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ANTHROPOLOGY

Large-scale processing of within-bone nutrients by Neanderthals, 125,000 years ago

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Diet played a key role in human evolution, making the study of past diet and subsistence strategies a crucial research topic within paleoanthropology. Lipids are a crucial resource for hunter-gatherers, especially for foragers whose diet is based heavily on animal foods. Recent foragers have expended substantial amounts of energy to obtain this resource, including time-consuming production of bone grease, a resource intensification practice thus far only documented for Upper Paleolithic populations. We present archaeological data from the lake landscape of Neumark-Nord (Germany), where Last Interglacial Neanderthals processed at least 172 large mammals at a water's edge site. Their (partial) carcasses were transported to this location for the extraction of within-bone nutrients, particularly bone grease. This "fat factory" constitutes a well-documented case of grease rendering predating the Upper Paleolithic, with the special task location devoted to extraction of nutritionally important lipids forming an important addition to our knowledge of Neanderthal adaptations.

INTRODUCTION

Diet played a key role in the development and expansion of the human niche, and studying past strategies to obtain proteins, lipids, and carbohydrates, as well as the relative importance of these macronutrients through time, constitutes important research topics in human evolutionary studies (*1*, *2*). Here, we present data on food processing by Last Interglacial Neanderthals, which show that these hunter-gatherers, similar to recent foragers, already focused heavily on the exploitation of within-bone nutrients—and particularly on bone grease—125,000 years ago.

Fat, especially within-bone lipids, is a crucial resource for hunter-gatherers in most environments, becoming increasingly vital among foragers whose diet is based heavily on animal foods, whether seasonally or throughout the year (*3*, *4*). When subsisting largely on animal foods, a forager's total daily protein intake is limited to not more than about 5 g/kg of body weight by the capacity of liver enzymes to deaminize the protein and excrete the excess nitrogen (*4*–*6*). For hunter-gatherers (including Neanderthals), with body weights typically falling between 50 and 80 kg (*7*, *8*), the upper dietary protein limit is about 300 g/day or just 1200 kcal, a food intake far short of a forager's daily energy needs. The remaining calories must come from a nonprotein source, either fat or carbohydrate (*4*, *9*). Sustained protein intakes above ~300 g can lead to a debilitating, even lethal, condition known to early explorers as "rabbit starvation." For mobile foragers, obtaining fat can become a life-sustaining necessity during periods when carbohydrates are scarce or unavailable, such as during the winter and spring.

There is very little fat in most ungulate muscle tissues, especially the "steaks" and "roasts" of the thighs and shoulders, regardless of season, or an animal's age, sex, or reproductive state (*6*). Mid- and northern-latitude foragers commonly fed these meat cuts to their dogs or abandoned them at the kill (*10*). The most critical fat deposits are concentrated in the brain, tongue, brisket, and rib cage; in the adipose tissue; around the intestines and internal organs; in the marrow; and in the cancellous (spongy) tissue of the bones (i.e., bone grease). With the notable exception of the brain, tongue, and very likely the cancellous tissue of bones, the other fat deposits often become mobilized and depleted when an animal is undernourished, pregnant, nursing, or in rut (*11*).

Exploitation of fat-rich marrow from the hollow cavities of skeletal elements, especially the long bones, is fairly easy and well documented in the archaeological record of Neanderthals [e.g., (*12*–*14*)]. On the basis of ethnohistoric accounts, as well as on experimental studies, the production of bone grease, an activity commonly carried out by women, requires considerable time, effort, and fuel (*15*–*19*). Bones, especially long-bone epiphyses (joints) and vertebrae, are broken into small fragments with a stone hammer and then boiled for several hours to extract the grease, which floats to the surface and is skimmed off upon cooling. For foragers heavily dependent on animal foods, bone grease provides a calorie-dense nonprotein food source that can play a critical role in staving off rabbit starvation (*11*).

The time depth of this practice is unclear. Presently, it has been documented as far back as 28,000 years ago (*20*), although it may well have a much deeper antiquity, extending into the Middle Pleistocene (*21*). Grease extraction has been suggested for various Middle Paleolithic faunal assemblages, such as Roc de Marsal, Les Pradelles, and Grotte du Noisetier in France. As shown by Morin (*3*), at these sites, a clear-cut interpretation is problematic because of equifinality issues, and convincing evidence from the Lower and Middle Paleolithic has yet to be published (*3*, *21*). Grease rendering is not easy to identify in the archaeological record. While it is sometimes possible to identify physicochemical alteration of bone tissue as a result of low-temperature cooking, diagenesis during long-term burial of bones can also mimic these modifications (*22*). Furthermore, grease

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rendering's most obvious characteristic—a high degree of cancellous bone fragmentation—can also result from a variety of postdepositional processes overprinting a faunal assemblage, hindering a clear-cut identification of the cause(s) of fragmentation (*3*, *21*, *23*).

Here, we present data from the Last Interglacial lake landscape of Neumark-Nord (Germany) (*24*, *25*). In this area, Neanderthals practiced bulk harvesting of a wide range of animal resources including forest elephants, the largest terrestrial mammals of the Pleistocene (*26*). Here, we focus on one of the richest locales, Neumark-Nord 2/2 (NN2/2). We present data showing that body parts from a minimum of 172 large mammals (mainly bovids, horses, and deer) were brought to NN2/2 for intensive lipid processing, an activity that took place over a comparatively short period within a very small water-edge location. This processing entailed marrow extraction, as well as the creation of tens of thousands of small bone fragments for the production of grease. This represents a well-documented case of this resource intensification practice predating the Upper Paleolithic and an important addition to the behavioral repertoire of Neanderthals.

Below, we situate these data within the broader record of Neanderthal subsistence activities in the Last Interglacial lake landscape of Neumark-Nord, where long-term and large-scale fieldwork over an area of about 30 ha has enabled us to create a "snapshot" of Neanderthal hunting and processing activities. Last, we contextualize the high-resolution evidence from this one locality with data on subsistence activities in the wider Neumark-Nord lake landscape, and we discuss the wider implications of this study for our understanding of Neanderthal subsistence strategies.

