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THE LAST INTERGLACIAL (EEMIAN) LAKELAND OF NEUMARK-NORD (SAXONY-ANHALT, GERMANY). SEQUENCING NEANDERTHAL OCCUPATIONS, ASSESSING SUBSISTENCE OPPORTUNITIES AND PREY SELECTION BASED ON ESTIMATIONS OF UNGULATE CARRYING CAPACITIES, BIOMASS PRODUCTION AND ENERGY VALUES

Abstract

The high-resolution palaeoenvironmental record from the last interglacial (Eemian) lakeland at Neumark-Nord (Saxony-Anhalt, Germany) holds the rare potential to study Neanderthal subsistence ca. 125,000 years ago in remarkable detail. Using the palynological record from the large lake Neumark-Nord 1 (NN1) and the adjacent small "pool" Neumark-Nord 2 (NN2) a sequence of lithic and faunal assemblages has been established, indicating Neanderthal presence in the lakeland throughout the Eemian. Calculations of the herbivore carrying capacity for the Neumark area during the Eemian reveal high biomass estimates. Using these estimates it was possible to calculate the structure of the source population, based on the faunal record rich in species and individuals, from littoral deposits assigned to the first mesocratic phase of the Eemian. The results can be used as a frame of reference for making inferences on subsistence opportunities and prey selection based on taphonomical and zooarchaeological studies of the Neumark-Nord faunal assemblages. In a broader perspective our study demonstrates the benefits from inferring energy values (kcal) and body mass (kg) as ancillary parameters to zooarchaeological analyses to understand the relationships between death assemblage and their habitats from which they originate.

Keywords

Last Interglacial, Eemian, zooarchaeology, taphonomy, thanatocoenosis, biocoenosis, carrying capacity, biomass, herbivore community structure, subsistence, prey selection, Neanderthals

Introduction

Palaeolithic Archaeology holds the potential to trace the roots of our behaviour far back in time through a diachronic perspective. With first attempts of placing the human "hunting way of life" in an evolutionary framework (Lee / De Vore 1968), reconstructing human subsistence in the Pleistocene became a major research agenda for Palaeolithic Archaeology. In the broadest sense subsistence comprises all the

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Fig. 1 The Great European Plain is one of the major topographical features of Europe characterized by an almost mountain-free landform. Today most of the Plain belongs to a temperate mixed and broadleaf forest biome. The area generally referred to as the North European Plain is roughly outlined with the black rectangle. – (Source: CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=1607793).

efforts undertaken to fulfil and maintain durably the basic demands of humans, most prominently and essential the appropriation and preparation of food (Sahlins 1972). Subsistence is constrained by the availability and distribution of resources in the environment. Thus, subsistence strategies, tactics or patterns decoded from the archaeological record can only be assessed with reference to the framing ecological conditions.

For most of the time in human history climate oscillations were more extreme than what we have experienced in the more recent past, i.e. the odd thousands of years of the Holocene. As a result, we witness landscapes and environments with no modern analogues to the ones in which earlier humans operated and evolved. This constitutes a challenge when connecting human behaviour and ecology in the archaeological context. However, on the North European Plain, relatively short interglacial climatic stages led to comparable environmental conditions, in which we can study the evolution of human ecology and the human niche, through time up to our present interglacial, the Holocene. Thus, the lakeland of Neumark-Nord is a rare high-resolution ecological and archaeological archive from the last interglacial (Eemian) offering ideal conditions to study Neanderthal adaptations to forested environments on the North European Plain (Gaudzinski-Windheuser / Roebroeks, 2014; Gaudzinski-Windheuser et al. 2014).

The earliest occupation of the North European Plain

The North European Plain covers parts of northern France, southeastern England, Belgium, the Netherlands, Germany, southern Scandinavia and Poland. Its limits and extent are defined more by the common use of the term than by strict geographical features. This region is part of the Great European Plain, which stretches from the northwestern foot of the Pyrenees in a long crescent through the North of Europe to the western foot of the Ural in the East (**fig. 1**). Its basic feature is the regular relief in an almost mountain-free landscape. Today this vast region belongs to the temperate mixed and broadleaf forest biome and, far to the southeast, the forest steppe zone.

During the Pleistocene the rather remote position of the North European Plain in the Old World constituted the terminal end of many human and other animal dispersals in Western Eurasia. The climatic oscillations of the Pleistocene, e.g. represented in Marine Isotope Stages (MIS), had enormous effects on the extant of land mass, geomorphology, hydrology and environments. During the pleniglacials of the cold stages large parts of the North European Plain were overthrust by glaciers several times. In contrast, during the full-interglacial warm phases sea levels were rising and mixed and broadleaf forest dispersed over the Plain. Nevertheless, with the onset of the 100 kya glacial-interglacial cycle about 1 mya ago, grassland-types of environments and steppe-tundras covered the European Plain most of the time. The drastic environmental, faunal, botanical and sedimentological responses to global climate change at these latitudes allows for a comparably fine subdivision of the terrestrial Pleistocene stratigraphy on the North European Plain (Litt et al. 2007). This constitutes an ideal framework for the study of hominin environmental responses, including the development of cultural and biological adaptation as well as expansion and contraction of the geographic range of human populations.

Depending on climate and environmental conditions, the North European Plain formed part of the biogeographic range of cold adapted faunal communities with core dispersal areas in the East or warm adapted faunal communities with core dispersal areas in the South (von Koenigswald 2003). When exactly humans became a part of these faunal communities on the North European Plain is still an issue. After phases of short-lived "Pioneer dispersals" around the Lower to Middle Pleistocene transition (exemplified by the evidence from Happisburgh, UK, Parfitt et al. 2005; 2010; Ashton et al. 2014), we can assume that from 600 kya onwards humans became frequent occupants of Central Europe, in the first instance during phases of favourable environmental conditions (Roebroeks 2006; Jöris 2014). From the middle part of the Middle Pleistocene onwards, humans seem to be present in significantly more challenging – cold dry – conditions, with sites no longer limited to the western (Atlantic) and southern (Mediterranean) parts of Europe, but also located in its more continental parts, east of the river Rhine (Haidle/Pawlik 2010; Kahlke et al. 2011; Cohen et al. 2012). Such a range expansion into more challenging environments might be related to the development of new strategies for survival (Hosfield 2016), including the introduction of fire as a fixed part of the human technological repertoire (Roebroeks/Villa 2011; Shimelmitz et al. 2014; MacDonald 2017). Establishing the exact spatiotemporal patterns of presence and absence and the factors determining these, including adaptations and alterations in subsistence and the process of "Neanderthalisation" (Hublin 2009), is still a big challenge.

For obvious reasons Northern Europe was depopulated during the pleniglacials, when glaciers expanded, and the remaining parts of the Plain became a hostile periglacial terrain. For most time segments of the Pleistocene the climate was cool and cool-temperate, and in particular drier, with dispersal of grassland and tundra steppe cover on the North European Plain as well as in the southerly adjacent low mountain range. Most of what we know about human subsistence stems from these environments. It seems that Neanderthals adapted their survival strategies well to these environments and focused on high nutritional resources which were predominantly stored in large herbivores (Gaudzinski-Windheuser/Kindler 2012). The low plant biomass production during most of the Pleistocene in these northern latitudes and the inferred high daily energy requirements of these humans (but see: Heyes/MacDonald 2015) may have enforced a "hunting way of live", which is so characteristic for the late Neanderthals. In addition, many anthropologists identify certain anatomical traits in Neanderthals as special adaptations to these cool climates in Europe (Churchill 1998; Aiello/Wheeler 2003; Weaver 2003). In this perspective, the process of "Neanderthalisation" can be perceived as an adaptation of a Middle Pleistocene European population to cool-dry to cool-temperate environments.

However, the earliest evidence for human presence in the northern parts of Europe, as well as on the North European Plain, derive from sedimentary contexts indicative of warmer interglacial climates with forested environments (Parfitt et al. 2005; Roebroeks 2005). At Happisburgh 3 (Parfitt et al. 2010; Ashton et al. 2014), humans seem to have remained in the area at the end of an interglacial about 800,000 years ago, when mainly deciduous forest became replaced by coniferous trees.

In the course of the Pleistocene these interglacials constituted the relatively short climatic optimum of a glacial cycle with climates and environmental conditions similar to today. Human presence on the North European Plain is also well attested for several interglacials. But, occupation pre-dating the Elsterian/Anglian glaciation (MIS 10 or 12) might have been restricted to the western part of the Plain, influenced by oceanic climate, while during the Holsteinian interglacial (MIS 9 or 11) areas which are more under continental climate influence, were also occupied (Haidle/Pawlik 2010; Kahlke et al. 2011; Cohen et al. 2012; Jöris 2014 following a MIS 12-11 correlation for this glacial-interglacial cycle, but see Geyh/Müller 2005; 2007; Litt et al. 2007; Bittmann 2012 supporting a MIS 10-9 correlation for the Elsterian-Holsteinian succession). However, due to the spread of forests during these interglacials in Europe, these environments are often considered as rather challenging environments for Neanderthals, based on reconstructions of the production and distribution of edible resources. Like modern-day temperate and tropical forests, Pleistocene interglacial deciduous forests within the Neanderthal range would have been characterized by a high primary biomass and a high primary production. Most of this richness would have consisted of trees and vegetational resources relatively expensive to process and only available over short periods of time. Meat must have been a critical food source. In contrast to the open mammoth steppe environments, herbivore mass in forested environments would have been significantly lower, while medium sized and larger mammals would have dispersed in forested environments. Thus, subsisting in these environments would have come with enormous risks and required high mobility (Gamble 1986; Kelly 1995; Binford 2001). Since the introduction of Gamble's (1986) model, which suggests that for most of the Pleistocene changing regional settlement histories are driven by environmental pressures, special attention has been devoted to the interglacials and particularly the last Interglacial, the Eemian (MIS 5e-5d, see Shackleton et al. 2003; Sier et al. 2011), to characterize Neanderthal ecology and ecological tolerance (e. g. Roebroeks/Conard/van Kolfschoten 1992; Speelers 2000; Gaudzinski 2004; Wenzel 2007; Gaudzinski-Windheueser/Roebroeks 2011). In recent modellings of abiotic factors shaping the Neanderthal range during the last interglacial, the North European Plain appears to be a rather unsuitable habitat, based on climate and terrain. Thus, the archaeological evidence in that region should be considered as representations of the tail of Neanderthal distribution during the Eemian (Benito et al. 2017). These results, although only based on abiotic parameters, emphasise again the importance of studying these "interglacial/warm/forest" Neanderthals on the North European Plain. This has the potential to provide a better understanding of their ecological tolerance as well as their flexibility, and plasticity in response to different ecological conditions.

The Eemian occupation of the North European Plain

For several reasons, the last interglacial, the Eemian, offers the best potential to reconstruct Neanderthal adaptations to forested environments on the North European Plain. Eemian terrestrial deposits are mainly found in regions which were previously covered by the Saalian ice sheet on the North European Plain. The retreat of the ice at the end of the Saalian glacification (MIS 6) released large amounts of water in the landscape and sub-surface, much of which was captured in a wide diversity of sediment traps on the North European Plain, such as kettle holes, meltwater channels and basins carved out at the end of the Saalian and beginning of the subsequent interglacial, due to isostatic movements and other geomorphological dynamics. Consequently, lakelands developed on the North European Plain and these lake basins filled up during the Eemian. The ice advance during the following Weichselian cold stage (MIS 4-2) did not penetrate as far south on the North European Plain as the Saalian ice did, so that Eemian basin deposits could survive unaltered in the underground in high numbers until today (Turner 2000). These Eemian basin deposits have a good chance to contain rather undisturbed high-resolution palaeoenvironmental and archaeological archives. But unfortunately, most of these basins are covered and protected by thick Weichselian deposits, mostly loess, preventing archaeological excavations and are only accessible by drilling.

The Eemian interglacial was defined by the palynological record in the region of Amersfoort (NL) (Bosch/Cleveringa/Meijer 2000). Today, the evidence from numerous Eemian deposits draws a very detailed and coherent picture about the plant succession during the Eemian reforestation on the European Plain (Turner 2000), which bears similarities to the recent Holocene and the penultimate interglacial, the Holsteinian, in terms of the dynamic sequence of the protocratic, mesocratic and teleocratic forest development phase during the interglacial cycle (Lang 1994). However, each interglacial has its own individual characteristics and progressions. In general, the Eemian is considered to have been as stable as the present Holocene, but warmer and wetter than today (Kaspar et al. 2005) and with higher sea levels than at present (Dutton/Lambeck 2012; Kopp et al. 2013). Thus, gradients of temperature and precipitation on the North European Plain might have been quite different from our recent interglacial, and thus, the mode of the reforestation and the spread of dense woodland during the Eemian might also have had its own unique dynamics. A rapid and uniform expansion of closed forests over the North European Plain is reconstructed from palaeobotanical evidence (Litt 2000; Turner 2000). For the virgin vegetation of the Holocene on the North European Plain the dominance of closed-canopy primeval forest or alternatively a mosaic of forests, open grassland, scrubs and groves maintained by large herbivores are proposed (Vera 2000; Birks 2005; Mitchell 2005). The large herbivore guild during the Eemian was more diverse than in the Holocene in Europe and contained several megaherbivores and a mix of browsers, grazers as well as mixed feeders indicative of mosaic environments (van Kolfschoten 1995; 1999; 2000). The potential of herbivores and other agents to create and maintain open habitats in interglacial forests are discussed by Svenning (2002). More recent studies also highlight the impact of herbivores on vegetation openness in past interglacials (Sandom et al. 2014; Bakker et al. 2016; and for a case study from Neumark-Nord 2: Pop/Bakels 2015). Thus, environmental reconstruction on a regional or even local scale is of particular importance from an archaeological point of view, when referring to Eemian environments as rather "uncomfortable" for Neanderthals to inhabit.

Eemian deposits on the North European Plain constitute high-resolution temporal and environmental archives compared to other Pleistocene periods. The temporal resolution is based on varve counting of Eemian sediments, which has allowed calculation of the durations of individual pollen stages (Erd 1973; Menke/Tynni 1984), and yielded solid data, which with ca. 11,000 years is relatively short (Müller 1974) (**tab. 1**).

Tab. 1 Interglacial forest development (Lang 1994), the subdivision of the Eemian based on Pollen Zones (Erd 1973; Menke/Tynni 1984) and their estimated durations (Müller 1974).

Interglacial Cycle (Lang 1994)	Forest phase	Eemian Pollen Zones		Duration (Müller 1974)
		Menke/Tynni 1984	Erd 1973	
Phase D (teleocratic phase)	*Pinus* phase	VII	9	~ 2,000 years
	Pinus-Picea-Abies phase	VI	8	~ 2,000 years
Phase C (mesocratic phase, 2. part)	*Carpinus-Picea* phase	Vb	7	~ 4,000 years
	Carpinus phase	Va	6	
Phase B (mesocratic phase, 1. part)	*Corylus-Taxus-Tilia* phase	IVb	5	~ 1,200 years
	Quercetum mixtum-Corylus phase	IVa	4	~ 1,200 years
Phase A (protocratic phase)	*Pinus-Quercetum mixtum* phase	III	3	~ 450 years
	Pinus-Betula phase	II	2	~ 200 years
	Pinus phase	I	1	~ 100 years

Neanderthal occupation during the Eemian is well attested at least for the German part of the North European Plain (Gaudzinski 2004; Gaudzinski-Windheuser/Roebroeks 2011). In contrast, in other parts of the Plain evidence of Neanderthal presence is still lacking, except for its southwestern tip in northwestern France where the fluvial tufa site of Caours close to the current mouth of the Somme river (Locht et al. 2014) and Waziers (Hérrison et al. 2015) are located. The last interglacial sea level rise and subsequent flooding of the channel separated Great Britain from the European main land, which may have prohibited a recolonisation immediately after the Saalian (Sier et al. 2015). The higher water levels during the Eemian also separated Denmark from northern Germany. Here, there is a complete lack of unambiguous evidence for Neanderthal presence during the Eemian as well as prior to or postdating the last interglacial (Egeland et al. 2014; Kellberg Nielsen 2017).

