteinii*, *Boselaphus tragocamelus*, *Hippotragus equinus*, *Hippotragus niger*, *Kobus ellipsiprymnus*, *Redunca fulvorufula*, *Redunca redunca*, *Syncerus caffer* and *Tragelaphus strepsiceros*, and the cervid *Axis porcinus* (Figure 7). This cluster consists of grazers and mixed feeders living in a variety of environments ranging from floodplains and savannahs to open woodlands. The *S. kirchbergensis* samples from the British MIS 7 sites, Weimar-Ehringsdorf and Weimar-Taubach fall most closely to the extant cervids *Axis axis* and *Cervus unicolor*, the bovids *Aepyceros melampus*, *Ammodorcas clarkei*, *Litocranius walleri*, *Ourebia ourebi*, *Tetracerus quadricornis* and *Tragelaphus angasii*, and the camelids *Camelus dromedarius* and *Lama glama*. This cluster is dominated by mixed feeders which incorporate a larger amount of browse in their diet. Most of these species live in relatively dry areas of open woodland and grassland.

When comparing the dietary flexibility of *S. hundsheimensis* with that of the other two *Stephanorhinus* species, it is clear that the former had a broader dietary range than either *S. kirchbergensis* or *S. hemitoechus*, ranging from an extreme browser to a mixed feeder with a considerable amount of grass in the diet. Our results therefore illustrate how the generalist subsistence strategy of *S. hundheimensis* (cf. Kahlke and Kaiser, 2011) contrasts with the more specialised strategies of *S. kirchbergensis* and *S. hemitoechus*. There is a clear indication of more browse in the diet of *S. kirchbergensis* compared to that of *S. hemitoechus*, whilst *S. hemitoechus* had the ability to subsist on a diet rich in grasses. However, it is too simplistic to describe *S. kirchbergensis* as a 'forest' rhinoceros and *S. hemitoechus* as a 'steppe' rhinoceros, assuming a browsing resp. grazing diet and taking these species as indicative of forested versus open landscapes. The 'forest' rhinoceros did not feed exclusively in forest areas, and likewise the 'steppe' rhinoceros was not exclusively a steppe grazer. The analysis of the dietary signature of these rhinoceros species in cases of sympatry and allopatry clearly demonstrates that their feeding traits, within a certain range of variation, relate to the characteristics of available food resources, which in turn reflect the range of habitats present in the regions considered during the Middle and Late Pleistocene interglacials.

The *S. hemitoechus* samples studied here do not appear in stratigraphic order in the DFA and the dendrogram (Figures 6 and 7). In the *S. kirchbergensis* samples, there is an increase in the size of the dentition, especially the m3 (Figure 5), and a weak trend towards a larger proportion of browse in the diet (Figure 6). The increased size of the dentition in *S. kirchbergensis* could find an explanation in the fact that in herbivores the dimensions of the teeth are related to the quantity and quality of the food. Larger occlusal surfaces enable more effective mastication of food (e.g. Janis, 1976, 1988; Van der Made, 2010; Anders and Von Koenigswald, 2013), providing a selective advantage when the proportion of low quality food resources in the diet increases. For the hindgut fermenter *S. kirchbergensis*, an increasing proportion of less-digestible browse in the diet may have necessitated a higher food intake (cf.

Steuer et al., 2010). However, dietary differences between the MIS 7 and MIS 5e *S. kirchbergensis* specimens are limited (Figure 6). Thus, there is little indication for a directional evolutionary process of increasing specialization of the two species as grazer resp. browser during the timespan considered. Instead, the individuals of the considered palaeopopulations reacted to changing environmental conditions within the limits of their feeding abilities.

The Bilzingsleben II samples present a suitable starting point for deciphering the relationships between the *Stephanorhinus* mesowear record, environmental factors and competitive interactions between the two species. The great similarity of the dietary traits of co-occurring *S. kirchbergensis* and *S. hemitoechus* individuals from this site must be explained by a high degree of spatial and temporal uniformity of food resources available to both species. Although the botanical evidence from the fossil layer of the *Stephanorhinus* remains is not sufficient for a detailed reconstruction of the contemporaneous vegetation (Erd, 1997), the geographic position of the site explains the apparent low habitat diversity of the region under fully developed interglacial (MIS 11) conditions. Bilzingsleben II lies within an area known as the ‘Zirkumherzynes Trockengebiet’, a relatively dry region in the rain shadow of the Harz Mountains (Figure 1). As is presently the case, during the Middle and Late Pleistocene interglacials Atlantic low-pressure systems controlled precipitation levels in Northwest and Central Europe (Kaspar and Cubasch, 2007). The mountains immediately northwest of Bilzingsleben protected the region against the prevailing winds from the west. As a mesoclimatic result, the area east and southeast of the Harz had a subcontinental climate, which in combination with the uniform morphological and edaphic characteristics of the region resulted in a relatively uniform vegetation pattern (T. Litt, pers. comm.). Based on these geomorphological considerations and the interglacial character of the mammalian fauna recovered from the site, which includes an abundance of large herbivores (Mania, 1991), the inferred vegetation consisted of subcontinental thermophilous woodland with rich undergrowth (T. Litt, pers. comm.). Such a habitat has a relatively high biomass and productivity in vegetation layers available to the rhinoceroses and other large herbivores. Both rhinoceros species are present in nearly equal numbers, indicating that *S. kirchbergensis,* which later appears to be a strong competitor, did not outcompete *S. hemitoechus* at this time. This may be due to the fact that its teeth were still small relative to its body size, while *S. hemitoechus* benefited from its smaller body size.