Neumark-Nord is located in eastern Germany, ~10 km south of the city of Halle, in an area that was covered by the Saalian glaciers during Marine Isotope Stage (MIS) 6 but out of reach of the subsequent (Weichselian) glaciation (Fig. 1). The area's location between the maximum extensions of the MIS 6 and MIS 2 glaciers is relevant for understanding the quality and quantity of well-preserved Last Interglacial basin sequences in this part of Europe. These sites developed within sediment-receiving structures created by a range of glacial and postglacial processes and exposed through quarrying. These basins have provided a rich paleoenvironmental record for the Last Interglacial (or Eemian), a warm-temperate period from which we have relatively few exposures elsewhere in Europe.

The basins NN1 and NN2 were found in the open cast (Tertiary) lignite mine of Mücheln (51°19′28″N, 11°53′56″E). From 1985 onward, the archaeologist Mania and his research group (*24*, *27*–*29*) investigated the large NN1 lake basin in a series of rescue interventions, until the end of the lignite mining activities in the mid-1990s. Mania also found the small basin NN2, about 100 m northeast of NN1, investigated by the current authors from 2004 to 2008.

Lake basin NN1 covered an area of about 24 ha, while NN2 represents what remains of a smaller and shallow water body, about 1.6 ha in documented size (Fig. 2). The infills of both basins cover the complete Last Interglacial, the duration of which has been calculated to be about 11,000 years for northern/central Europe (*30*) [but see (*31*)]. This has been further subdivided into distinct Pollen Assemblage Zones (PAZs), which reflect its characteristic vegetation succession (*30*, *32*). On the basis of stratigraphic and geochronological position, paleobotanical data, and alternating lake transgressions and regressions during the individual PAZs, the find bearing deposits of both basins can be correlated in high spatial and temporal resolution (*33*–*35*).

Hominins left abundant traces of their presence in this lake-dotted landscape, especially in the early parts of the Last Interglacial, i.e., during PAZ III and PAZ IV, with a total duration of ~2850 years. During this period, the vegetation surrounding the water bodies was largely open (*36*). Winter temperatures were roughly similar to those historically documented, as suggested by a study (*37*) of the rich plant record from the sites (average coldest month of −2° to 0°C, currently −1° to 0°C). Summer temperatures reached higher values, with the average for the warmest month (July) estimated to

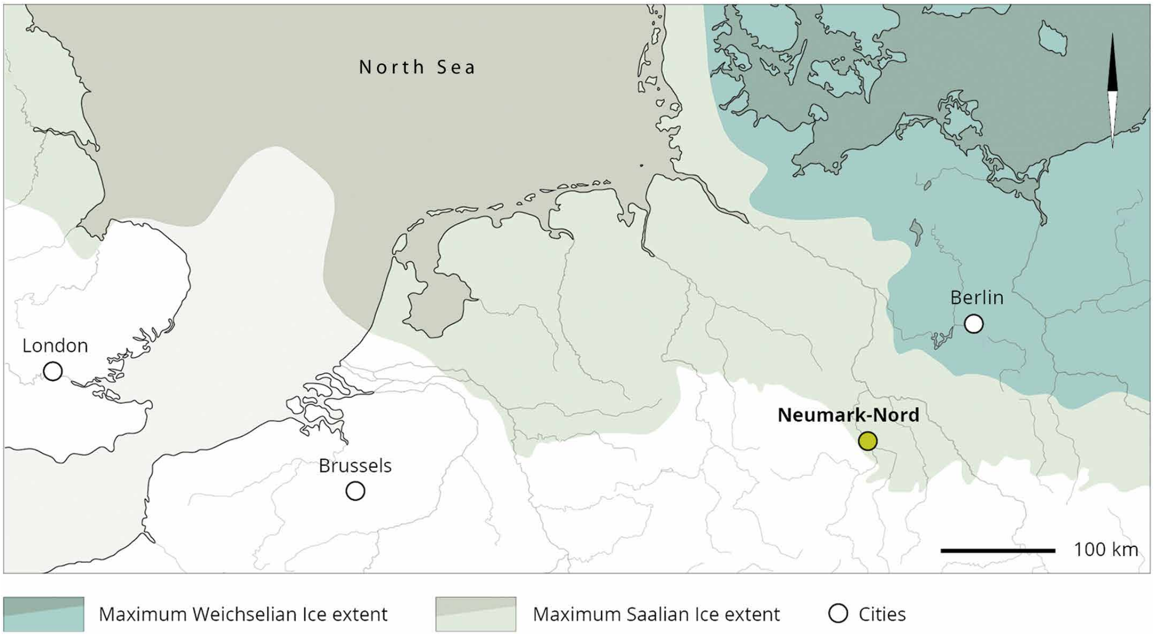


Fig. 1. Location of Neumark-Nord (Germany). The site's position is depicted relative to the maximum extent of the Saalian and Weichselian glaciations.