A number of Eemian archaeological sites deposited in basin sediments or travertine are known from the North European Plain (Gaudzinski 2004; Gaudzinski-Windheuser/Roebroeks 2011). Unfortunately, most of these sites were excavated a long time ago, and most of the archaeological and, in particular, zooarchaeological material must be considered extremely biased rather than thoroughly excavated (Gaudzinski 2004). It is a precarious task to draw conclusions about Neanderthal subsistence strategies from faunal analysis of these collections. Evidence from single-carcass elephant sites like Lehringen (Lower Saxony, Germany), including the recovery of a wooden lance and artefacts (Thieme/Veil 1985) and Gröbern (Saxony-Anhalt, Germany) may indicate that weak and isolated elephant individuals wading in shallow water – possibly using water to support their heavy weight – became an easy target of Neanderthals (Gaudzinski 2004). The species rich fauna from the travertine of Taubach (Thuringia, Germany) points to a similar strategy. The fauna of this collection is dominated by forest rhino (*Stephanorhinus kirchbergensis*, MNI = 76) and brown bear (*Ursus arctos*, MNI = 51) (Bratlund 2000). Neanderthals occupied the travertine area repeatedly during the early phases of the Eemian. Mainly young and subadult rhinos and brown bears of all age classes were hunted (Bratlund 2000). Lehringen, Gröbern and Taubach point to a subsistence strategy during the Eemian, which was different to the preferred game repertoire of Neanderthal in cool to cool-temperate environments (Gaudzinski 2004). Large pachyderms, such as elephants and rhino, seem to have become more important in the nutrition of Eemian Neanderthals (but see Smith 2015). To avoid risky and dangerous manoeuvres, weaker individuals were targeted, both older and young ones. Regarding the brown bear, one may conclude that in the search for high nutritional resources in the Eemian environments the hunting focus of Neanderthals diversified to include defensive and/or solitary large mammals, such as elephants, rhinos and bears for the benefit of lower handling cost and higher return rates (Gaudzinski-Windheuser/Roebroeks 2011; Smith 2015). In contrast, evidence from the recently excavated Somme River valley site of Caours in northern France suggests that the environmental change of the last interglacial had limited influence on Neanderthal subsistence strategies. During the Eemian as well as the Weichselian Pleniglacial in northern France hunting preferentially focussed on medium sized herbivores (fallow deer, reindeer, red deer) and subsistence varied in terms of the main prey taxa present in different environments (Locht et al. 2014).

However, we should keep in mind that hunting is more than just killing an animal. Ideally, prey choice, subsistence strategies and the ecological niche humans occupied should be considered in the frame of faunal community structure and prey abundance at a given time, as well as the specific ethology of individual species. Killing reindeer and red deer in an open grassland environment might involve completely different hunting tactics and might be embedded in completely different systems of land-use and organisation than killing fallow deer and red deer in forested environments.

Analysis of the material from our recently excavated small Eemian basin Neumark-Nord 2 and the adjacent large lake Neumark-Nord 1 enables us to study in some detail subsistence opportunities and

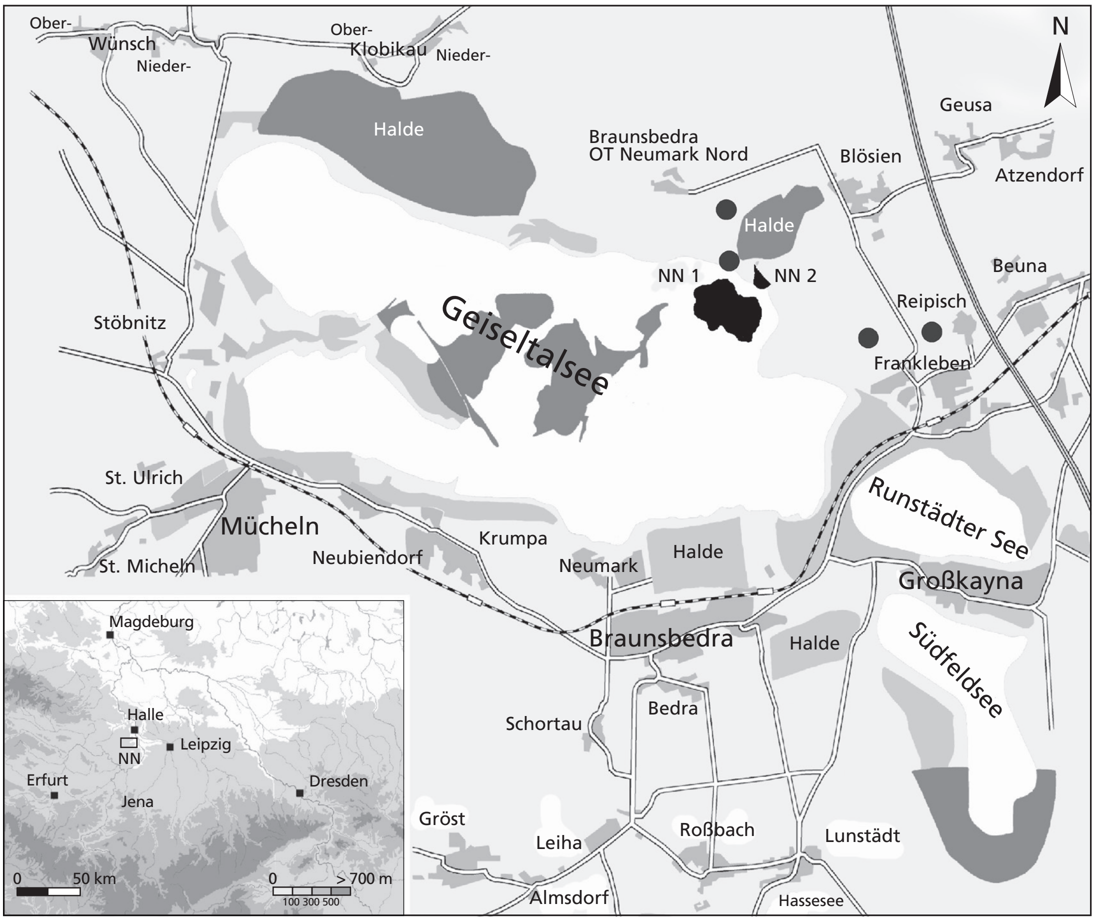

Fig. 2 Location of the Eemian lake basin Neumark-Nord 1 (NN1) and the small pond Neumark-Nord 2 (NN2) within and along the recent Geiseltalsee, Saxony-Anhalt, Germany. The black dots indicate potential basin structures documented by field surveys. The box inset indicates the position of the Neumark-Nord lakeland on a larger regional scale.

Neanderthal behavioural adaptations in forested environments during the Eemian on the North European Plain.

The Eemian lakeland of Neumark-Nord

The Eemian site of Neumark-Nord 2, as well as the adjacent synchronous basin Neumark-Nord 1, are located approximately 10 km south of Halle and 35 km west of Leipzig in Saxony-Anhalt, Germany (51°19′28″N, 11°53′56″E; **fig. 2**). The first Eemian basin, Neumark-Nord 1 (NN1) was uncovered in 1985 in the former lignite open cast mine Mücheln. Thanks to the perseverance and motivation of the research group "Bilzingsleben / Neumark-Nord", founded by and around Dietrich Mania, this basin was investigated and excavated in a continuous marathon against the machines, large-scale bucket-wheel excavators, until the end of mining activities in the mid-90s. NN1 became famous through its unique thanatocoenosis, consisting of numerous (almost) complete large mammal skeletons within the lake basin (Mania et al. 1990; 2010a; Meller 2010). These skeletons were uncovered and in parts damaged by bucket-wheel excavators, and an unknown but probably high number of these skeletons were most likely destroyed without being noticed in the course of quarrying at NN1 (Mania 2010a; Mania / Thomae / Altermann 2010; Mania et al. 2010b). During subsequent reclamation works of the mine to create the Geiseltalsee, which is completely flooded today covering an area of approx. 18 km², Mania also discovered the second basin, Neumark-Nord 2 (NN2), about 100 m northeast of NN1. NN2 was completely uncovered on a wedge like terrace during levelling of the northeastern embankment of the Geiseltalsee at the end of the 1990s. Thorough multidisciplinary investigations and archaeological excavations began in 2004 by the Landesamt für Denkmalpflege und Archäologie Sachsen Anhalt, and continued from 2006 to 2009 in collaboration with the Faculty of Archaeology, Leiden University and MONREPOS Archaeological Research Center and Museum for Human Behavioural Evolution (Gaudzinski-Windheuser / Roebroeks 2014).

Lake basin NN1 covered an area of about 24 ha, while basin NN2 represents a small and shallow pond, of about 1.6 ha in size. The north-south extent and the western margins of NN2 were fully recovered, while former mining activities had already destroyed the easternmost limits of the basin (Hesse / Kindler 2014). Prior to the large-scale excavations of NN2 there had been some debate about the chronostratigraphic position of the interglacial deposits of basin NN2. Multidisciplinary analyses at NN2 and correlations with the record of NN1 however established beyond any doubt a synchronic filling during the Eemian (Strahl et al. 2011; Gaudzinski-Windheuser / Roebroeks 2014). In the area of the Geiseltalsee more basin structures below Weichselian loess deposits are known, which may be part of the extended Neumark lakeland (Hesse / Kindler 2014).

The archaeological record of the recently investigated basin NN2 is an ideal starting point to study Neanderthal occupation and subsistence in the Eemian lakeland area around the current Geiseltalsee.

NN2 – Stratigraphy, basin dynamics, and correlations with NN1

Multidisciplinary studies and excavations at NN2 provide a high-resolution coverage of dynamic processes in the development and filling of the basin, as well as environmental changes during the Eemian (Strahl et al. 2011; Gaudzinski-Windheuser / Roebroeks 2014; Pop / Bakels 2015; Pop et al. 2015). Results of these investigations, including sedimentology, micromorphology, pollen analyses and palaeomagnetism, establish the temporal and spatial context for all archaeological studies at NN2.

The largest extent of basin NN2 is 90 m NE-SW and 60 m NW-SE, with asymmetrical inclinations of the slopes on the northern and southern margins (**fig. 3**, Hesse / Kindler 2014). At the steeper southern part of the basin the sediments build a

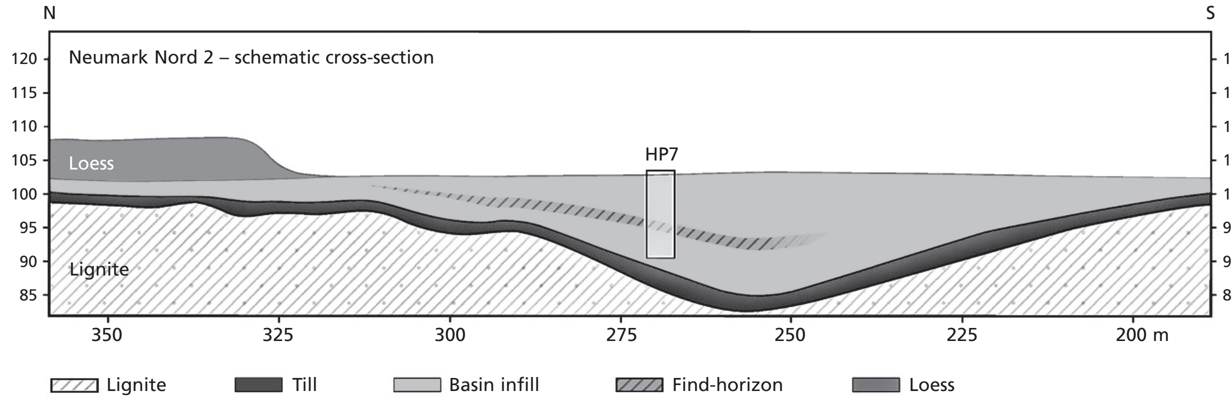

Fig. 3 Schematic north-south cross section of the Neumark-Nord 2 basin and its infill including the stratigraphic position of the archaeological find horizon NN2/2. The box inset refers to the main profile HP7 section. Vertical axis: height in meters above sea level. Horizontal axis: position of the NN2 basin in the excavation grid (in meters).

homogenous almost unstratified infill. In contrast, at the more gently sloping northern part sediments are partly fine laminated and fine sandy layers on the northern margin develop continuously into finer silty deposits towards the centre. The aim of the various multidisciplinary studies was a profile section near the centre of the basin, with the complete succession of the basin infill (main profile 7 = Hauptprofil 7 = HP7) (**fig. 3**) (Strahl et al. 2011; Hesse/Kindler 2014). Eemian archaeological deposits were exclusively restricted to the areas north of HP7. Excavations in these areas were connected by an additional trench to HP7. This provided the opportunity to place the archaeological deposits within the stratigraphy at the basin centre and the Eemian pollen succession. (Sier et al. 2011; Strahl et al. 2011; Bakels 2014; Hesse/Kindler 2014; Pop/Bakels 2015).

NN2 is separated from NN1 by a lignite diapir, that swelled on the western extensions of basin NN2 (Thomae 2003; Thomae/Rappsilber 2010; Wansa/Strahl/Rappsilber 2014). Although NN1 was a large lake and NN2 only a small pond, the infill of basin NN1 is much thicker, but their sedimentology and palynology are highly comparable (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). Both basins developed on a Saalian till. The lowermost layers belong to the Saalian Pleni- and Late Glacial. The infill of NN2 consists of clastic lake silt sediments, at NN1 various types of gyttjas were originally described (Mania 2010a; Mania et al. 1990; 2010a; 2010b; Mania/Thomae/Altermann 2010), but only in the upper part of the sequence, as well as at NN2, the proportion of organic detritus is significantly high (Wansa/Strahl/Rappsilber 2014). The water table in both basins was fluctuating, with several transgressions and regressions (Mania/Mai 2010; Mania/Thomae/Altermann 2010; Mücher 2014; Pop/Bakels 2015; Pop et al. 2015). Thus, different sandy margin deposits with archaeological layers were buried. For the correlation of the NN1 and NN2 deposits (Wansa/Strahl/Rappsilber 2014) Jaqueline Strahl refers in her pollen analyses to a regional standard classification for Eastern Germany for the late Saalian (Strahl/Hermsdorf 2008) and the Eemian (Erd 1973). In the pollen profile established by Corrie Bakels the terminology of Menke and Tynni (1984) was used (e. g. Sier et al. 2011; Bakels 2014; Pop/Bakels 2015). Both pollen profiles at NN2 and the conclusions drawn from them are in good agreement with each other. Only the location of boundaries between certain pollen stages at NN2 may differ. Based on the palynological synchronisation the archaeological and faunal record at NN1 and NN2 can be linked and Neanderthal occupations in the lake landscape of Neumark-Nord can be attributed to different pollen zones (**fig. 4**).