Compared to Bilzingsleben II, the dietary signals of the two *Stephanorhinus* species from Weimar-Ehringsdorf (MIS 7/5e) are significantly more differentiated (Figure 6). The latter fossil site is located in a wetter region of the central German Thuringian Basin, on the flank of a tectonic graben forming the valley of the River Ilm. The abundant floral remains from the find layers of the Ehringsdorf *S. kirchbergensis* (Mammal Fauna 2) and *S. hemitoechus* (Mammal Faunas 2-3, 7-8) specimens reveal a generally high diversity of habitats in the vicinity of the site (Vent, 1974). However, in comparison with the lower and middle parts of the Lower Travertine (Mammal Fauna 2; see section 3.1.), the Upper Travertines (Mammal Faunas 7-8) experienced intensified subcontinental climatic influences. Due to this environmental trend and the time-transgressive nature of the Ehringsdorf *S. hemitoechus* sample (Table 1), a wide diversity of rhinoceros habitats is represented in the divergence of the dietary signal. In particular, the relatively grazer-like signature of the *S. hemitoechus* sample reflects the influence of the more subcontinental climate of the Upper Travertine.

The three British MIS 7 sites are all of fluvial origin, although the Selsey channel was of a smaller scale than the Thames River (Ilford and Crayford). The latter part of MIS 7, from which these sites date, is known to have been relatively dry and continental in northwest Europe, with somewhat lower temperatures than in most other late Middle Pleistocene interglacials (Ruddiman and McIntyre, 1982; Petit et al., 1999; Desprat et al. 2006). This part of the interglacial witnessed an influx of animals adapted to open environments into northwest Europe, whilst forest-adapted animals withdrew (Schreve, 2001a, 2004; Auguste, 2009). The British MIS 7 samples display the largest dietary difference between the two *Stephanorhinus* species within the time span considered. In comparison with the Weimar-Ehringsdorf specimens, the British MIS 7 *S. kirchbergensis* sample is shifted towards the mixed feeder end of the spectrum (Figure 6), whilst *S. hemitoechus* has the dietary signature of a grazer. This indicates that the availability of browse was limited, in accordance with other environmental proxies which are indicative of open environments in the British Isles (Schreve, 2001a). Even though its optimal diet seems to have incorporated more browse (see below), *S. kirchbergensis* was able to increase the grazing component in its diet, and be a strong enough competitor to force *S. hemitoechus* to consume greater proportions of abrasive foodstuffs.

During at least part of MIS 5e, the *Stephanorhinus* species show a mostly disjunct distribution, with *S. kirchbergensis* occurring in Central Europe, whilst *S. hemitoechus* is common in western parts of the continent and in the British Isles. Under these conditions, *S. kirchbergensis* at Weimar-Taubach consumed a significantly higher percentage of browse than *S. hemitoechus*. The geomorphological characteristics of this site are similar to those at Weimar-Ehringsdorf, situated only 2 kilometres northwest of Taubach, providing a similar diversity of habitats. Nevertheless, the absence of the only other temperate-adapted rhinoceros species and the diverse range of available foodstuffs ameliorated the environmental conditions for *S. kirchbergensis*.

Of the British MIS 5e sites with *S. hemitoechus* fossils, Victoria Cave, Kirkdale Cave and Joint Mitnor Cave are all located on the boundary between an upland area and a lowland area, providing a diverse habitat of plateaus, slopes, valleys and floodplains. Raygill Fissure, and to a lesser degree Tornewton Cave are situated in a diverse upland landscape with plateaus, valleys and streams. In contrast, the site of Barrington lies in a lowland area with lower habitat diversity, with open environments along the river and possibly woodland further away from the active stream (Gibbard and Stuart, 1975). Although we studied only a single lowland site and we cannot exclude that other lowland sites show a different pattern, interestingly, these different levels of habitat diversity can be traced in the mesowear scores for these sites: the upland samples are classified as mixed feeder, whereas the lowland sample is classified as grazer, although it is not displaced towards the grazer end of the spectrum as much as the British MIS 7 *S. hemitoechus* sample (Figure 6).

Since further environmental proxies are only available for the Barrington site, we cannot exclude the possibility that these sites date from different phases of the same interglacial. However, this scenario seems unlikely based on the fully developed interglacial character of the faunal assemblages: the ecologically demanding *Hippopotamus amphibius* is recorded from all sites, and other 'temperate indicators' such as *Palaeoloxodon antiquus, Sus scrofa, Dama dama* and *Capreolus capreolus* are also present in the upland sites. Since the large herbivore faunas from the upland and lowland sites are very similar, the difference in the mesowear scores could reflect the availability of foodstuffs in the environment. A more diverse habitat would have provided a wider range of resources, enabling *S. hemitoechus* to subsist on a mixed feeder diet, whilst a more homogeneous environment with open grassland forced the species to graze.