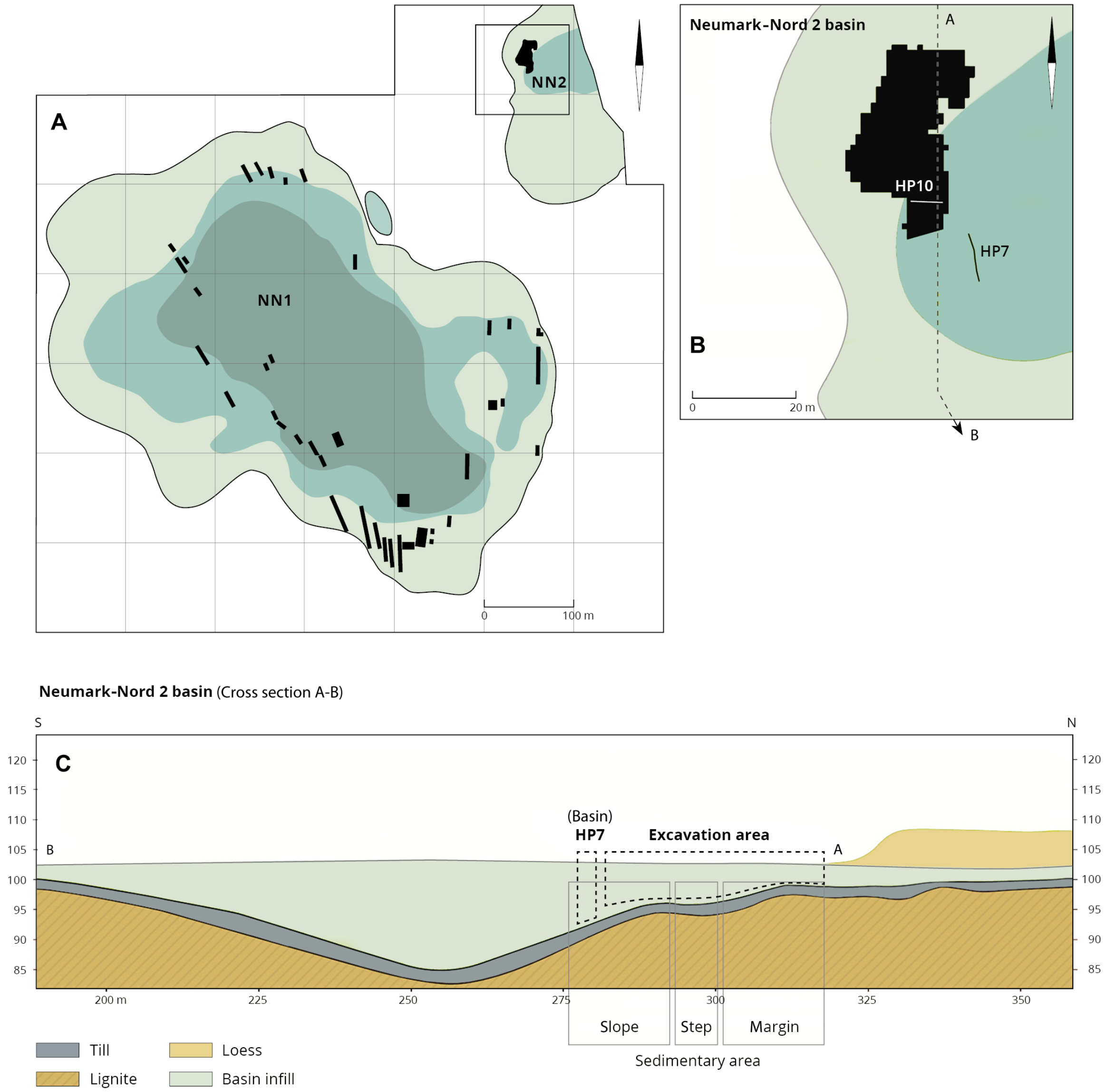


Fig. 2. The NN1 and NN2 basins. Topographic map of the NN1 basin (**A**) and the small NN2 basin (**B**), with indicated the locations of the NN1 archaeological rescue interventions (black rectangles) and the position of the NN2 excavated area (in black). On the basis of (*35*), with data derived from figure 38 of (*24*) and (*29*). A N-S cross-section through the NN2 basin is shown in (**C**) [modified from (*41*)], the basin infill situated between the basal Saalian till deposits and the overlying Weichselian loess.

have been +19° to +25°C compared to +17.5°C for recent values. Traces of a more ephemeral hominin presence in this lake landscape date to the *Carpinus* (hornbeam) phase (PAZ V), characterized here by a closed-canopy forest vegetation.

Apart from isolated bones and lithics scattered throughout the interglacial sequence, three main find contexts characterize the paleontological and archaeological record of the Eemian here: (i) in the lake margins of the two basins, high-density concentrations of flint artifacts and highly fragmented bones; (ii) in the extensive littoral zones of NN1, at some distance from the lake proper, partly articulated and disarticulated bones from individual large mammal skeletons, not always associated with lithics, distributed over small areas (these include the recently published *Palaeoloxodon antiquus* finds from Neumark Nord 1 (*26*); (iii) in gyttja deposits in the central part of NN1 basin, articulated skeletons, partially preserved skeletons of single individuals, and skeletal remains from multiple individuals, mostly of *Dama dama*, some with cut marks and hunting lesions (*38*).

At NN2, find level NN2/2B yielded a high-density flint and bone concentration—the focus of this contribution—that formed along the northern margin of the water body. It contained 16,524 flint artifacts, ~98% of these consisting of small (<50 mm) debitage from on-site knapping of flint nodules sourced from the local glacial deposits, with a total weight of 44.4 kg (*39*). Larger flakes were retouched into simple scrapers and/or denticulates. The site also yielded an exceptional series of manuports, elements of a percussive toolkit with anvils and hammerstones, including pieces up to 2.2 kg in weight (*40*) (see the Supplementary Materials for details on the lithic assemblage). Alongside evidence for Neanderthal knapping activities at NN2/2/B, 118,774 heavily fragmented and cut marked faunal remains were recovered, representing a minimum number of 172 large mammals, including horses [minimum number of individuals (MNI) = 56], bovids (MNI = 45), and cervids (MNI = 54).

Elsewhere, we have published detailed overviews of the NN2 sedimentary infill, based on a series of multidisciplinary studies of the location (*25*, *41*), and limit ourselves here to the general picture. The basin formed through the intrusion of Tertiary brown coal deposits, lignite, into the overlying Quaternary sediments. This created an undulating surface containing many depressions in the area such as NN2, which functioned as a sediment trap during the Last Interglacial. In contrast to the meters-deep NN1 lake, the NN2 basin was mostly a small pond with varying water tables, up to about 1 m in depth. Continuous subsidence and concomitant infilling kept the basin in its bowl-like shape for the major part of the Eemian.

The artifact-bearing deposits, situated in lithological unit 8, were documented in a number of sections throughout the 2004–2008 excavations. A key section here is Hauptprofil 7 (HP7), exposing the deepest part of the infill (Fig. 2). This section was sampled for a range of dating and paleoenvironmental analyses and for sedimentological and soil-micromorphological studies, while a set of high-resolution paleomagnetic samples was also acquired [see (*25*)]. All samples were collected from the very same part of the HP7 section, enabling a direct comparison of results on a 5-cm stratigraphic sampling interval over the entire sequence. All data indicate a geologically rapid infilling of the shallow basin, with sedimentation an almost continuous process, without pronounced soil formation in periods of nondeposition (*42*). Calcareous silt loams were deposited by overland flow, mainly by after flow, in a very calm sedimentary setting in placid water, with only short interruptions during which the depression fell dry. This low-energy sedimentation did not cause any discernible lateral movement of the archaeological material (*43*, *44*). The main find level (NN2/2B) was excavated over an area of 491 m^2. Along the basin's northern margin, this unit is only 20 cm thick, but it increases in thickness and complexity toward the center, where it develops into several, partly laminated, substrata with a total thickness of up to 1 m.