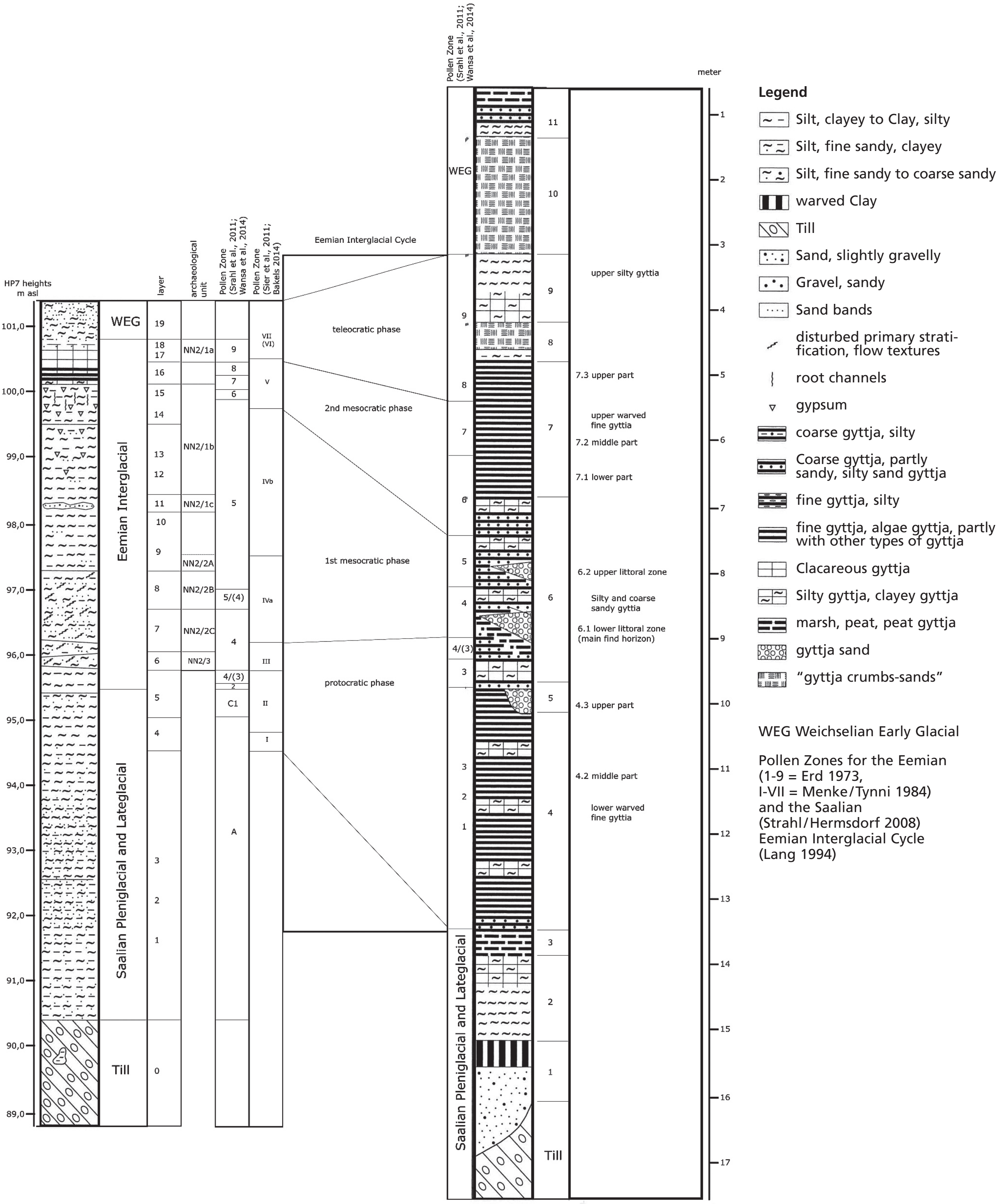

Fig. 4 Correlation of the stratigraphy and archaeological units at Neumark-Nord 1 (NN1) and Neumark-Nord 2 (NN2) based on the palynological sequences in both basins (according to Sier et al. 2011; Strahl et al. 2011; Bakels 2014; Hesse/Kindler 2014; Wansa/Strahl/Rappsilber 2014; Gaudzinski-Windheuser et al. 2018). The record of the individual archaeological units and their chrono-stratigraphic relations are discussed in the text.

The archaeological and faunal record from NN1 and NN2

Investigation and excavation at NN1 and NN2 followed completely different schedules. NN2 was investigated after reclamation works in the lignite mine, extensive and thorough year-round excavation of the northern part of the basin was possible. At NN1 during active mining the constant cutting of bucket-wheel excavators opened large surfaces but only for short periods of time, permitting only rescue excavations and the collection of uncovered complete and partially compete skeletons. An overview of excavation areas, the location of skeletons within basin NN1, and results of faunal analyses at major archaeological littoral zones at NN1 (layers 6.1 and 6.2) and NN2 (NN2/2B) are given in **figure 5**. The fauna from NN2 and NN1 represents the typical Eemian-fauna. Ungulate species include: straight-tusked European forest elephant (*Palaeloxodon antiquus*), three species of rhinoceros (*Stephanorhinus kirchbergensis, Stephanorinus hemitoechus* and *Coelodonta antiquitatis*), wild boar (*Sus scrofa*), horse (*Equus* sp.), aurochs (*Bos primigenius*), potentially steppe bison (*Bison priscus*) (identified by a horn fragment from NN1), potentially elk (*Alces* sp.) (identified by a complete distal metapodial from NN2/2), giant deer (*Megaloceros giganteus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama geiselana*) and roe deer (*Capreolus capreolus*). Car-

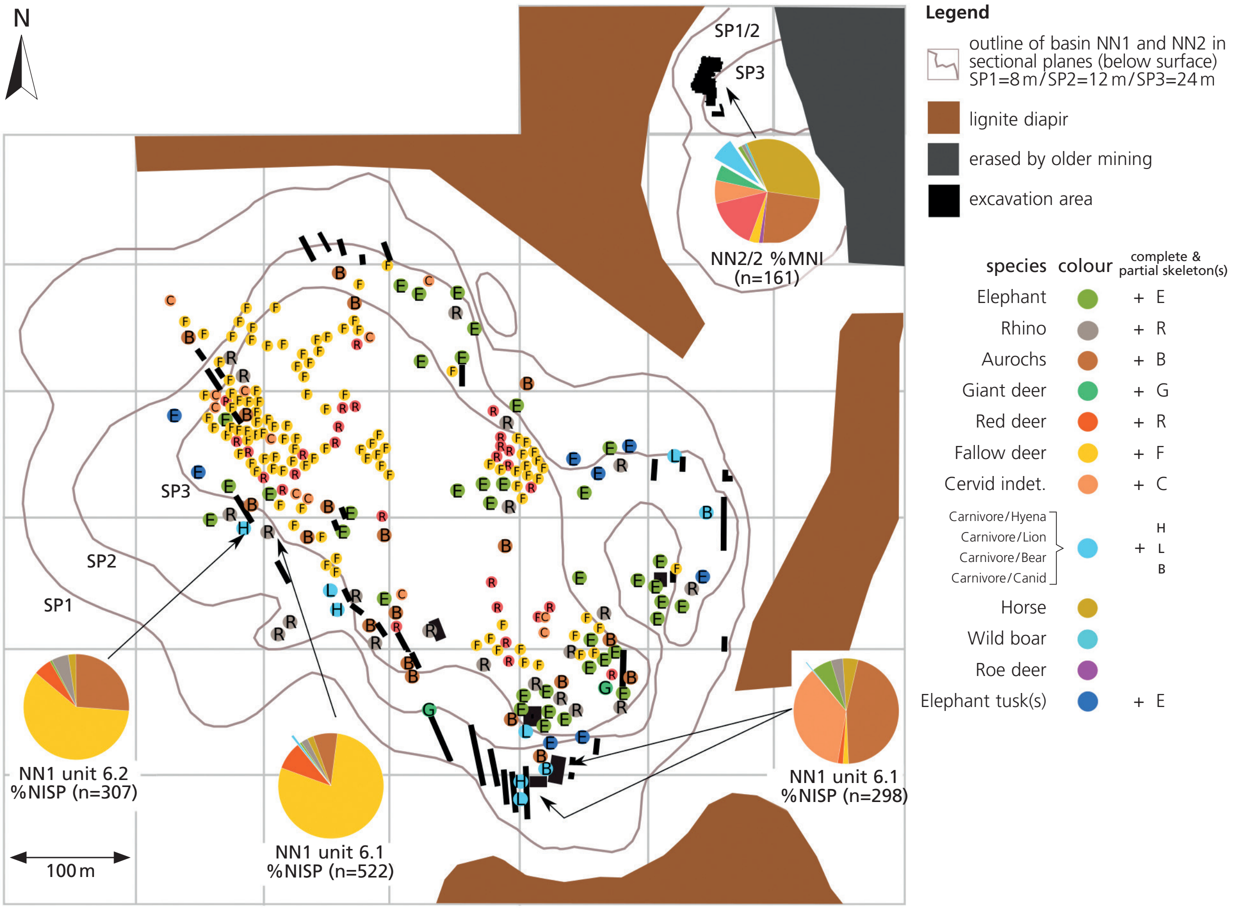

Fig. 5 Topographic map of the large lake basin Neumark-Nord 1 (NN1) in the center and the small "pool" Neumark-Nord 2 (NN2) in the upper right corner, with spatial distribution of (partial) mammal skeletons in basin NN1 (colored dots) and archaeological excavation areas (black rectangles). The pie charts indicate species distribution in selected excavation areas, at NN2 for the main find horizon NN2/2B (expressed as %MNI = minimum number of individuals), at NN1 for the lower littoral zone (unit 6.1) and upper littoral zone (unit 6.2) (expressed as %NISP = number of identified specimens per taxon). – (The synopsis is based principally on figures and data presented in Mania et al. 2010a; Meller 2010.).

Tab. 2 Estimated MNI of carnivores and ungulates in the different archaeological units in basin Neumark Nord 1 (NN1) and Neumark-Nord N2 (NN2) (Sources: Mania et al. 2010a; Meller 2010; own data) (Pollen zones see table 1.)

Basin	NN1											NN2					
Archaeological Unit	unstratified	**4.2** middle part lower warved fine gyttja	**4.3** upper part lower warved fine gyttja	**6** silty and coarse sandy gyttja	**6.1** lower littoral zone (main find horizon)	**6.2** upper littoral zone	**7.1** lower part upper warved fine gyttja	**7.2** lower to middle part upper fine warved gyttja	**7.3** upper part upper fine warved gyttja	**9** upper silty gyttja		NN2/3	NN2/2B	NN2/1c	NN2/1b	NN2/1a	
Pollen Zone	indet	1,2,3	1,2,3	(3),4,(5)	4	5	6	7	8	9		3	4	5	5 (6)	8,9	
Bones present	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	sum	yes	yes	yes	yes	yes	sum
Taxon/MNI																	0
Lion				1	2						3		1				1
large Felid											0		1				1
Hyena					1	1					2			1			1
Bear					1						1		8				8
Wolf					1						1		1				1
Fox	1										1		1				1
											0						0
Elephant		1	3	9	52		4	3			72		2	1			3
Rhino				2	9	2					13		2				2
Wild boar											0		1				1
Horse					>3						3	1	56	2			59
large Bovid				2	8	1	2			1	14		40	2			42
Cervid (*Capreolus* size)											0		2				2
Cervid (*Capreolus-Dama* size)											0		3				3
Cervid (*Dama* size)	26		1	26	>3		94	2	2		154		5	2			7
Cervid (*Dama-Cervus* size)	5						8				13		9	1			10
Cervid (*Cervus* size)	9		2	6	>3		24		1	1	46		26	2			28
Cervid (*Cervid-Alces-Megaloceros* size)											0	1	3				4
Cervid (*Alces-Megaloceros* size)					1	1					2		5				5
Sum	**41**	**1**	**6**	**46**	**84**	**5**	**132**	**5**	**3**	**2**	**325**	**2**	**166**	**11**	**0**	**0**	**179**

nivore species include: lion (*Panthera leo spelaea*), hyena (*Crocuta crocuta spelaea*), cave bear (*Ursus spelaeus*), brown bear (*Ursus arctos*), wolf (*Canis lupus*) and fox (*Vulpes Vulpes*). An estimation of the Minimal Number of Individuals (MNI) during each Eemian Pollen phase based on our analyses and data reported in Meller (2010) and Mania et al. (2010a) is presented in **table 2**. The diversity of species present at Neumark-Nord, especially during the *Corylus*-phase of the Eemian, may reflect high primary production and high degrees of resource partitioning (Fritz/Duncan 1994; Britton et al. 2012; 2014).

From the Saalian sequence at NN1 no remains of larger mammals are reported, also at NN2 no larger mammal bones were recovered from Saalian deposits. The transition from the Saalian to the Eemian at NN2 is only sparsely attested by sediments according to Strahl (Strahl et al. 2011). In contrast, Bakels (2014) has described a thicker and finer subdivision for the protocratic phase, probably by incorporating additional samples from a section (HP10) 8m away from HP7. Here, a sandy littoral zone was deposited near the centre of the basin (layer 6) and an area of 4m² was excavated (NN2/3), yielding 71 lithic artefacts and 170 bones, belonging to at least one horse and one large cervid, a robust red deer or larger sized species. The beginning of the Eemian at NN1 is located in the lowermost parts of the lower varved fine gyttja (layer 4). In the middle and upper part of this gyttja remains of at least four forest elephants, one fallow deer and two red deer were uncovered. At the end of the protocratic phase of the Eemian (Pollen Zone 3) fluvial sandy deposits (layer 5) cut into the lower varved gyttjja (Mania/Thomae/Altermann 2010) at NN1. There is also evidence for changes in the flow regime from malaocological evidence (Strahl et al. 2011).

The transition to the first part of the mesocratic stage (Pollen Zone 4) is documented at NN2 in the top of lake silts of layer 5 according to Strahl (Strahl et al. 2011), or in layer 7 by Bakels (2014) and at NN1 on the bottom of the silty and coarse sandy gyttja (layer 6). From the lake deposits at NN1 attributed to Pollen Zone 4 complete and partially preserved skeletons of 46 mammals were found, 26 fallow deer, 9 elephants, 6 red deer, and 2 aurochs and rhinos. Intersected in the gyttja is a first littoral deposit, spreading horizontally up to 150m (layer 6.1, lower littoral zone). The lower littoral zone is the main archaeological horizon at NN1, where most of the archaeological excavations took place and most of lithic artefacts were found. Complete and partially complete skeletons are dominated by elephants, with an MNI (minimal number of individuals) of 52. Detailed zooarchaeological information from the faunal record is pending. NISP-data are available from two excavation sites, where bones of different sized cervids and aurochs dominate. Also, horse is attested, which is absent from the record of complete and partially complete skeletons at NN1. At NN2 the deposits of alternating sand and silts contain scattered lithics and bones (NN2/2C).