6. Conclusions

Stephanorhinus kirchbergensis and *S. hemitoechus* were embedded in a dynamic process of temporo-spatial replacements and interspecific differentiation of Middle to Late Pleistocene rhinoceroses in the western Palaearctic. Both their anatomical features (see section 2) and the obtained mesowear scores show significantly higher dietary specializations compared to the Early to early Middle Pleistocene *S. hundsheimensis*. This is consistent with the idea that the 100 ka periodicity in the global climatic record caused a sustained environmental continuity compared to the preceding 41 ka regime and thus promoted the development of more specialized subsistence strategies (Kahlke and Kaiser, 2011).

The presence of the rhinoceros species considered here is often taken as a first indication of the character of the vegetation prevailing in their respective habitats. However, our studies demonstrate that species identity alone is not sufficient to establish the real dietary traits of a *Stephanorhinus* palaeopopulation. The occurrence of the ‘forest’ rhinoceros *S. kirchbergensis* in a faunal assemblage by no means indicates exclusively forested habitats. Similarly, the 'steppe' rhinoceros *S. hemitoechus* did not occupy steppe landscapes only. Instead, the reconstruction of past rhinoceros diets on the level of extended samples from stratigraphically well-defined palaeopopulations of different European regions sheds light on the impact of habitat diversity and the effect of interspecific competition with closely related rhinoceros species on feeding behaviour.

Whilst both *S. kirchbergensis* and *S. hemitoechus* had already developed advanced dietary specializations compared to that of the “indigenous” *S. hundsheimensis* when they first entered Europe, there is little evidence of progressing dietary specialization of the two newcomers over the late Middle and Late Pleistocene. A moderate size increase of the molar row in *S. kirchbergensis* over this period may have provided some advantage. The mesowear signals of both species indicate a mixed feeder diet, similar to that of extant mammal species in relatively open habitats. In comparison with *S. hemitoechus*, *S. kirchbergensis* generally consumed more browse. Nevertheless, both species maintained a level of dietary flexibility, with *S. kirchbergensis* including more or less browse in its diet depending on the quality of the habitat, and *S. hemitoechus* shifting from mixed feeder to consuming more grass when necessary. Although this indicates they preferred different habitats, clearly both species were capable of surviving on a range of diets in a range of environments.

Low habitat variability forced *S. kirchbergensis* and *S. hemitoechus* to consume very similar diets, as is evidenced by the sympatric Bilzingsleben II populations. Increasing habitat variability correlates with an increasing degree of divergence in feeding traits both within and between *Stephanorhinus* species. At Weimar-Ehringsdorf, Weimar-Taubach, and the British

MIS 5e upland sites, high habitat variability was combined with relatively high precipitation, allowing *S. hemitoechus* to consume its optimal mixed feeder diet, and *S. kirchbergensis* to incorporate more browse. Low habitat variability pushed *S. hemitoechus* towards consuming more grass even in the absence of *S. kirchbergensis,* as reflected by the British MIS 5e lowland sites. This pattern therefore holds regardless of whether both species were co-occurring or only one species was present, although the disjunct distribution pattern during MIS 5e appears to have presented optimum conditions for both species. However, in some cases the impact of habitat variability on dietary composition was modified by the presence of a closely related competitor. Thus, *S. kirchbergensis* from British MIS 7 sites, with low precipitation levels, was able to survive on less browse, thereby displacing co-occurring *S. hemitoechus* towards a grass-dominated diet.

Similar patterns of dietary variation related to habitat characteristics and competitive interactions have been observed in a range of other fossil species, such as Neogene equids (Kaiser, 2003) and bovids (Solounias and Hayek, 1993; Merceron et al., 2004, 2006; Kostopoulos and Karakütük, in press), Early and Middle Pleistocene Proboscidea (Rivals et al., 2012; Rivals et al., in prep.) and Late Pleistocene cervids (Rivals and Solounias, 2007; Rivals et al., 2010). As in the rhinoceros species with highly specialised feeding traits studied here, these animals had a considerable dietary flexibility and adapted their diet according to the availability of food resources in different habitats (Kaiser, 2003; Rivals and Solounias, 2007; Tütken et al., 2013).

For Middle to Late Pleistocene *S. kirchbergensis* and *S. hemitoechus* of Central and Northwest Europe, it appears likely that the diet consumed was not simply the result of a directed time-transgressive evolution. Even as specialists they retained a certain amount of ecological flexibility as part of their subsistence strategy. Rather, within the range of each species' ecological tolerance, diet was controlled by environmental parameters, with a particular role for habitat variability. Whilst these rhinos obviously had a preferred optimal diet, in most cases they had to make do with what was available in their environment, following the timeless proverb “You'll have to take pot luck!”

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