The rich NN2/2B assemblage accumulated over a short period. Pollen analysis (*33*) allowed us to situate unit 8 in the *Corylus* zone IVa2 of the Eemian (*41*), with an estimated duration of 1200 years (*32*). In HP7, this PAZ zone is recorded in deposits with a thickness of 130 cm, indicating a sedimentation rate of 0.11 cm/year (*41*). Assuming constant sedimentation during pollen zone IVa, we can calculate that unit 8 and its associated archaeology accumulated within a maximum period of between 288 (*34*) and 455 years (*33*), a high temporal resolution for a Pleistocene archaeological context of that age. Since some large, well-preserved faunal elements such as a complete bovid skull were recovered encased in ~60 cm of finely laminated sediments (see Supplementary Text), sedimentation rates occasionally must have been substantially higher than the estimate mentioned above.

Most archaeological finds were uncovered along the rim of the basin and from an adjacent step in the basin's slope [see Fig. 2 and (*35*)]. The excavation proceeded over a length of 30 m from the northern margin to the central part of the basin in the south (Fig. 2). Along its northern margin, the find-bearing unit consists of a fine-grained sandy silt layer of 10 to 20 cm in thickness. From here, unit 8 proceeds downslope toward the basin center, where the layer dissolves shortly behind our main sampling profile HP7. Between the edge of the water body and the center, the basin morphology contains a step. In this area, sediment thickness increases up to 1 m of sandy silts and silts. More than two-thirds of all the finds recovered during excavation were recorded in this ~15 m–by–5 m large "step area."

In this area, the excavations documented very dense clusters of bone fragments, flint artifacts, and manuports, sometimes more than 1000 single finds/m^2. Studies of the horizontal distribution of the finds, together with some lithic and bone refits and an absence of any substantial lateral movement, strongly suggest that we are dealing with a distribution of archaeological material in primary context, formed in a low-energy sedimentary setting, with no displacement due to hydrodynamic sorting (*43*, *44*). Many of these finds, bone fragments, flint artifacts, and pebbles, formed several notably dense semicircular concentrations with diameters of 40–80 cm within this step area (Fig. 3).

RESULTS

Assemblage composition, fragmentation, preservation, and taxonomy

During excavation, 19,650 of the total of 118,774 faunal remains were recorded in three dimensions. Most of the faunal material was obtained through dry and wet sieving of the find bearing sediments. This guaranteed the recovery of most, if not all, faunal remains initially deposited, resulting in a faunal assemblage minimally biased by excavation methodology and recovery. The ratio of 1:6 between three-dimensionally recorded finds and those retrieved by sieving already illustrates the degree of fragmentation of the material. Two-thirds of the bone material stems from a small part of the step area at the northern edge of the basin, with dense semicircular find concentrations (see Fig. 3).

Measurements of 26,003 bone specimens show that two-thirds is smaller than 3 cm in maximum dimension (n = 18,171) and almost half of the material is smaller than 2 cm (n = 11,553) (figs. S1 and S2). This sample comprises 5884 long bones, 1645 cranial elements—predominantly teeth (fragments)—3815 flat bones, and 670 short bones. The bulk of the remaining 13,989 unidentifiable bones constitutes the small fraction of the assemblage. Most of these specimens show a thin compacta with spongy structure inside and derive from cancellous bone portions, the epiphysis, proximal and distal shaft portions of long bones, parts of the skull and mandibles, all axial and thoracic bones, and elements of the foot. Consequently, only a small number of bone remains (n = 8850) could be identified to a specific taxon and bone element, representing only 7% of the entire NN2/2B faunal assemblage. The identified taxa represent almost the entire Eemian large mammal community known from the North European Plain [see (*45*)].

Most of the specimens can only be attributed to body size classes through the robustness of the compact bone. For subdividing the different cervid taxa, we defined special size classes, which lump taxa that may overlap in bone size and thickness of the compact bone (table S1).

A minimum number of 172 individuals was calculated, in which horses (MNI = 56), large bovids (MNI = 45)—all diagnostic bones representing *Bos primigenius*—and red deer–sized cervids (MNI = 26) dominate (see Table 1). Bones of all taxa display traces of human modification (see below and table S2).

Analysis of breakage patterns [see (*46*)] of 8675 long bone fragments reveals predominantly that bone fragmentation occurred when specimens were fresh, resulting in a low fracture freshness index score