Habitat settings and preservation conditions hamper the detection of a clear-cut boundary between Pollen Zone 4 and 5 at NN2 (Strahl et al. 2011). Thus, in the lower 30cm of layer 8 at HP7 a transitional phase between both Pollen Zones is placed and the upper parts are attributed to PZ 5. This result differs from Bakels (2014) interpretation of the NN2 pollen record, in which the boundary between Pollen Zone 4 and 5 is located higher in the profile. In the northern part of the basin, layer 8 contains the archaeological main find horizon NN2/2B (see **fig. 3**). Along the margin, layer 8 forms a 20cm thick sandy deposit, which becomes complex and thicker downslope, with laminated substrata up to 1m in depth. The upper part of this find horizon dissolves downslope towards the center of the basin. In the area of HP 7 the remaining sediments are disturbed and finger out, leaving a ca. 50cm thick silt loam deposit with isolated sandy lenses. The archaeological record from NN2/2B comprises almost 20,000 lithic artefacts and tools (Pop 2014; Pop et al. 2018) as well as and more than 118,000 faunal remains. From detailed faunal analyses a MNI of 166 large mammals are calculated (Kindler et al. in prep.), mostly horses, aurochs and red deer. Archaeological material from the basal part of the subsequent layer 9, which could be reworked in a slightly upwards position, are attributed to archaeological unit NN2/2A.

Tab. 3 Overview of the position of different archaeological units at Neumark-Nord 1 (NN1) and Neumark-Nord 2 (NN2) in the Eemian Interglacial Cycle.

Interglacial Cycle (Lang 1994)	Forest phase	Archaeological Deposits		Duration (Müller 1974)
		NN1	NN2	
Phase D (teleocratic phase)	*Pinus* phase	NN1.9 (upper gyttja)	NN2/1a	~ 2,000 years
	Pinus-Picea-Abies phase	NN1.7 (upper gyttja		~ 2,000 years
Phase C (mesocratic phase, 2. part)	*Carpinus-Picea* phase	NN1.7 (upper gyttja)		~ 4,000 years
	Carpinus phase		NN2/1b NN2/1c	
Phase B (mesocratic phase, 1. part)	*Corylus-Taxus-Tilia* phase	NN1.6.2 (upper littoral)		~ 1,200 years
	Quercetum mixtum-*Corylus* phase	NN1.6.1 (upper littoral)	NN2/2B	~ 1,200 years
Phase A (protocratic phase)	*Pinus-Quercetum mixtum* phase	NN1.4 (lower gyttja)	NN2/3	~ 450 years
	Pinus-Betula phase			~ 200 years
	Pinus phase			~ 100 years

In the stratigraphy of HP7 at NN2 Pollen Zone 5 extends through the sequence to Layer 14 (Bakels 2014; Strahl et al. 2014). An additional archaeological unit was excavated (NN2/1c). Apart from lithic artefacts 4,724 highly fragmented, intensively weathered and abraded bones were uncovered. At least a part of the assemblage might consist of material reworked from earlier find scatters. From the few larger bones which could be determined to species during excavation a MNI of 8 larger mammals can be estimated. Anthropogenic marks on the bone surfaces are present. Additional small-scale excavations in the area of HP7 above NN2/1c, yielded bone fragments and lithic artefacts summarized as NN2/1b. In sum 752 mostly fragmented bones and teeth are scattered through the sequence of archaeological unit NN2/1b.

Pollen Zone 5 in basin NN1 comprises the middle part of the silty and coarse sandy gyttja (layer 6). Here, a second littoral deposit is intersected (upper littoral zone, layer 6.2.). One rhino skeleton associated with lithic artefacts and a partially destroyed skeleton of a large bovid were found here. Additional bones belong to a second rhino, a giant deer and hyena. From an excavation in the southwestern part of the upper littoral zone 309 bone specimens are reported, with 60 % of the NISP belonging to fallow deer (see **fig. 5**).

The second part of the mesocratic phase (Pollen Zones 6 and 7) is documented in thick deposits at NN1, beginning in the upper part of layer 6 and covering most parts of the following upper fine varved gyttja (layer 7). In HP7 at NN2, both Pollen Zones are much thinner and the deposits are characterized by a transition from clastic lake silts to more organic sediments. Bones and lithics from the uppermost parts of archaeological unit NN2/1b may belong to PZ6. At NN1 the lower part of layer 7 has yielded the most impressive record of complete and partially complete skeletons. Cervids are dominating with more than 100 individuals, mostly fallow deer, compared to only 4 elephants and 2 large bovids. In the middle part of layer 7, attributed to PZ7, additional skeletons of 3 elephants and 2 partial preserved cervids were unearthed.

The teleocratic phase characterising the end of the Eemian (Pollen Zones 8 and 9) begins at NN2 after the deposition of organic material (Bakels 2014), while Strahl detected the boundary within the organic layer (Strahl et al. 2011). Four lithic artefacts and a few bone fragments can be attributed to Pollen Zone 9 and are summarised as archaeological unit 2/1a. At NN1, PZ8 and 9 again cover thick sediment deposits. Two (partial) skeletons of fallow deer and one of red deer belong to PZ8. A destroyed skeleton of a red deer, a skull and other remains of an aurochs were found in the uppermost Eemian deposits in PZ9.

In summary, there is ample archaeological evidence for Neanderthal presence in the lakeland of Neumark-Nord as shown by lithic artefacts from different layers and Pollen phases during the Eemian interglacial cycle at NN1 and NN2 (**tab. 3**). Combining the current faunal records from NN1 and NN2, different compositions of the ungulate thanatocoenoses for the main phases of the Eemian interglacial cycle are evident (**fig. 6**). The highest diversity in ungulate taxa is recorded during the first mesocratic phase during which the main archaeological units at NN1 and NN2 accumulated. In addition, a larger carnivore assemblage is preserved only during the first mesocratic phase (**fig. 7**). To assess the characteristics and "quality" of these thanatocoenoses, to establish a finer temporal sequence, and to derive information on Neanderthal occupations at Neumark during the Eemian, the environmental settings and specific locations within the basins in which the different faunal assemblages were deposited are essential.

Establishing a palyno-stratigraphic sequence of thanatocoenoses at NN1 and NN2

Lake NN1 and the pond NN2 are characterized by fluctuating water tables during the Eemian. These regressions and transgressions formed and preserved littoral zones within the basins. Due to the close proximity of the basins, identical environmental conditions during sedimentation can be expected. However, due to their different morphologies and their specific depositional background, changes in the water table were not inevitably synchronous. In terms of different hydrological situations, the elevation of both basins also has to be considered.

NN2 and also NN1 originate presumably from kettle holes (Wansa / Strahl / Rappsilber 2014). The melting ice activated the diapiris of the lignite in the underground flanking the basins. Basin NN1 is much deeper, the elevation of the Saalian till at the base of both basins is not less than about 4 m higher in NN2. In addition, late Saalian deposits at NN2 are about 1.5 m thicker than in NN1 (Wansa / Strahl / Rappsilber 2014). At the beginning of the Eemian we have to assume that basin NN1 was located about 5 m deeper in the landscape than NN2. Not surprisingly, the interglacial deposits are much thicker at NN1 and the final infilling of the basin occurred earlier at NN2, considering the comparably thin deposits during PZ6-9 at NN2.

Due to its size and elevation the catchment area of water must have been much larger in the lake NN1. If the basins were influenced by changing ground water tables, NN2 should have been more prone to drying out than NN1. Also seepage water from the higher elevated NN2 could have drained down to NN1. In addition, there is a zone of low elevation between the diapirs separating NN1 and NN2 (see **fig. 5**). Here, the outermost extensions of NN2 were truncated during mining and subsequent reclamation works (Thomae / Rappsilber 2010; Wansa / Strahl / Rappsilber 2014). At least intermittent connections of both basins via this breach can't be excluded.

Transgressions and regressions in basin NN1 and NN2 had a major influence on the preservation of the archaeological and faunal records. Their origin, composition and genesis must be linked to specific lake phases. Neanderthal activities should principally be attributed to dry areas within the basins, while subsequent submergence preserved the archaeological record of these activities. Four characteristics of major find contexts throughout the stratigraphy of the basins can be summarized: (1) In littoral zones, associations of lithics and highly fragmented bones are distributed over comparable larger areas. (2) In littoral zones, disarticulated bones from single individuals, partially associated with lithics are also distributed over small areas. (3) Articulated skeletons, partially preserved skeletons of single individuals, and skeletal remains from multiple individuals are found in gyttja deposits at NN1. Articulated cervid skeletons undisturbed by rotary excavators typically display overflexion of head and neck, convex bending of the thorax and parallel leg posture. (4) Finally, bones and lithics are scattered

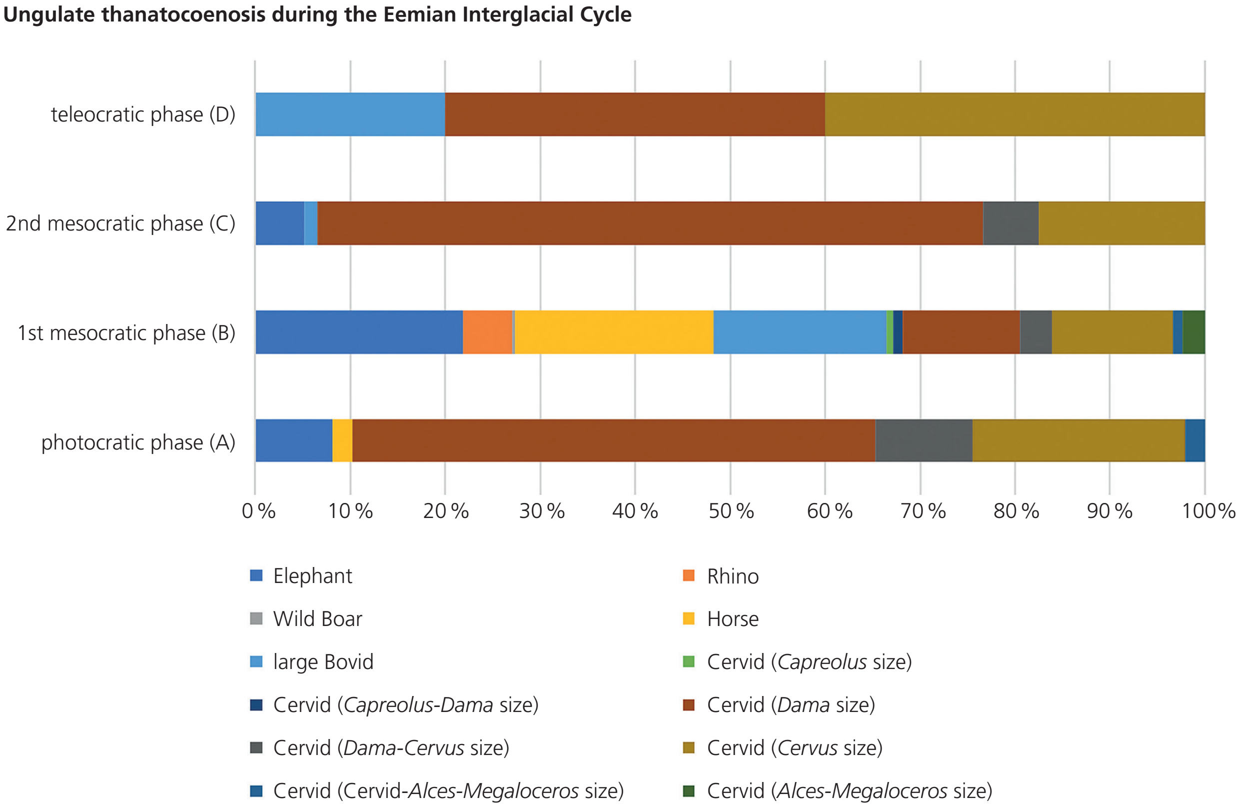

Fig. 6 Composition of the ungulate thanatocoenoses (based on estimates of MNI = minimum number of individuals) in the Neumark lakeland during the Eemian Interglacial Cycle.

in comparatively low numbers through the Eemian sequence.

At the transition to the Eemian protocratic phase, marshland developed in the NN1 basin. The faunal record at Neumark-Nord starts in PZ3 with the thanatocoenosis comprising the few individuals from layer 4 at NN1 during a first Eemian lake phase (Mania 2010a). The fauna is deposited in the gyttja within the basin or near the margins of the former lake. Lithic artefacts are not reported from these deposits. The regression during PZ3 dried out the basin completely. Even so, fluvial sediments accumulated (layer 5) during PZ 3 and subsequently transgression of a second lake phase began (base of layer 6). At NN2 in similar stratigraphic position fluvial depositions are supposed (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). According to Strahl (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014) the early phases of the Eemian in NN2 are represented in thin horizons with evidence of hiatuses. In contrast, Bakels (2014) has described a thicker and finer subdivision for the protocratic phase beginning with marshland development and a first sandy find horizon (find layer NN2/3) close to the center of the basin. For NN2/3 deposition during transgression is reconstructed (Pop/Bakels 2015). In Bakels palynostratigraphy, NN2/3 is attributed to PZ3. Thus, the first sandy littoral horizon at NN2 could correspond to the second lake phase at NN1, with maximum expansion of the water body in NN1.

At NN1, the second Eemian lake phase continues into the first part of the mesocratic phase (PZ4). During a major regression the lower littoral zone and major archaeological horizon (layer 6.1) formed around a waterbody in the centre of the basin. The last occurrence of terrestrial molluscs is recorded (Strahl et al. 2011) in the lower part of the stratigraphy in HP7 at NN2 and above NN2/3. The deposits are characterized by disturbance within the sediments (Wansa/Strahl/Rappsilber 2014; Mücher

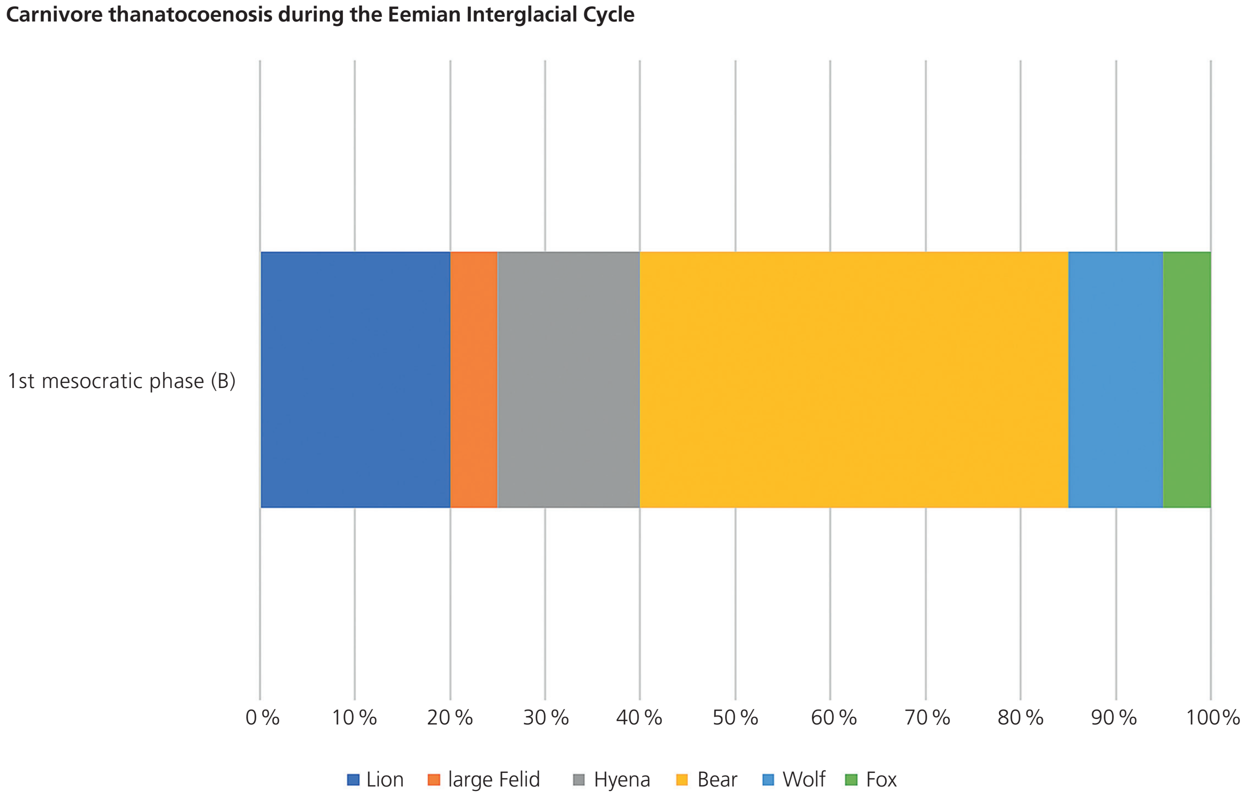

Fig. 7 Composition of the carnivore thanatocoenosis (based on estimates of MNI = minimum number of individuals) in the Neumark lakeland during the first mesocratic phase of the Eemian Interglacial Cycle.