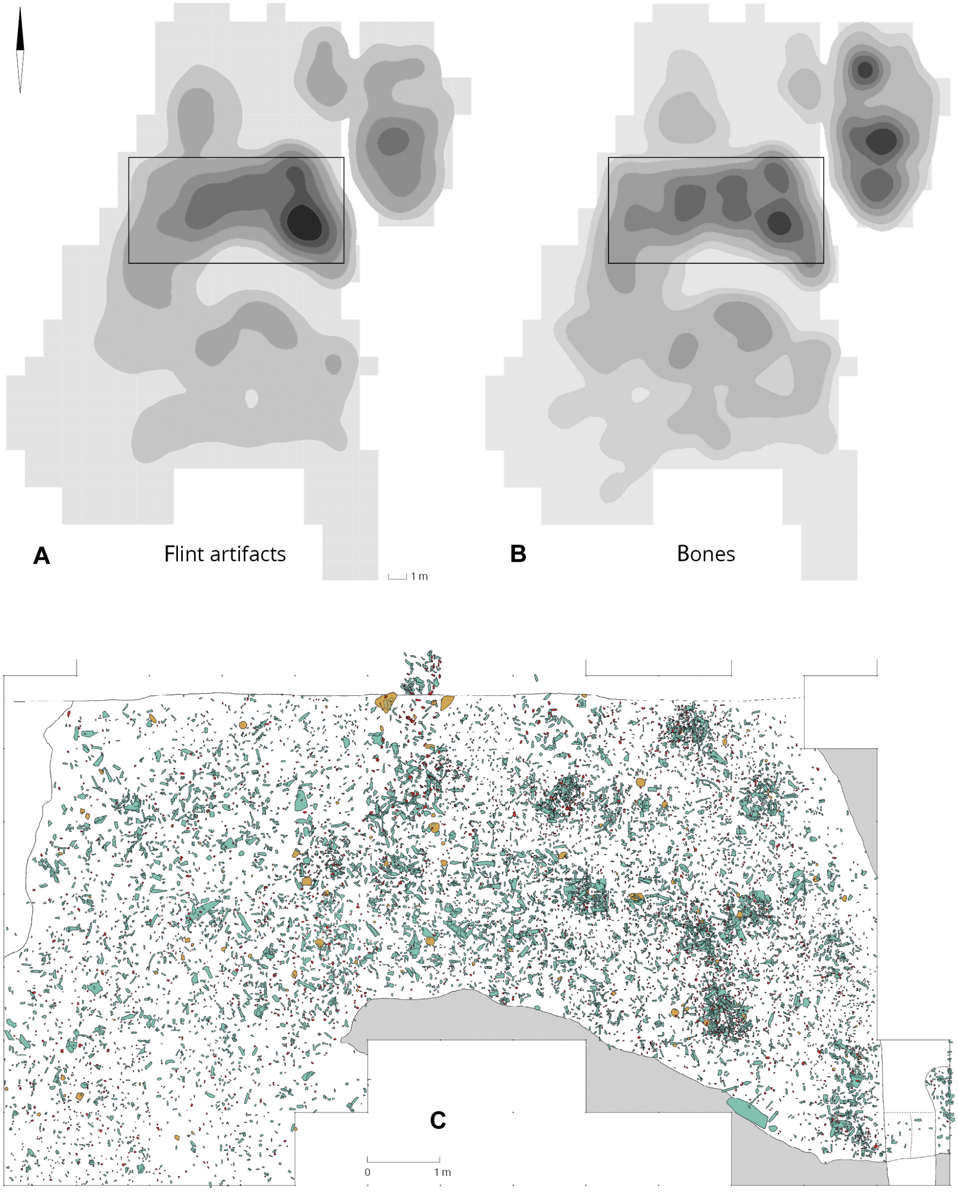


Fig. 3. Spatial distribution of lithics and faunal remains. (**A**) Interpolated density map of the NN2/2B flint artifacts (n = 16,524). (**B**) Interpolated density map of the NN2/2B faunal remains (n = 118,774). (**C**) Magnified plan of the step area with all three-dimensionally recorded bone, lithic, and manuport specimens (bone, light blue; lithic, dark blue; manuport, orange).

(*47*) of 1.02 (table S3). The high fragmentation of the bone assemblage already occurred in a very early phase of the biostratinomic chain, with some additional overprinting when bones were still fresh and, again to a lesser degree, when bones had dried out (table S4). Thus, the high fragmentation of the bones was mostly related to predepositional rather than postdepositional processes.

Covering of the bones by sediments must have been quick, as indicated by the excellent preservation of bone surfaces and an almost uniform absence of advanced stages of climate-induced weathering throughout the site. Most of the bone surfaces display only signs of a very initial stage of weathering, if any at all (see fig. S3 and tables S5 and S6). Some bones show minor traces of bone surface abrasion, a phenomenon that occurs more often in the northern ("margin") part of the excavation, where the find-bearing sediment layer is thin; abrasion is almost completely absent in the area of the step (fig. S3). This abrasion of bone surfaces can result from movement of bones in contact with sediment particles, e.g., by trampling. The margin might have been an area of more intense animal (including human) traffic and movement, while, alternatively, the bones may simply have suffered more from trampling because of a thinner and somewhat more coarse-grained sediment cover. In sum, as with fragmentation, weathering and abrasion indicate a short pre- and syndepositional phase that shaped the assemblage condition before the bones became submerged and covered by protective sediment.

Table 1. List of taxonomically identified specimens in the NN2/2B assemblage. For each taxon, number of identified specimens (NISP) and MNI are provided, as well as the corresponding percentages.

Taxon	NISP	MNI	NISP (%)	MNI (%)
Panthera leo	3	1	0.03	0.58
Large felid (cf. *Panthera* sp.)	1	1	0.01	0.58
Ursus sp.	44	8	0.50	4.65
Canis lupus	14	1	0.16	0.58
Vulpes vulpes	3	1	0.03	0.58
P. antiquus	23	2	0.26	1.16
Stephanorhinus sp.	34	2	0.38	1.16
Sus scrofa	7	1	0.08	0.58
Equus sp.	2824	56	31.91	32.56
B. primigenius	3233	45	36.53	26.16
Cervid (total)	2664	54	30.10	31.40
Cervid (detail)				
Capreolus size	19	2	0.71	3.70
Capreolus-Dama size	51	3	1.91	5.56
Dama size	312	6	11.71	11.11
Dama-Cervus size	732	9	27.48	16.67
Cervus size	1386	26	52.03	48.15
Cervus-Alces-Megaloceros size	130	3	4.88	5.56
Alces-Megaloceros size	27	5	1.01	9.26
Cervid indet.	7		0.26	
Total	**8850**	**172**	**100**	**100**

Skeletal element representation and indices

The high degree of bone assemblage fragmentation prevents the clear-cut identification of skeletal elements and taxa and even limits the attribution of bone fragments to body size classes and general bone type. Only about 7.5% of the fauna (8850 of the total 118,779) can be attributed to a specific taxon or taxonomic group and skeletal element. Skeletal representation is established for the most abundant taxa [in respect to number of identified specimens (NISP) per taxon and to MNI]: horse (*Equus* sp.), large bovid (cf. *B. primigenius*), the group of smaller cervids (*Capreolus-Dama-Cervus* size group), and larger cervids (*Cervus-Alces-Megaloceros* size group) (tables S7 to S10, respectively). NISP, minimum number of elements (MNE), MNI, and minimum number of animal units (MAU) are unevenly distributed among the different elements. While cranial portions (isolated teeth, skull, and mandible) and long bones are abundant, axial/thoracic elements and foot bones (carpals/tarsals and phalanges, except metapodials) are more rare. Rib fragments are plentiful but represent only a few individuals: Rib and vertebrae fragments, as well as pelvic elements and scapula-blade fragments, form a considerable part of the identifiable bones, but their numbers are far smaller than one would expect had complete carcasses been deposited at the site. For *Equus* sp. and *B. primigenius*, on average, an NISP of 4.5 is needed to account for one bone element; in the larger and smaller cervids, it is 2.7 and 2.9, respectively. The skeleton of these four taxa consists of about 230 bones (± depending on the definition and separation of bones). With these numbers, the individuals of these four taxa, if complete, would already contribute 138,989 bones to the assemblage. In addition, carpals and phalanges are relatively easy to identify and, if once present, should occur in higher numbers, even in this fractured assemblage. In sum, bone elements with high values of within-bone nutrients, such as long bones, mandibles, and crania, occur in high numbers. Body parts with a relatively high amount of meat around the bones, such as the vertebral column and rib cage, are less frequent—possibly well hidden among the unidentified fragments—and low-nutrient parts, such as foot bones, are underrepresented (Fig. 4).

Correlations with utility indices help illuminate the taphonomic processes and human agency that shaped skeletal element representation [see, e.g., (*12*, *48*)]. For all four taxa, we tested indices related to bone mineral density, overall food utility index (FUI; as a proxy for meat), marrow content, and unsaturated marrow index (UMI) (see the "Zooarchaeology - Faunal Assemblage and Analyses" section in Supplementary Text for details and figs. S22 to S33 for results). Correlations were (highly) significant for bone mineral density, marrow, and UMI ($P < 0.001$), except for horse marrow ($P = 0.02$), and marrow from large cervids ($P = 0.002$) but insignificant for meat (P values between 0.17 and 0.97). However, only ~20% of skeletal element survivorship can be explained by differences in structural density ($r^2 = 0.16$ to 0.22 across the four taxa; mean = 0.1875). In contrast, correlation with the marrow index was notably stronger ($r^2 = 0.54$ to 0.75; mean = 0.625). The UMI showed the highest explanatory power, accounting for over 80% of skeletal element representation ($r^2 = 0.78$ to 0.87; mean = 0.825). These strong, significant correlations support the interpretation of selective transport of marrow-rich bones to the site. However, such a selection may mimic a bone density–dependent preservation pattern (*12*, *49*).

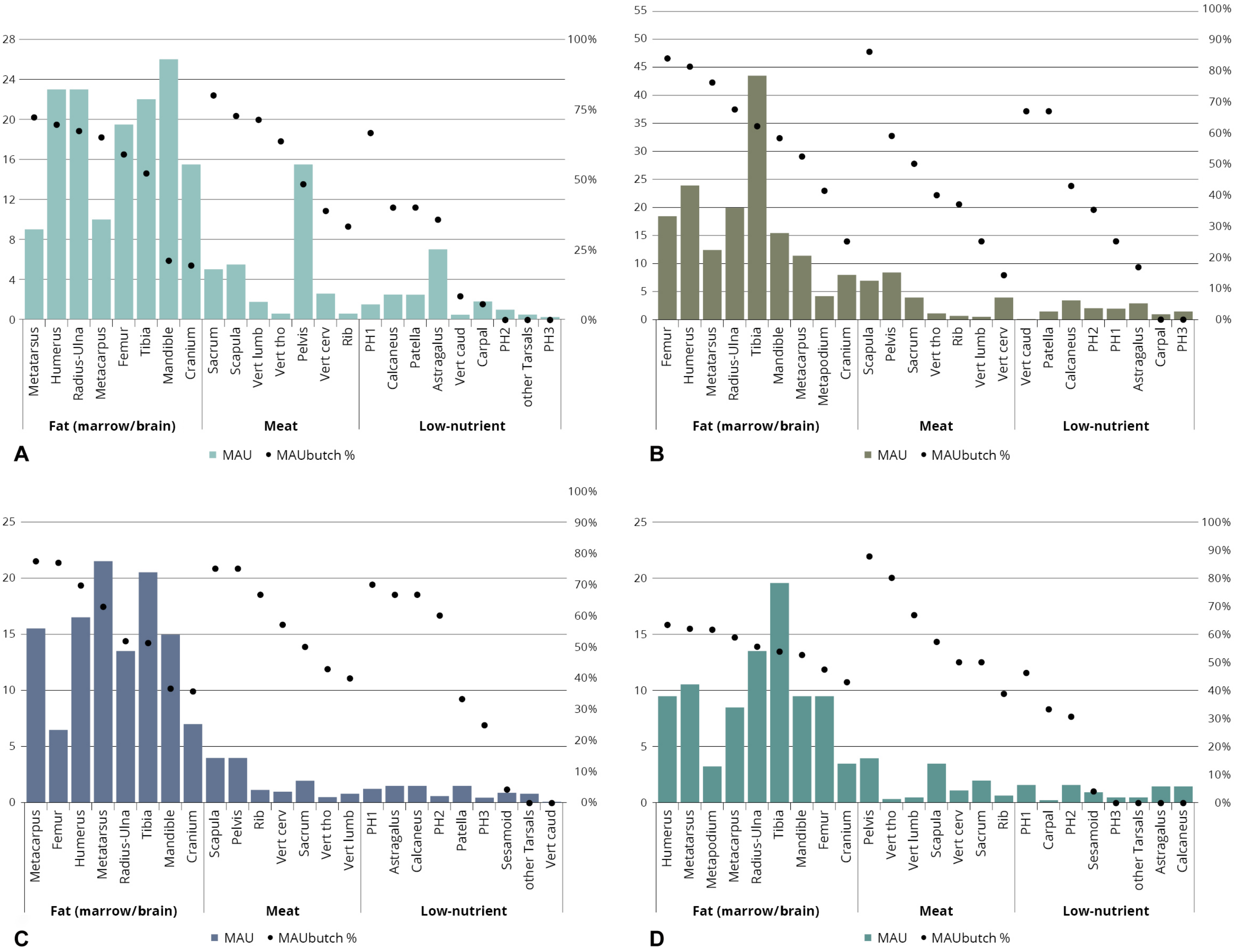
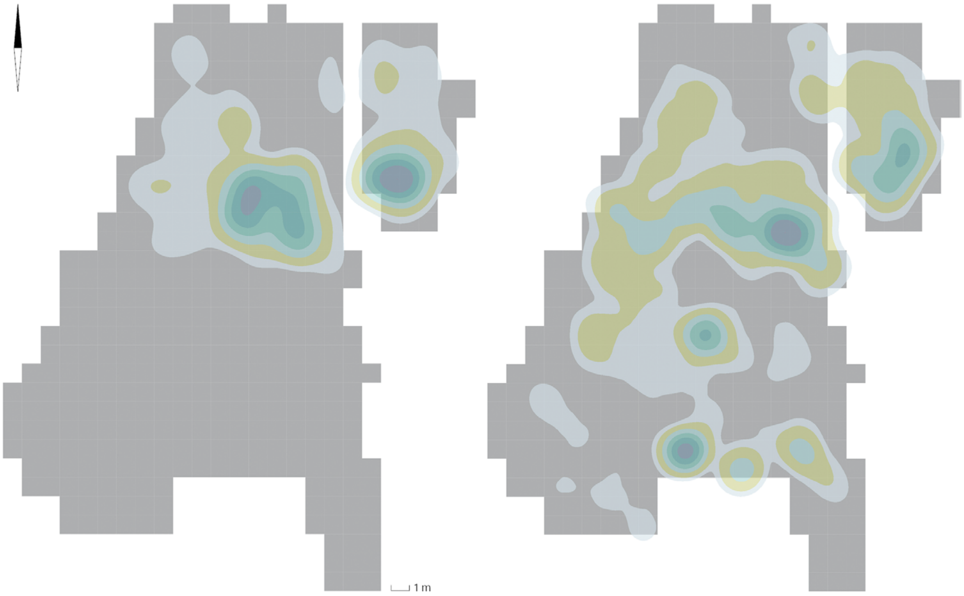