2014) and alternations of transgressing and regressing water (Pop/Bakels 2015). At the top of these deposits the basin had dried out completely (Mücher 2014). Thus, within layer 7 in NN2 an equivalent to the lower littoral zone of NN1 could be deposited. During the subsequent transgression at NN1, the third Eemian lake phase, the water body reached maximum expansion, once again. Higher up in the stratigraphical succession at NN2 transgression is also reconstructed for the archaeological main find horizon NN2/2B (Wansa/Strahl/Rappsilber 2014; Pop/Bakels 2015). In Bakels (2014) pollen zoning NN2/2B still belongs to PZ4, but according to Strahl's reading of the pollen profile (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014) the transition to PZ5 is already present in the lower part of NN2/2B.

Pollen Zone 5 is represented in thick sediment deposits at NN2 in Strahl's pollen zoning as well as in Bakels'. In the lower parts of PZ5 there is a steady and continuous sedimentation of finer grain sizes and the disappearance of the disturbances within the sediments are related to higher water tables than those reconstructed in the lower parts of the stratigraphy (Strahl et al. 2011; Wansa/Strahl/Rappsilber 2014). Starting in layer 10 there is recurrent evidence of desiccation of the basin NN2 and pedogenesis occurs (Bakels 2014; Mücher 2014; Wansa/Strahl/Rappsilber 2014). At NN1, during PZ5, another major regression reduced the level of the lake and the upper littoral zone (6.2) formed around the water body at the centre of the basin. Thus, the sandy find horizon NN2/1c, scattered finds from archaeological unit NN2/1b at NN2 as well as the finds from the upper littoral zone from NN1 could have been deposited in temporal proximity (Wansa/Strahl/Rappsilber 2014).

The second part of the mesocratic phase and the teleocratic phase is compressed at NN2 but comprises thicker deposits at NN1. At the beginning of this phase a change to more organic components within the sediments is recorded in both basins. Basin NN2 seems to be filled up to its greatest extent, with evidence of extreme shallow water and development of marshland. Extreme shallow waters and eutrophication is reconstructed at NN1 for layer 7 (PZ6, 7, and 8). The lake spreads again to its maximum expansion. The largest accumulation of cervid skeletons is from PZ6. During the second half of the Eemian no littoral zones have been formed and preserved within the basins. According to Bakels, PZ 6 begins slightly lower down in the profile of HP7 at NN2, in contrast to Strahl's observations. Thus, isolated finds from the uppermost part of NN2/1b may already belong to PZ6. Finally, archaeological unit NN2/1a covers the teleocratic phase at the end of the Eemian.

Discussing Neanderthal occupations at NN1 and NN2

In the deeper parts of the Eemian deposits, the lake at NN1 reached maximum expansion during the protocratic phase. Within the lake almost intact skeletons of four elephants, one fallow deer and two red deer were uncovered. At NN2 a first lake transgression followed a phase of marshland in the basin. Near the centre of the basin, remnants of a littoral zone were excavated. The 4 m² site yielded artefacts and cut marked bones of at least one horse and one very large cervid, either a large male red deer, a giant deer or an elk.

The first part of the mesocratic phase is characterized by alternating more open and more closed environments. In addition, several regressions and transgressions were filling up the basins and also almost drying them out occasionally. Due to these changes, littoral horizons in both basins formed and persevered, like the lower littoral zone (6.1) and the upper littoral zone (6.2) at NN1 and NN2/2B in basin NN2. At NN1, the skeleton remains from the littoral zones are mainly from elephant, rhino and aurochs. According to Mania (2010a) and Mania et al. (2010a) at least one aurochs and one rhino were butchered at the spot. In contrast, from the evidence inside the basin, fallow deer skeletons dominate. Analyses of the cervids show that at least two of them show cut marks. At NN2, during this phase, the main archaeological unit NN2/2B formed. The fauna is purely anthropogenic in origin without any significant involvement of other biotic agents. The carnivore bones present in the accumulation also show butchery marks. Our analyses have demonstrated that Neanderthals were active here during all four seasons (Kindler et al. in prep.). The MNI of all taxa in the death assemblage is 166, amongst them 56 horses, 40 aurochs and 53 individuals of different sized cervid taxa (Kindler et al. in prep.). Although we lack substantial faunal data from the excavation areas at NN1, the NISP composition at three sites in the upper and lower littoral zones also indicates high numbers of horses, aurochs and cervids, in the size range of red deer and fallow deer (see **fig. 5**). For the two littoral zones at NN1 more open vegetation is reconstructed, for NN2/2B more closed vegetation (Mania et al. 2010a; 2010b; Pop/Bakels 2015). Thus from palyno-stratigraphical comparisons, the littoral zones at NN1 and NN2 are most likely not contemporaneous and they formed during several relatively short time intervals of a few hundred years during the mesocratic phase (Mania et al. 2010a; 2010b; Sier et al. 2011; Kindler/Smith/Wagner 2014; Wansa/Strahl/Rappsilber 2014). Higher in the profile at NN2, is a smaller and less well preserved lithic and faunal assemblage, with anthropogenic modifications, NN2/1c, whose genesis hasn't been fully assessed yet. But after the formation of NN2/1c the basin was almost filled and had a tendency to dry out completely. Artefacts and bones still occur sporadically in these deposits and are assigned to NN2/1b. The uppermost level of NN2/1b reaches into the second part of the mesocratic phase, also often referred to as the Eemian maximum, characterised by the spread of the most thermophilus plant species. From here to the end of the teleocratic phase at NN2 the sediments are compressed, marshland developed and finally a last shallow water pool. During profile trenching tiny splinters of bone and four artefacts were found in deposits dating to the teleocratic phase, labelled NN2/1a. Extreme shallow waters and phases of eutrophication are reconstructed at NN1 for the second part of the mesocratic phase. The lake spreads again to maximum expansion. The largest accumulation of cervid skeletons, 128 individuals, were deposited in a fine varved gyttja within the lake during the second mesocratic stage. Eight of these skeletons show cut marks and two individuals display hunting lesions (Gaudzinski-Windheuser et al. 2018). The final deposition of elephant skeletons occurs during this phase, in the succeeding teleocratic phase only one bovid and four cervid skeletons were deposited.

Neanderthal presence in the Neumark lakeland is attested by lithic artefacts and anthropogenic bone modifications for all four phases of the interglacial cycle and during phases of more open and more closed environments. However, the characteristics, quantities and "qualities" of lithic and faunal assemblages at NN1 and NN2 vary tremendously. These differences can be linked to spatial and temporal changes in sedimentation, dependent on environment, topography and basin morphologies. The littoral horizons at NN1 and NN2 were deposited during relatively short periods of time with high sedimentation rates (Sier et al. 2011; Wansa / Strahl / Rappsilber 2014) within the basins. Analyses of orientation of lithics and bones at NN2/2B revealed deposition with low-energy and no significant re-distribution of finds by hydrodynamic flows (Pop et al. 2015; García-Moreno et al. 2016). At NN1 the presence of complete skeletons and the distribution of skeletal parts from single individuals over small areas also indicate, that dislocation of finds during or after deposition played a minor role here. The same accounts for complete and partially complete skeletons deposited in the inner part of the lake NN1. High sedimentation rates, but low energy flows allowed the preservation of these unique thanatocoenoses and archaeological units, that reflect occupation and activities of Neanderthals in dry areas inside the depressions of the basins. In contrast, when the basins were completely filled with water or covered by marshland, Neanderthals were forced to operate outside the basins in the Neumark lakeland. The erosional deposits forming the infill of NN1 and NN2 derive from these areas. Sporadic finds of lithics and / or modified bones scattered in the basins infills – especially during the second part of the mesocratic and teleocratic phases – indicate Neanderthal presence in the lakeland, but the evidence doesn't provide any spatial and temporal resolution for littoral deposits.

The preservation of complete and partially complete skeletons from gyttja deposits inside basin NN1 is still puzzling. An interpretation of this unique faunal record based on a comprehensive taphonomical and zooarchaeological analyses is still missing. Most of the specimens belong to fallow deer (*Dama dama geiselana*). For the origin of this *Dama*-record different scenarios were postulated. In the "hunting accidents" scenario the cervids were driven into the lake basin and died there (Mania et al. 1990). In the "natural die off" scenario, an accumulation over several thousands of years was reconstructed culminating in an assemblage which should represent a mix of different natural and anthropic processes (Mania 2010b; Mania et al. 2010b). The "poison scenario" builds on the evidence of cyanobacteria present in NN1 sediments. Animals in the Neumark lakeland, especially young fallow and red deer bulls during the rut, died by poisonous water caused by the cyanobacteria (Pfeiffer 1999; Braun / Pfeifer 2002; Pfeiffer-Demel 2010a; 2010b). This scenario appears attractive at first glance, since it exerts particular events for the origin of a unique thanatocoenosis. Deadly cocktails produced by cyanobacteria can kill a substantial amount of animals in short amounts of time (de Boer et al. 2015; Bengis et al. 2016). However, there is additional evidence challenging the "poison scenario" at Neumark. Pfeiffer-Demel (2010a) thinks that the cervids died soon after drinking at the shore line. With rising water tables the bloated cadavers drifted in the lake, sank to the bottom and became deposited there. This process must occur within days during early stages of decomposition. In contrast, the posture of undisturbed skeletons is typical for desiccation during decomposition (Mania et al. 1990). The occasional presence of cut marks, rodent gnawing and root etching on bones of some cervid skeletons also indicates decomposition and subsequent deposition of the carcasses on dry land and not in water (Gaudzinski-Windheuser 2010; Gaudzinski-Windheuser et al. 2014). In addition, the liability to drink high amounts of polluted water varies between different mammal species. Cyanobacterial blooms usually become deadly cocktails, when wind drift accumulates high amounts of these bacteria at the shores of a waterbody. In a recent study of mortality due to repetitive cyanobacterial blooms in South Africa, it was mainly zebra, wildebeest and white rhino, that died (Bengis et al. 2016). Amongst the Eemian larger ungulates at Neumark, both horse and aurochs need substantial amounts of fresh water, while cervids can meet their water requirements from water stored in the plants they consume. However, remains of horses didn't contribute to the skeleton thanatocoenosis at all and remains of aurochs appear in comparable low numbers. Frequent are elephants in the Neumark thanatocoenosis, while in the recent South African study not a single elephant was poisoned. Elephants wade deeper into water bodies to drink and therefore don't consume the cyanobacteria floating at the shores (Bengis et al. 2016). Thus, it becomes complicated to incorporate the cervid taphonomical data into the structure of the skeleton thanatocoenosis in the "poison scenario". But also for the "hunting scenario" and "natural die-off scenario" we still lack supporting zooarchaeological and taphonomical data for coherent contextualisations. Hunting lesions recently detected on a cervical vertebra and a pelvis of two fallow deers clearly demonstrate close range hunting of these individuals during the 2nd mesocratic phase (layer 7) (Gaudzinski-Windheuser et al. 2018). However, data on cut marks from the thanatocoenosis show that the carcasses were only marginally exploited. Given that the cadavers were decomposing and depositing on dry land it is also surprising that evidence of carnivore involvement and scavenging is almost non-existent. Although Neanderthal involvement becomes more and more visible, the exact origin(s) and processes shaping the skeleton thanatocoenosis at NN1 still remain enigmatic. Work on the thanatocoenoses of the skeleton is still in progress and it will take some more time to analyse the material of other taxa present at NN1.

Nevertheless, the NN1 and NN2 evidence provides a uniquely large and clear window into the faunal community of the lakeland about 125,000 years ago, as well as the activities of Neanderthals in an early last Interglacial setting, including anthropogenic fires (Roebroeks/Bakels 2015; Pop et al. 2016). In the current state of research at Neumark and referring to the record of NN2/2B, the high-resolution palaeoenvironmental data, the rich and generally well-preserved fauna heavily exploited by humans, and the virtual absence of carnivore marks suggest a Neanderthal "permanence" or at least "dominance" in the Neumark-Nord lakeland, and the distinct possibility to document spatial variability in faunal exploitation over a large area. This variability is well attested when comparing the number of individuals encountered at NN1 and NN2/2B. Horse, aurochs and red deer dominate in the assemblage of NN2/2B, while at NN1 it is elephant and fallow deer. This may point to specific prey preference, even when assuming that Neanderthals are responsible for the thanatocoenosis from NN1, they took little benefit from their efforts and left the carcasses and remains almost untouched.

Crucial for an assessment of subsistence strategies are the opportunities an ecosystem or biotope offers, i.e. community structure, prey abundance and distribution. Reconstructions of these variables from death assemblages are challenging due to biases by taphonomic processes and other factors, such as differences in mortality rates in individual taxa and temporal resolution (e.g. Behrensmeyer/Western/Boaz 1979; Behrensmeyer/Dechant Boaz 1980; Western 1980; Lyman 1994; 2008; Kidwell/Rothfus 2010; Kidwell/Tomasovych 2013). As an additional frame of reference to discuss subsistence opportunities the carrying capacity (CC) for the Eemian in the Neumark lakeland and the biomass deposited in the thanatocoenosis are calculated.

Deducing subsistence opportunities in the Neumark lakeland from ungulate carrying capacity and biomass

From an ecological perspective human subsistence must meet the energetic and dietary demands of individuals. Based on isotopic studies, Neanderthals are characterised as humans relying heavily on animal resources (e.g. Richards et al. 2008; Wissing et al. 2016; but see also Smith 2015), but regional variation in diet composition may have existed. Recent studies of ancient DNA present in dental calculus on Neanderthal teeth supports the notion of a meat-based diet for the higher latitudes of the Neanderthal range, while two individuals from Spain appeared to have had a quite vegetarian lifestyle (Weyrich et al. 2017). Prey abundance must have been a crucial variable in Neanderthal subsistence. Energy production and energy flow in ecology is in general expressed in weight (e.g. kg) or calories (e.g. kcal) in a certain area (e.g. km²). Deducing biomass and energy values from archaeofaunas can contribute to better understanding of Neanderthal subsistence and ecology. In a zooarchaeological perspective these calculations can be used as ancillary key figures, when comparing and interpreting minimal numbers of individuals (MNI) in faunal assemblages (see Lyman 2008).