Fig. 4. Skeletal element representation of main taxa. Skeletal element representation for *Equus* sp. (**A**), *B. primigenius* (**B**), and larger (**C**) and smaller (**D**) cervids, based on MAU—numbers on the left *y* axis—divided by nutrient content (fat-rich, meat-rich, and low-nutrient yields), with black dots indicating the percentages of butchery traces per skeletal element (right *y* axis).

Consideration of intraelemental survivorship provides a more nuanced estimate of density-dependent survivorship (*3*, *21*, *50*). The epiphysis-shaft ratio (ESR) of all long bones is 1:5 for *Equus* sp., 1:6 for *B. primigenius*, and 1:10 for both small and large cervids. Correlation of ESR values per long bone element with respective bone density [following (*3*)] shows strong significance for *Equus* sp. ($r^2 = 0.48$, $P = 0.026$) and *B. primigenius* ($r^2 = 0.48$, $P = 0.025$). For both cervid taxa, however, no significant correlation was found (small cervids: $r^2 = 0.001$, $P = 0.79$; large cervids: $r^2 = 0.27$, $P = 0.12$) (see the "Zooarchaeology - Faunal Assemblage and Analyses" section in Supplementary Text for details). Given that bone mineral density values are similar across horses, bovids, and cervids (*49*), preservation biases between taxa are unlikely. All bones were recovered from the same depositional context formed within a narrow time interval, ruling out taphonomic variability due to environmental change. Although the correlations for horses and bovids are significant, only about half of intraelemental survivorship is explained by density. Considering the high degree of fragmentation, identification biases or carnivore activity may have played a role. However, these results strongly suggest that Neanderthals were a substantial factor influencing skeletal representation (see below).

Together, skeletal element representation and correlations with various indices suggest that the NN2/2B faunal assemblage was shaped primarily by differential transport of carcass parts by Neanderthals, guided by within-bone nutrient content (e.g., brain, marrow, fat, and grease). Preservation or fragmentation based on structural density or selection for meat-rich parts appears less influential. Thus, carcass portions or selected bones were generally brought to the site after initial butchery, although we cannot rule out that some of the at least 172 individuals were completely butchered on site.

Additional support for carcass part transport to the lake margin comes from weight estimates of the taxa found at NN2/2B. The spatial distribution of selected body parts and bone types also indicates a focus on bone processing. Marrow- and grease-rich long bones are clearly clustered in area B, while foot bones (excluding metapodials) are more widely dispersed across the excavation area (see Fig. 5).



A Heatmap of all long bones ($n = 9584$)   **B** Heatmap of all foot bones ($n = 418$)

Fig. 5. Spatial distribution of faunal remains at NN2. Distribution of the identified long bones (**A**) and of the foot bones (**B**), excluding metapodials. A more clustered distribution of the long bone fragments is clearly visible.

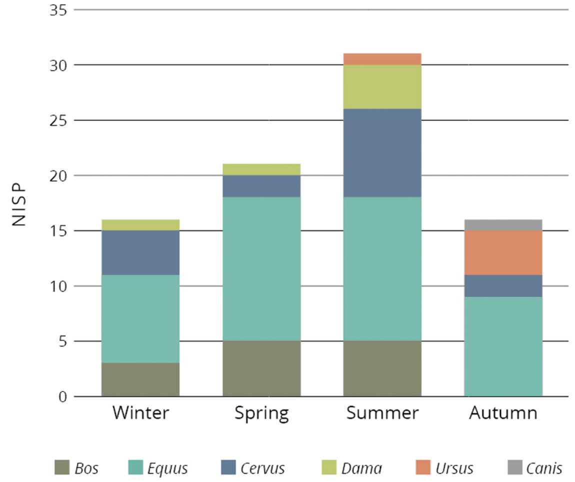


Fig. 6. Season of death of different taxa. Season of death based on dental and bone development data from 84 specimens (NISP) of different taxa, representing an MNI of 47 (see table S15).

Skeletal element representation at NN2/2B is best explained by differential transport by Neanderthals based on within-bone nutrients (brain, marrow, fat, and grease) and not by preservation and fragmentation nor meat/muscle tissue. Thus, the introduction of parts of carcasses or even of selected bones to the site occurred in general after butchery, although we cannot entirely rule out the possibility that some of the minimally 172 individuals were completely butchered at the location.

The spatial distribution of selected body parts and bone types further supports a focus on bone processing. The marrow- and grease-rich long bones show a clear clustering in area B, while foot bones (excluding the metapodials) are more dispersed all over the excavated area (Fig. 5).

Age structure and seasonality

Assessment of age at death of individuals by tooth crown height measurement, tooth wear, as well as ontogenetic development of teeth, tooth replacement, and bone growth can yield data on prey age classes and hunting seasons. Horse mortality falls in the range of a living-structure mortality pattern. Cervids and bovids fit the prime-age mortality pattern in a triangular representation of mortality (*51*). However, acknowledging the high fragmentation of the material and the differences in composition and morphology between horse and ruminant teeth, not fully developed juvenile and heavily worn teeth of senile bovids and cervids may have been fractured more than the respective teeth of horses. Given these considerations, hunting strategies in the interglacial habitats at and around Neumark-Nord may have differed from Neanderthal sites in mainly cold to cool-temperate settings, which are indicative of selective targeting of adult, energy-rich individuals (*52*).

Seasonality data (Fig. 6 and table S15) obtained from 84 bones and teeth (MNI = 47) from horses, bovids, cervids, bears, and wolves also testify to the exploitation of fetal, newborn, and young juvenile individuals. The data do not indicate a specific hunting season for horses, bovids, and cervids, as all seasons are represented by the ungulates. While the cutmark evidence suggests that the carnivores (MNI = 5) were butchered for consumption, their almost exclusive autumn signal may indicate that they were also hunted for their pelts as coat condition peaks before the onset of winter. The bears (MNI = 8) may also have been hunted in autumn for their fat deposits. The seasonal data demonstrate that hunting events took place throughout the year across the Neumark-Nord landscape.