For estimations of body weight the catalogue of data compiled by Smith et al. (2003) for late Quaternary mammals can be used. In addition, Thompson and Henshilwood (2014) have collected data on edible calorie values for different sized African ungulates. Combining their data for different species an approximately 600 kcal per kg ungulate body weight can be derived, which is used to transform the body weight of a species into its calorie content.

Prey abundance is controlled by primary production, which is influenced by a variety of factors like soil substrate, precipitation, temperature and insolation (Churkina/Running 1988; Nemani et al. 2003). Based on these variables a theoretical estimation of the carrying capacity, i.e. the maximum amount of biomass, for an ecosystem can be calculated. From a comparative data set of 95 recent faunal communities Rodriguez et al. (2014) developed an equation to calculate large herbivore biomass production expressed in kg/km² based on temperature and rainfall. Calculation of large herbivore biomass (Rodriguez et al. 2014) based on rainfall follows the equation:

$$\mathrm{maxB(P)} = 18.3\ \mathrm{P} - 3993 \qquad (1)$$

Calculation of large herbivore biomass based on temperature follows the equation:

$$\mathrm{maxB(T)} = 1634\ \mathrm{MAT} - 12502 \qquad (2)$$

where maxB(T) is maximum ungulate biomass as limited by mean annual temperature. The equation doesn't fit for mean annual temperatures below 8° C. Estimating large herbivore carrying capacity (CC) at a certain locality should be based on the minimum value obtained in both equations:

$$\mathrm{CC} = \mathrm{Min}\ (\mathrm{maxB(P)};\ \mathrm{max(BT)}) \qquad (3)$$

For the Eemian on the North European Plain and in Central Europe estimations of temperature and precipitation are based on palaeobotanical data, including data from Neumark-Nord and/or data obtained in the larger region around Neumark-Nord (Zagwijn 1996; Aalbersberg/Litt 1998; Kaspar et al. 2005; Kühl et al. 2007). Results from climate simulation models for that region are in overall concordance with the botanical results (Kaspar/Cubasch 2006). For the first half of the Eemian the region of Neumark-Nord was influenced by (sub)continental conditions. Summer mean temperatures were higher, but winter mean temperatures lower than today. For the second half of the Eemian a change to (sub)oceanic conditions is reconstructed, with a lower amplitude between summer and winter temperatures, i.e. lower mean temperatures in summer and higher mean temperatures in winter. An increase in precipitation in both parts of the Eemian is reconstructed, for the first half above 600 mm and below 700 mm, for the second half probably above 700 mm.

The results of CC calculations for Neumark-Nord are given in **table 4** using the range of mean annual temperature and rainfall today and different values for reconstructed Eemian climate conditions in the region. The results suggest, that ungulate biomass during the Eemian was limited by mean annual temperature at Neumark-Nord. The number of herbivores in recent ecosystems is usually below the estimated CC. The same may account for Pleistocene ecosystems. However, CC values give an indication of the highest biomass values, which may serve as a very first reference to characterise and compare recent and past ecosystems. Comparing the recent and the past is always prone to faulty and misleading conclusions. In particular, past interglacials are in many ways different from our recent interglacial. On the other hand, in recent settings we can observe mechanisms shaping biocoenoses, in past settings we observe mechanisms shaping thanatocoenoses, which usually reflect a biased extract of the living community. Nevertheless, death assemblages originate from processes operating in biocoenoses. Especially, when reconstructing human subsistence from death assemblages reference to past biocoenoses is needed. Thus, and at best, observations in both settings should complement each other and broaden perspectives.

Given a wetter and warmer climate during the Eemian at Neumark-Nord, CC could have been considerably higher than today. The ungulate biomass could have been about three times higher compared to recent climatic conditions in the Neumark area (**tab. 4**). Thus, diversity of species and the high numbers of individuals in the Neumark thanatocoenoses can be linked to high ungulate biomass production. However, observed biomass usually oscillates below calculated CC, especially in forested environments, in which primary plant biomass production is vertically structured and thus limits food availability for ungulate species (Rodriguez et al. 2014).

For comparison, there is limited data on recent ungulate biomass production on the North European Plain, simply because native environments with free roaming ungulates are almost absent in Europe today. About 900 km east of Neumark-Nord one of the last refugia for European ungulates was established in 1932, the Biolawieza Primeval Forest (BPF). The park covers about 1,450 km^2 in eastern Poland and western Belarus today, but doesn't represent a virgin interglacial forest (Mitchell / Cole 1998). In BPF five ungulate species, European bison, elk, red deer, roe deer and wild boar can live undisturbed and coexist with their predators, wolf and lynx. Fallow deer was introduced to the Biolawieza forest in the 19th century, eradicated during the first world war and never re-introduced since then. At Bialowieza an almost complete, historical annual animal census from 1830 up to 1993 is documented (Jedrzejewska et al. 1997). In BPF ungulate biomass is controlled by temperature, the number of predators and the effects of changing political situations in the 20th century, which led to severe poaching and repression of wild game by increasing numbers of livestock in the forest. Highest mean annual temperature during that times was 8.5 degrees giving an estimated ungulate CC of 1,180 kg / km^2. The highest observed ungulate CC in the historical census, with more than 10,000 individuals of different species in the final year (1992/93), is 1,307 kg / km^2 and 7.4 individuals per km^2 using the compilation of body mass in late Quaternary mammals (Smith et al. 2003). This means more than 4 million calories per km^2 (600 kcal per 1 kg ungulate body weight) including almost 600 cattle individuals still roaming in the park (**tab. 5**).

These results suggest that calculated CCs in forested environments on the Northern European Plain can be reached, especially when acknowledging that at Bialowieza only an impoverished interglacial fauna has survived and domesticates still reduce the biomass of the wild game.

Tab. 4 Ungulate carrying capacity (kg / km^2) using the range of different temperature and precipitation estimates for the region of Neumark-Nord during the Eemian.

Temperature (°C) maxB(T)	CC	Precipitation (mm) maxB(P)	CC
9.1 (recent)	2,367		
10	3,838		
		453 (recent)	4,297
		500	5,157
11	5,472		
		550	6,072
		600	6,987
		700	7,902

The thanatocoenoses at Neumark-Nord reflect mortality in a lakeland during the course of the Eemian. Waterholes are essential for most larger mammals and should be considered as magnets for herbivores and their accompanying predators. Much hunting and killing occurs around waterholes. The role of surface water for the structure and dynamics of herbivore communities is addressed in recent studies in African settings from different ecological perspectives, including biomass production and its spatial distribution around and in the near vicinity of water holes, drinking behavior, competition and niche portioning, as well as hunting and predation (Western 1975; Valeix/Chamaillé-Jammes/Fritz 2007; Valeix et al. 2007; 2009a; 2009b; Crosmary et al. 2012; Hayward/Hayward 2012). From this perspective, the Neumark depositional environment, high biomass production and high numbers of individuals in a diverse herbivore fauna provide ideal references to inspect the structure of the Eemian herbivore community and potential Neanderthal subsistence and hunting behaviour in more detail.

For the ungulate species present in the Neumark thanatocoenoses weight estimations are based on data compiled by Smith et al. (2003) (**tab. 6**). Inferring a 600 kcal per 1 kg ungulate (Thompson/Henshilwood 2014) the calorie value for each taxon can be derived. Against the background of the overall larger size of ungulate species at Neumark compared to their Holocene counterparts (Döhle 2010; Palombo/Albayrak/Marano 2010; van der Made 2010), the values were slightly adjusted for some species, but the values are still based on conservative estimations. Because of high fragmentation of bones and size overlap between cervid species (Pfeiffer 1999), unambiguous taxonomic identification in the thanatocoenosis of NN2/2B is mostly impossible, so the cervids were subdivided into different body size and weight classes (Kindler et al. in prep.). The cervids and all other taxa are lumped in six size classes, from taxa less than 100 kg up to the size of elephants with 6,000 kg.

Species diversity and quantity of individuals is poor in the protocratic and teleocratic phase of the Eemian at Neumark. In the second mesocratic phase many individuals were deposited, but species diversity is limited (see **tab. 2** and **fig. 6**). In contrast, the record of the first mesocratic phase is rich in species and individuals and comprises different death assemblages, with different taphonomic histories. The records from the littoral zones at NN1 and NN2/2B, although most likely consecutive in their temporal formation, should permit a synthetical view on the community structure during the first 2,400 years of the mesocratic phase of the Eemian, because evident biases in the individual thanatocoenoses can be off set against and complement each other. The different death assemblages at NN1 and NN2 formed

Tab. 5 Weight (kg) and calorie (kcal) values for the Bialowieza ungulate population. Census data are taken from Jedrzejewska et al. (1997), body weight estimates are taken from Smith et al. (2003).

Bialowieza Primeval Forest/Bialowieza National Park (BNP), Poland/Belarus (size: 1,450 km²)					
Taxon	Census 1992/93	Weight (Individuum)	Weight (Population)	Kcal (Individuum)	Kcal (Population)
Wisent	554	500	277,000	300,000	569,400,000
Elk	200	355	71,000	213,000	155,490,000
Red deer	4,177	156	652,656	93,750	637,500,000
Roe deer	2,630	23	59,175	13,500	82,620,000
Wild boar	2,571	117	300,807	70,200	381,747,600
Dom. cattle	594	900	534,600	540,000	4,504,680,000
sum	**10,726**		**1,895,238**		**6,331,437,600**
per km²	**7.40**		**1,307**		**4,366,509**

Tab. 6 Body weights estimates for ungulate taxa from Neumark-Nord using data for late quaternary mammals as a reference (Smith et al. 2003).

Smith et al. 2003			Neumark-Nord (NN)	
Taxon	Species	Weight (kg)	Taxon	size class
Elephantidae	*M. imperator*	10,000		
Elephantidae	*M. columbi*	8,000		
Elephantidae		6,000	Elephant (*P. antiquus*)	size 7 (>2,500 kg)
Elephantidae	*M. primigenius*	5,500		
Elephantidae	*L. africana*	3,940		
Rhinocerotidae	*C. sinum*	2,949		
Elephantidae	*E. maximus*	2,720		
Rhinocerotidae	*S. kirchbergensis*	2,000	Rhino (*S. kirchbergensis, S. hemitoechus, C. antiquitatis*)	size 6 (<2,500 kg)
Rhinocerotidae	*R. sondiacus*	1,750		
Rhinocerotidae	*R. unicornis*	1,602		
Rhinocerotidae	*D. sumatrensis*	1,266		
Rhinocerotidae	*D. bicornis*	1,180		
Bovidae		1,000	large Bovid (*B. primigenius, B. priscus*)	size 5 (<1,000 kg)
Bovidae	*B. priscus*	900		
Bovidae	*B. taurus*	900		
Cervidae	*A. latifrons*	850		
Cervidae	*M. algericus*	800		
Cervidae		800	Cervid (*Alces-Megaloceros* size) (large specimens: *Alces* sp., *Megaloceros* sp.)	size 5 (<1,000 kg)
Bovidae	*B. bison*	579		
Bovidae	*B. bonasus*	500		
Cervidae		500	Cervid (*Cervus-Alces-Megaloceros* size) (very large specimens: *Cervus elaphus,* small specimens: *Alces* sp., *Megaloceros* sp.)	size 4 (<600 kg)
Equidae	*E. grevyi*	409		
Equidae	*E. quagga*	400	Horse (*Equus* sp.) Horse (*Equus* sp.)	size 4 (<600 kg)
Cervidae	*A. alces*	359		
Equidae	*E. zebra*	287		
Equidae	*E. burchelli*	276		
Equidae	*E. caballus*	250		
Cervidae	*C. elaphus*	218		
Cervidae		180	Cervid (*Cervus* size) (*C. elaphus*)	size 3 (<300 kg)
Cervidae	*C. elaphus*	167		
Cervidae	*C. elaphus*	157		
Cervidae	*C. elaphus*	120		
Suidae		120	Wild Boar (*S. scrofa*)	size 3 (<300 kg)
Suidae	*S. scrofa*	117		
Cervidae		100	Cervid (*Dama-Cervus* size) (small speciemens: *C. elaphus,* large specimens: *D. d. geiselana*)	size 2 (<100 kg)
Cervidae		80	Cervid (*Dama* size) (*D. d. geiselana*)	size 2 (<100 kg)
Cervidae	*D. dama*	56		
Cervidae	*D. dama*	49		
Cervidae		45	Cervid (*Capreolus-Dama* size) (small speciemens: *D. d. geiselana*, large specimens: *C. capreolus*)	size 2 (<100 kg)
Cervidae	*C. capreolus*	22.5	Cervid (*Capreolus* size) (*C. capreolus*)	size 2 (<100 kg)

Tab. 7 MNI for ungulate taxa at NN2/2, weight estimates (kg) and energy values (kcal).

Species	size class	MNI	Weight (Ind) kg	Weight (Pop) kg	kcal (Ind) $\times 10^6$	kcal (Pop) $\times 10^6$	kcal sum size class (Pop) $\times 10^6$	species per size class
Elephant	size 7 (>2,500 kg)	2	6,000	12,000	3.6	7.2	7.2	1
Rhino	size 6 (<2,500 kg)	2	2,000	4,000	1.2	2.4	2.4	1
large Bovid	size 5 (<1,000 kg)	40	1,000	40,000	0.6	24	26.4	2
Cervid (*Alces-Megaloceros* size)		5	800	4,000	0.48	2.4		
Cervid (*Cervus-Alces-Megaloceros* size)	size 4 (<600 kg)	3	500	1,500	0.3	0.9	14.34	2
Horse		56	400	22,400	0.24	13.44		
Cervid (*Cervus* size)	size 3 (<300 kg)	26	180	4,680	0.108	2.808	2.88	2
Boar		1	120	120	0.072	0.072		
Cervid (*Dama-Cervus* size)	size 2 (<100 kg)	9	100	900	0.06	0.54	0.888	4
Cervid (*Dama* size)		5	80	400	0.048	0.24		
Cervid (*Capreolus-Dama* size)		3	45	135	0.027	0.081		
Cervid (*Capreolus* size)		2	23	45	0.0135	0.027		
sum		**154**		**90,180**		**54.108**		
					without Elephants	**46.908**		

most likely within time windows of only a few hundred years, based on estimation of sedimentation rates (Mania et al. 2010a; 2010b; Sier et al. 2011; Kindler / Smith / Wagner 2014; Wansa / Strahl / Rappsilber 2014) and thus provide insights into mortality in a biocoenosis due to Neanderthal hunting and other processes during relatively short time intervals. During that time more than 280 individuals of different ungulate taxa identified so far, were deposited in an area covering approx. 0.4 km² (**tab. 2** and **fig. 5**). An additional frame around the question of the duration of accumulation can be established for NN2/2B with reference to the energy flow between prey and Neanderthals. An exclusively anthropogenic origin of this faunal assemblage is reconstructed. Except elephants all species identified bear traces of exploitation by Neanderthals. The minimum number of 152 identified ungulate individuals of different species bearing butchery marks represents 78,180 kg and 46,908,000 kcal (**tab. 7**). A considerably higher daily energetic expenditure for Neanderthals compared to modern humans is debated (e.g. Heyes / MacDonald 2015). For modern hunter-gatherers a total daily energy intake of 3,000 kcal per individual is assumed (Sebastian et al. 2002). In **figure 8** calculations for a daily intake of 3,000 kcal and 5,000 kcal and different proportions of meat in daily diets are used to calculate for how long groups of different sizes can subsist on the calories deposited at NN2/2B. Although Neanderthal group size in the Neumark lakeland is unknown, both tables show, that the calories deposited at NN2/2B can reflect ungulate meat consumption within a maximum of a few decades or a generation. This illustrates, that a predator, in this case Neanderthals, active in habitats with high herbivore biomass can produce large bone assemblages in areas of prey aggregation, like water holes, in rather short amounts of time. Given high mortality at Neumark because of herbivore aggregation at

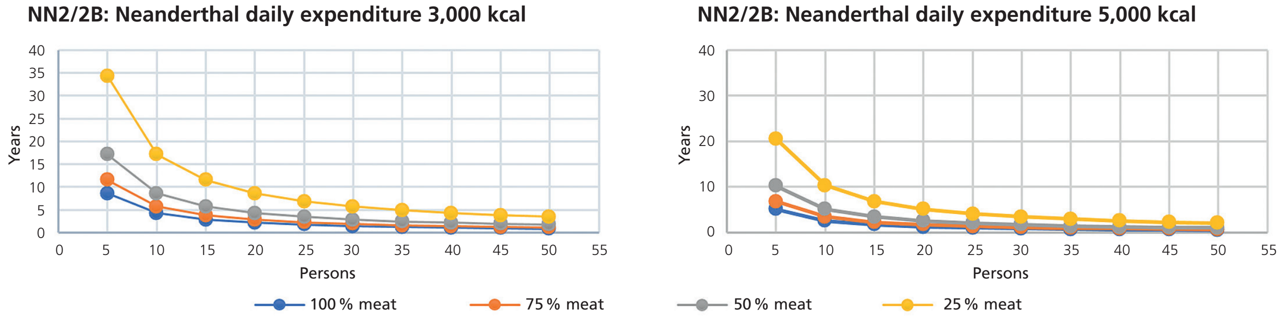

Fig. 8 Estimates of the number of years different-sized groups could subsist on the calories deposited at NN2/2B, based on a daily energetic expenditure of 3,000 kcal (left) and 5,000 kcal (right) and varying proportions of meat in daily foods.

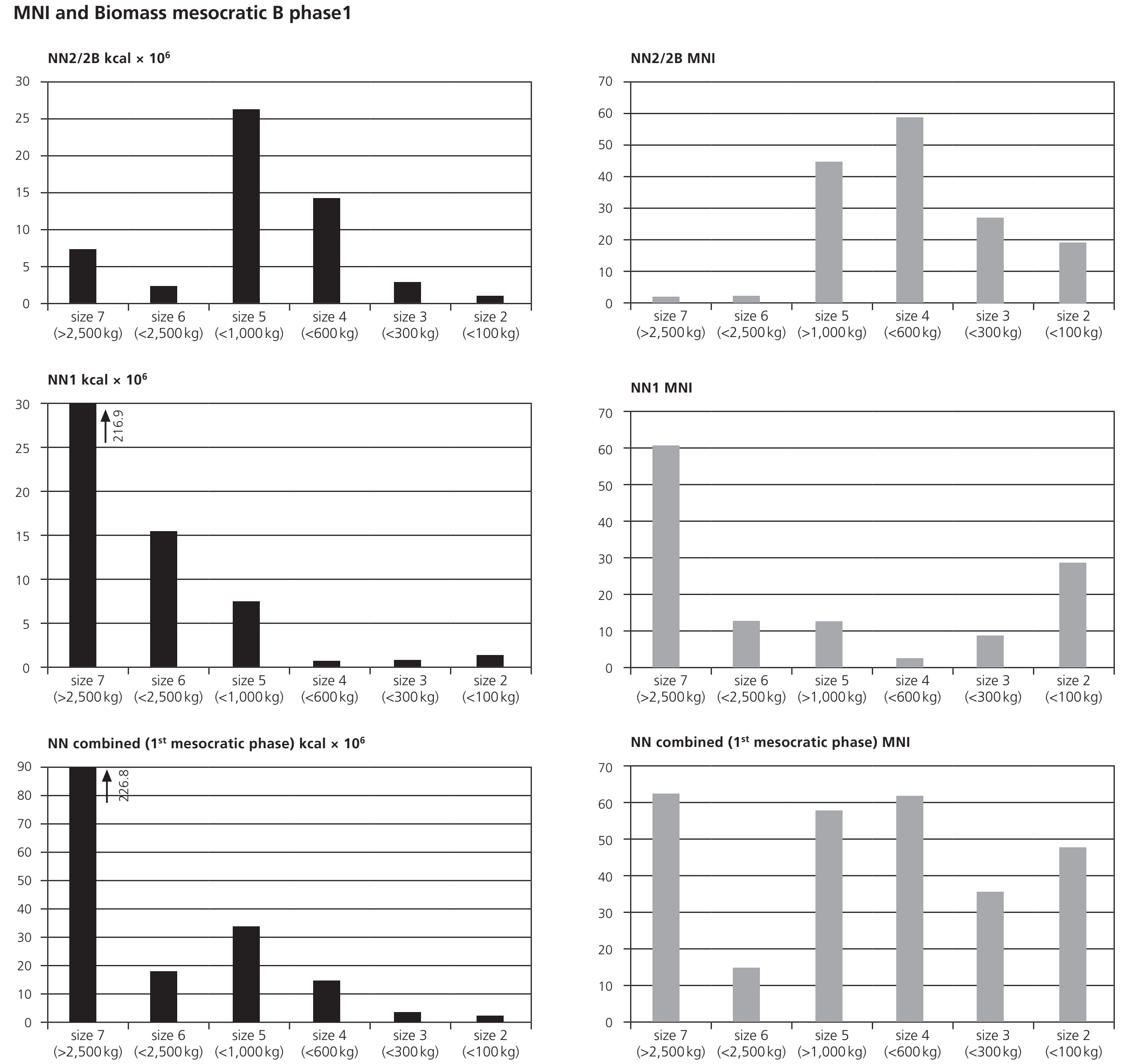

Fig. 9 Thanatocoenoses of the first mesocratic phase of the Eemian at Neumark-Nord. Top row: NN2/2B. Middle row: NN1, unit 6. Bottom row: NN2/2B and NN1, unit 6 combined. Left column: Calories (kcal). Right column: Minimal number of individuals (MNI). Species represented by size class are listed in table 6.

Tab. 8 Reconstruction of the living ungulate community during the first mesocratic phase at Neumark-Nord (MNI dead × Birth/Death rate × Correcting factor). Birth/Death rates are taken from Western (1980) and adjusted for the species and their estimated weight at Neumark. The correcting factor expresses the susceptibility for taphonomic destruction per size class and is calculated from ratios of observed and expected carcasses presented by Western (1980). Species represented by size class are listed in table 6.

Weight	MNI dead	Birth/Death rate	Correcting factor	Population (N)	proportion population (N)	kcal × 10^6 per size class (geo. mean)	kcal × 10^6 in stable population	proportion population (kcal)
size 7 (>2,500 kg)	63	8	0.167	968	0.104	3.60	3,484.56	0.696
size 6 (<2,500 kg)	15	9	0.167	228	0.025	1.20	273.55	0.055
size 5 (<1,000 kg)	58	12.5	0.181	919	0.099	0.54	492.96	0.098
size 4 (<600 kg)	62	22.5	0.33	1,586	0.171	0.27	425.47	0.085
size 3 (<300 kg)	36	25	1	2,700	0.291	0.09	238.09	0.048
size 2 (<100 kg)	48	30	2	2,880	0.310	0.03	92.19	0.018
				9,280	1	5.73	5,006.81	1

water holes, Neanderthal hunting, and the actions of other predators, the individual thanatocoenoses during the first mesocratic phase could have formed during much shorter time intervals as expressed by calculations of sedimentation rates of the burying deposits. Apart from the question of the exact temporal frame for a thanatocoenosis – something that we will most probably never achieve in a Palaeolithic context –, the species and individual rich faunal assemblages from the littoral horizons are in concordance with time restricted accumulations of mortality within the biocoenosis during the first mesocratic phase. Thus, estimations of the structure of the living community should at best incorporate all death assemblages of the first mesocratic phase.

The combined thanatocoenosis summarizes the minimal number of individuals (MNI) and energy (kcal) per size class from the NN2/2B and unit 6 from NN1 (**fig. 9**). The record from NN2/1c and NN2/1b are not taken into consideration, because their depositional contexts are still not fully assessed. Most individuals belong to elephant (size class 7) and horse (size class 4) followed by aurochs (size class 5), fallow deer (size class 2), red deer (size class 3) and considerable fewer individuals from rhino (size class 6). Considering biomass, elephants exceeds by far over all other taxa, followed by aurochs, rhino and horse. The deer species contribute only a minor portion to the biomass deposited in the death assemblage.

Neotaphonomic studies in eastern and southern Africa have clearly demonstrated the relationships between living community and death assemblage (Western 1980; Western/Behrensmeyer 2009; Hutson 2012; 2016; Miller et al. 2014). The proportions of individuals per species in a death assemblage are influenced by differences in birth and mortality rates as well as in differences in the susceptibility for taphonomic destruction. Both variables are dependent on body size of a species (Western 1980; Western/Behrensmeyer 2009). In general, species with lower body weight have higher birth rates and vice-versa. In a stable population the birth rate must correspond to the mortality rate. In contrast, bones of larger species are more robust against taphonomic loss than bones of smaller species. Western (1980) provides data on birth rates for different sized mammals and ratios for observed and expected individuals per species in the Amboseli National Park, Kenya. For the neotaphonomic study in Amboseli the living community from which a death assemblage originates is known, while the structure of the biocoenosis during the first mesocratic phase at Neumark can only be derived from the thanatocoenosis alone. But from the data provided by Western (1980) the observed mean birth rates per size class present at Neumark can be used to account for different mortality rates and the mean differences between observed and expected individu-

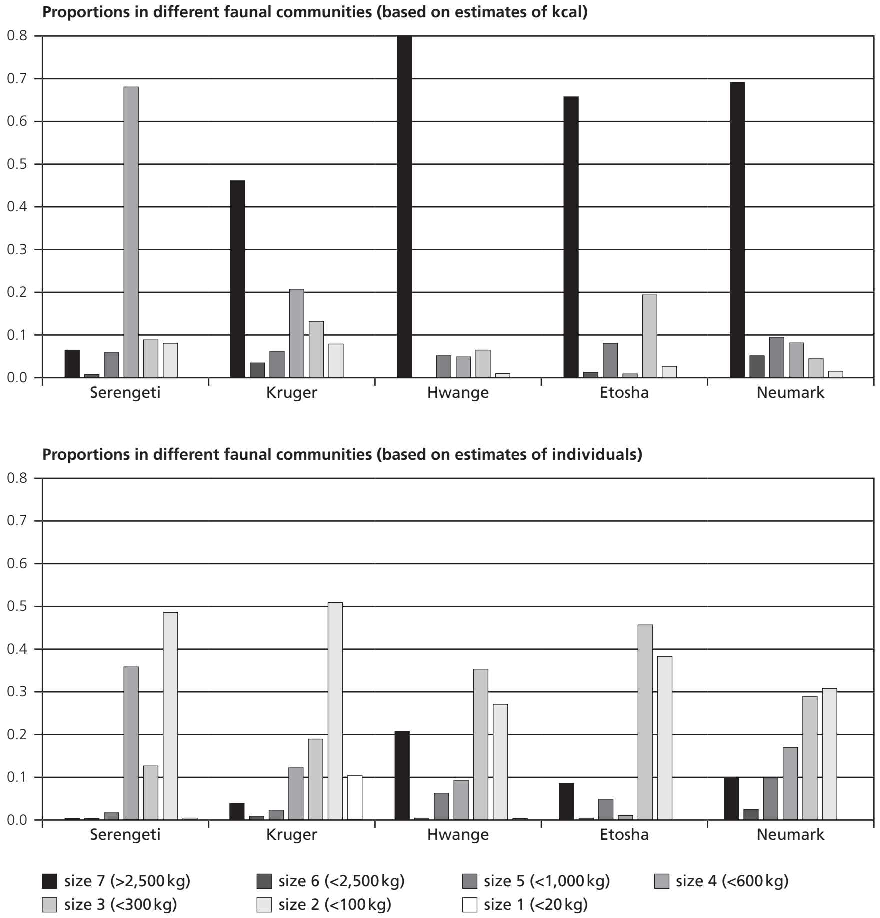

Fig. 10 Proportions of species of different size classes as calculated for the living community of the first mesocratic phase at Neumark compared with census data from African National Parks. Above: proportions based on estimates of calories (kcal). Below: Proportions based on estimates of individuals. – (Sources: Serengeti ecosystem, residential individuals only: TAWIRI 2010; Kruger National Park: SANParks 2012; Hwange National Park: Chamaillé-Jammes et al. 2009; Etosha National Park: Lindique and Lindique 1997).

als per body size class can be used as a correcting factor to account for different survivorship due to taphonomic processes. With these two variables a source population for the thanatocoenosis can be calculated (**tab. 8**). The number of individuals in the calculated source population is not necessary identical to the factual number of individuals in the past living community, because the number of individuals in the death assemblage should in the long run increase in time, although the number of individuals in the living community will remain stable. But the proportions of taxa in the calculated source population should reflect the past community structure more accurately as the proportions of biomass and individuals in the thanatocoenosis. The proportions of body size groups in the reconstructed source population for Neumark are in good agreement with the distribution of taxa in recent African ungulate communities with elephants as the heaviest species (**fig. 10**). In the reconstructed Neumark living population most individuals represent red and fallow deer, followed by horse, elephant, aurochs and finally rhino (**fig. 11**). Elephant is the dominant species in this community, storing approximately 70 % of the biomass, while the other taxa contribute less than 10 % of biomass to the reconstructed living community respectively (**fig. 11**). Mortality at Neumark is not evenly distributed across taxa, when considering their proportions in the death assemblage and their proportions in the reconstructed community. Mortality among the large taxa, elephants, rhino, and aurochs is around 6 %, among the deer less than 2 % and among horses around 4 %. This pattern may be related to different drinking behaviours between the taxa. Elephants, rhino and horses and most likely the aurochs need fresh water. Red and fallow deer can satisfy their water needs by extracting fluids from consumed plants, but at least red deer are known to wallow in water bodies. Thus, differences in mortality between taxa could be related to differences in the spatial diffusion and frequencies of taxa approaching the lake margins and thus different probabilities to die at the spot as well as to prey selection of specific predators, including Neanderthals. It is only during the first mesocratic phase of the Eemian, that carnivore bones contributed to the thanatocoenosis, but there is only ample evidence for butchery by Neanderthals (Gaudzinski-Windheuser et al. 2014). Thus, while the reconstructed source population of the

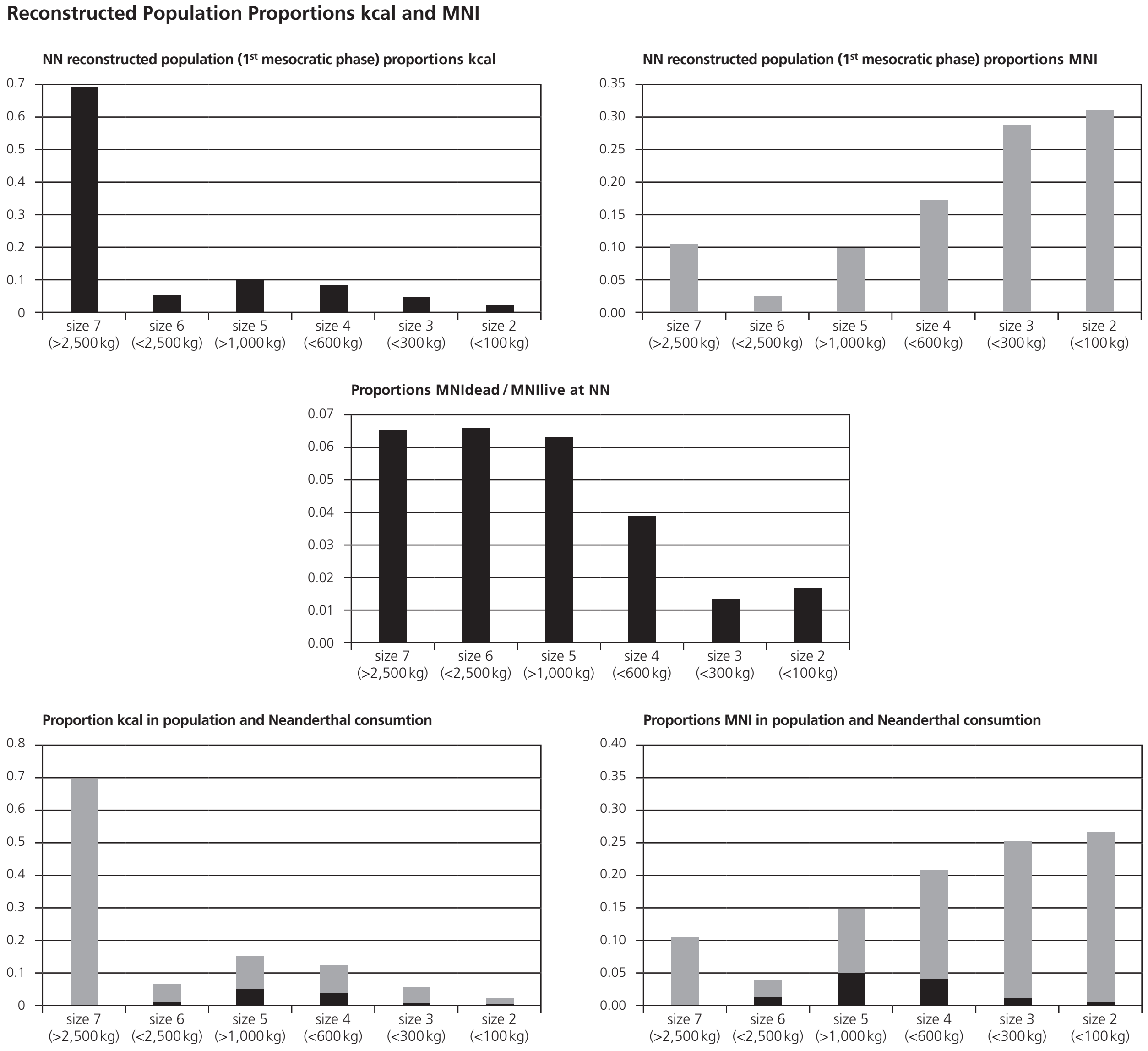

Fig. 11 Top row: Proportions of size classes in the reconstructed living community during the first mesocratic phase of the Eemian at Neumark. Top left: Calories (kcal). Top right: Minimum number of individuals (MNI). Center: Proportion of the observed dead individuals and the calculated living individuals at Neumark. Bottom row: Proportions of taxa consumed by Neanderthals plotted against the proportions of size classes in the reconstructed living population: Bottom left: Calories (kcal). Bottom right: Minimum number of individuals (MNI). Species represented by size class are listed in table 6.

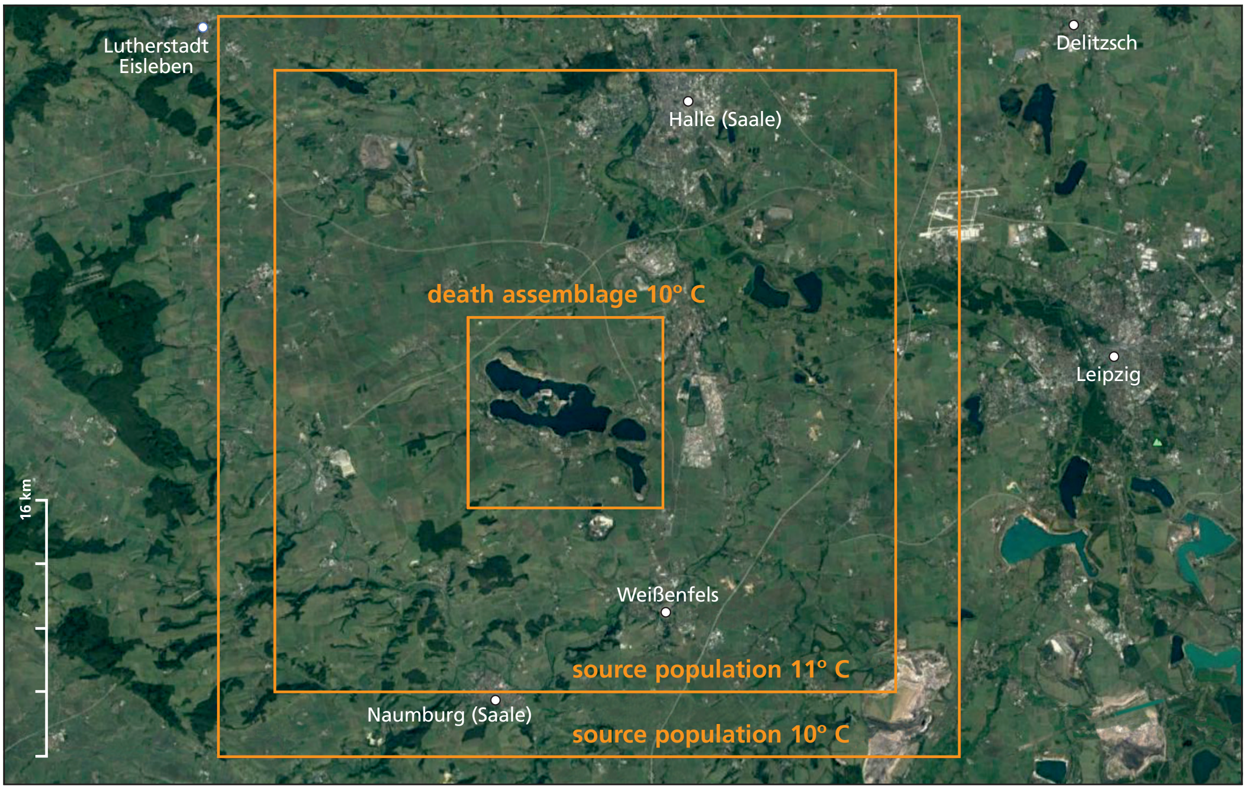

Fig. 12 The region of the Neumark lakeland today, with the Geiseltalsee in the center (snapshot from Google Earth) and the minimal catchment areas of the combined thanatocoenosis of the first mesocratic phase of the Eemian at Neumark and of the reconstructed source population based on the carrying capacity at 10° C and 11° C mean annual temperature.

first mesocratic phase can serve as a frame of reference to highlight subsistence opportunities in terms of ungulate resources, a closer look at the evidence of herbivore exploitation we have so far, can illuminate potential Neanderthal prey selection.

For an estimation of spatial diffusion, the area occupied by the reconstructed source population of the Neumark thanatocoenosis can be calculated by dividing the biomass by the carrying capacity. The results should be considered as the minimum catchment area of the source population and the individuals of the death assemblage (**fig. 12**). Based on CC for 10° C for Neumark the source population must have occupied an area of approx. 2,200 km² and for the combined thanatocoenosis of the first mesocratic phase of the Eemian an area of approx. 130 km² is required. The results illustrate again the high biomass distribution in the surroundings of the Neumark lakeland and point to opportunities for Neanderthals to subsist on a diverse ungulate community rich in individuals on a rather local scale and with low residential mobility.

How Neanderthal worked with these opportunities may become visible by putting the proportions of biomass and individuals in the source population in relation to their proportions in the Neumark thanatocoenosis with traces of human interference, these being the individuals from NN2/2B and individuals from the NN1 thanatocoenosis for which butchery is proposed and those bearing clear cut marks on bones (**tab. 9** and **fig. 11**). Evidence of human interference is lacking for elephants. Nevertheless, the proportions of anthropogenic modification per size class sum up to 12 % of the entire size and biomass of the source population. Anthropogenic modification correlates with biomass and not with the proportions of individuals in the source population. Highest proportions are documented in size class 5 (aurochs) and size class 4 (horse). This focus can be a result of a trade-off between risk, handling costs and return rates. Ungulate species react differently in their behavioural adjustments to hunting and predation risks at water holes (e.g. Valeix et al. 2009a; Crosmary et al. 2012). Permanent Neanderthal presence and intense hunting of a single species at Neumark could have lead ultimately to the species' avoidance of the water bodies. Although a strong focus on prey of 300 to 1,000 kg can be reconstructed for Neanderthals at Neumark, additional harvesting in other size classes could compensate for the risk of chasing away preferred prey from the Neumark lakeland. Thus, the limiting factor influencing Neanderthal occupation of the Neumark lakeland would have been the responses of prey to their presence and hunting pressure. Shifting hunting grounds and habitation areas could have been an additional strategy to avert the risk to deter prey from approaching the Neumark water bodies.

Conclusions and Prospects

The high-resolution palaeoenvironmental archive of the Neumark-Nord lakeland has preserved evidence of Neanderthal presence during all Eemian substages. In the first instance the "quality" of the archaeological record can be related to the specific taphonomical conditions of the depositional environments. Nevertheless, changes in structure and composition of vegetation and with that faunal communities during the Eemian may have affected Neanderthal land-use, mobility and subsistence, which must be considered when analysing patterns in the archaeological record.

The record from Neumark-Nord gives a rare opportunity to integrate ecological factors from the faunal evidence, when reconstructing Neanderthal subsistence strategies during the Eemian interglacial. Calculations of carrying capacities demonstrate high ungulate biomass production limited by mean annual temperatures during the Eemian. Species richness and niche partitioning between taxa observed during the first mesocratic phase at Neumark is a direct outcome linked to high primary production. During this phase large mammal community structure was most probably analogous to recent African faunas rich in or dominated by elephants, i.e. taxa with high body weight contribute most of the biomass and taxa with low body weight contribute more individuals to the community. Species richness, the distribution of biomass and individuals in the community gives a wide array of subsistence opportunities. In this context, the current zooarchaeological data from the first mesocratic phase shows a clear focus on aurochs, horse and large cervids, subsidized in descending order by rhino, size class 3 cervids, and size class 2 cervids. Subsistence on ungulates is biomass oriented and to a lesser degree determined by the abundance of individual taxa in the community. Trade offs between risk, handling cost and return rates are certainly major variables influencing this subsistence strategy and prey choice. Putting the number and biomass of ungulate individuals in a spatial context it becomes apparent, that Neanderthals in the Neumark area could subsist on a local scale, i.e. with a low residential mobility, with the presence of waterholes attracting animals and guaranteeing an almost continuous presence of prey.

Currently, we can qualify aspects of subsistence just for the archaeological record of NN2/2B. Narrowing down the temporal resolution of the archaeological levels is fundamental for a detailed assessment. For the littoral zones at NN1 and NN2 during

Tab. 9 Minimal number of individuals (MNI) and calories (kcal) per size class with evident modifications from butchery in the combined thanatocoenosis of the first mesocratic phase of the Eemian and their proportions in the reconstructed source population.

Neanderthal consumption: first mesocratic phase/size class	MNI	kcal × 10^6	proportion in source population
size 7 (>2,500 kg)	0	0.00	0.000
size 6 (<2,500 kg)	3	3.60	0.013
size 5 (<1,000 kg)	46	24.69	0.050
size 4 (<600 kg)	62	16.64	0.039
size 3 (<300 kg)	30	2.65	0.011
size 2 (<100 kg)	20	0.64	0.007
sum	**161**	**48.21**	**0.120**

the first mesocratic phase accumulation within few centuries are reconstructed. Biomass and energy values contribute to a better understanding of the duration of occupation. The fauna from NN2/2B is rich in species and individuals. The respective data derived from the MNI and biomass indicate a much shorter "chronology of occupation(s)" during which a larger group of Neanderthals could have been supplied. Qualifying the origin of NN1 can expand our knowledge. Here, the composition of the thanatocoenoses from the so-called butchery areas and the causes of death for the skeleton thanatocoenosis are of major interest. The differences are striking. Due to the preservation of (partly) complete skeletons elephants are dominating in the first mesocratic phase, but are, at the current state of knowledge, almost absent from the butchery areas. In contrast, not a single horse is among these skeletons, but horse constitute most of the MNI from NN2/2B. Independent from the causes of death, one must ask, why these skeletons haven't been scavenged and dismembered by humans and carnivores, beside a few cut and gnaw marks. Carnivores were present in the Neumark lakeland and were also exploited at NN2/2B, but it has to be established, which role carnivores played in the Neumark faunal community. It is unclear in which ungulate size classes the different predators mainly operated and how this interrelates with Neanderthal subsistence and prey selection. At present, it seems that the whole lakeland was under "Neanderthal control" during the first mesocratic phase. Prudence must be exercised, when comparing the records from different Eemian substages at Neumark-Nord, especially with the record from the second mesocratic phase rich in cervid skeletons. Although some aspects of the thanatocoenoses share similar general taphonomical patterns, species diversity is considerably lower and the number of individuals per species different in the second mesocratic phase, specifically the high numbers of fallow deer. With changes in vegetation during both phases, and potentially denser forest canopy cover in the second mesocratic phase, the structure of the living ungulate community must have also changed and thus, the source population for both thanatocoenoses might be quite different. Against this background, we also have to assume shifts in Neanderthal subsistence in response to environmental change.

Nevertheless, in a broader perspective the record from Neumark-Nord reveals new aspects of Neanderthal subsistence and challenges concepts of Neanderthal adaptations in forested environments in North and Central Europe (e.g. summarised in Gaudzinski-Windheuser / Roebroeks 2011). Compared to well-known Neanderthal subsistence habits on the North European Plain during cool and cool-temperate climatic conditions, we may conclude that during interglacials Neanderthals still focussed on the exploitation of large mammal resources, but strategies of land-use and the patterns of settlement have differed. When temperature and precipitation is the crucial variable for ungulate biomass production, at least for the early part of the Eemian, with alternating patches of vegetation openness, we can conclude higher ungulate biomass compared to cool- and cool-temperate climate phases. Thus, prey is more abundant, less dispersed in the landscape and migration distances are shorter. Neanderthals could subsist on a more local basis, indicated e.g. by the catchment area of the ungulate population during the first mesocratic phase of the Eemian at Neumark. Following standard models of predator-prey relationships (e.g. Begon / Mortimer / Thompson 1996), higher production in prey biomass might also affect Neanderthal populations, causing them to increase at a local scale.

The vast and almost inexhaustible paleoenvironmental and archaeological record from Neumark-Nord teaches us that analysing Neanderthal subsistence strategies must be framed in the habitat, in which subsistence was exercised. Carrying capacities, calculations of biomass and calorie values are good auxiliary proxies to build bridges between thanatocoenoses and biocoenoses. When we succeed in placing Neanderthals in different and changing past living communities, we will reach a new level of detail and accuracy in the reconstruction of their subsistence, ecological tolerance and variability at Neumark and elsewhere in the Neanderthal world.

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