Combining the spatial concentration of the material with the high sedimentation rate and the swift pre- and syndepositional biostratinomic processes, we infer a short time window for the formation of the

NN2/2B assemblage. While there likely were recurrent episodes during which (parts of) carcasses were brought to the site for processing, the data suggest that these events took place during a very short period (see Discussion).

Anthropogenic and other bone surface modifications

Analysis of the bone surfaces showed that the frequency of anthropogenic modification is extremely high in the NN2/2B faunal assemblage, visible as a result of its excellent state of preservation, with only minor weathering and abrasion of bones (see the Supplementary Materials for detailed description). Bones of all size classes and taxa, as well as all bone types and fragment sizes, display cut marks and/or hammerstone-induced impact damage (Figs. 7 and 8). Considering the well-represented horse, bovid, and cervid assemblage, about 40% of the bones (excluding teeth) show anthropogenic modifications (Fig. 9 and tables S7 to S10). Against the background of the high fragmentation and the high NISP and MNE with cut marks and impacts, we can infer that all individuals deposited at the site were butchered. Cut and scraping marks appear in clusters of multiple marks, indicating skinning, disarticulation, and defleshing. Many bones show dense scatters of cut marks, probably originating from cleaning the bone surface. Impact notches, impact flakes, and loading points are also frequent on bones containing marrow cavities. Shallow striations appear regularly on bones with and without cut marks. These are fine incisions on the bone surfaces that lack the typical shape of cut marks. The striations may result from abrasion of the bone surfaces that flattened cut mark morphology and/or thorough removal of the periosteum (see Supplementary Text for a detailed discussion). Carnivore modifications were only identified on 11 specimens within the equid, bovid, and medium-sized cervid remains. Three specimens displayed carnivore traces overlying cut marks, while five elements exhibited carnivore gnawing that occurred postdesiccation. Carnivore involvement shaping the skeletal element profile, e.g., by removing epiphyses, can be ruled out. The few traces observed point to carnivore access to bone fragments when (most of) the assemblage was already deposited. Tooth marks from micromammals are absent. Bones of micromammals occur in low numbers, and not a single burrow was observed throughout the NN2 sequence, also underlying the rapid formation of the assemblage and its encasing matrix after Neanderthal activities at the site.

Additional evidence for intensive processing of mammal tissue and within-bone resources comes from heated bone specimens. Most of these heated bones ($n = 1953$, i.e., 1.64% of the faunal assemblage) are also clustered in the dense concentration area (fig. S12). These specimens, exclusively belonging to the <2-cm size class with 99% measuring <1 cm, exhibit thermal modification on all surfaces, indicating fragmentation before heat exposure. In conjunction with heat-altered lithics, thermally modified pebbles, and charcoal fragments, these heat-affected bones likely represent the remnants of degraded combustion features at this location. This spatial concentration of fire-related proxies provides additional support for interpreting this area as a focused activity zone characterized by intensive processing of mammal carcasses.

DISCUSSION

Many Paleolithic sites are characterized by faunal assemblages with an abundance of small bone fragments, which hinders the identification of specific bone elements and species. While containing clear evidence of human activities, at most of these sites, the involvement of nonhuman bone-altering agents—such as carnivores, trampling, and postdepositional processes—in bone fragmentation cannot be definitively excluded. Consequently, drawing unambiguous conclusions regarding the formation of these assemblages and the specific role of human actors remains challenging. In this context, the NN2/2B site is notable for its high-resolution environmental, spatial, and chronological framework, which enables a more nuanced contextualization and interpretation of the data, distinguishing it from the majority of other Palaeolithic sites.

The faunal material from NN2/2B represents an exceptionally rich and well-preserved anthropogenic assemblage. It shows minimal evidence of postdepositional disturbance and a near-total absence of carnivore activity. Together with the 16,524 flint artifacts, stone manuports, and the abundant evidence for fire use in the form of heated lithics, heated bones, and charcoal, it constitutes a scatter in primary context that accumulated at the edge of the NN2 water body. Its high degree of bone fragmentation of grease bearing elements occurred, while bones were still fresh and can confidently be ascribed to cultural activities aimed at comminution of the faunal remains. Most of the material derived from a minimum of 172 large mammals, which accumulated over a short period within a remarkably small area of only about $50m^2$.

Given its primary archaeological context, excellent state of preservation, virtual absence of nonanthropogenic biotic modifications, limited spatial distribution, and fast sedimentation of its encasing matrix, the formation of the bone assemblage may have resulted from a relatively short use (or uses) of the locality, rather than of multiple episodes spread out over an extended period of time. The very fast formation of the assemblage is also illustrated by a well-preserved and complete bovid skull, encased in 69 laminations (fig. S5).

We lack the data to provide a precise estimate of the actual duration of the event or events that took place there, nor can we offer additional insights about the continuous or discontinuous nature of the occupation within this brief period. This places limits on the behavioral inferences we can draw from the assemblage. What we can say with some confidence is that the zooarchaeological, taphonomic, and spatial patterns provide evidence for a specialized focus on the systematic extraction of lipids at NN2/2B from a very substantial quantity of bones derived from a large number of ungulates of several different species.

Disentangling bone grease rendering from other taphonomic processes presents certain challenges, as recently emphasized by Blasco *et al.* (*21*) and references therein, particularly because bones subjected to grease extraction often become unidentifiable or are entirely removed from the assemblage. At NN2/2B, however, we find abundant evidence of intensive anthropogenic fragmentation during the nutritional phase, with virtually no overprinting by carnivores. Rapid deposition is indicated by environmental, anthropogenic, and biotic surface modifications. Correlation between bone mineral density and bone destruction provided mixed results, which are best interpreted as the outcome of selective carcass transport and the high fragmentation of the assemblage. Conversely, indices such as the UMI yielded robust and statistically significant results supporting this interpretation [see also (*12*)]. Morin (*3*) [see also (*53*, *54*)] has proposed a set of criteria for identifying bone grease rendering in archaeological assemblages, based on actualistic experiments. While these experimental frameworks provide valuable comparative data, we caution against applying them uncritically to

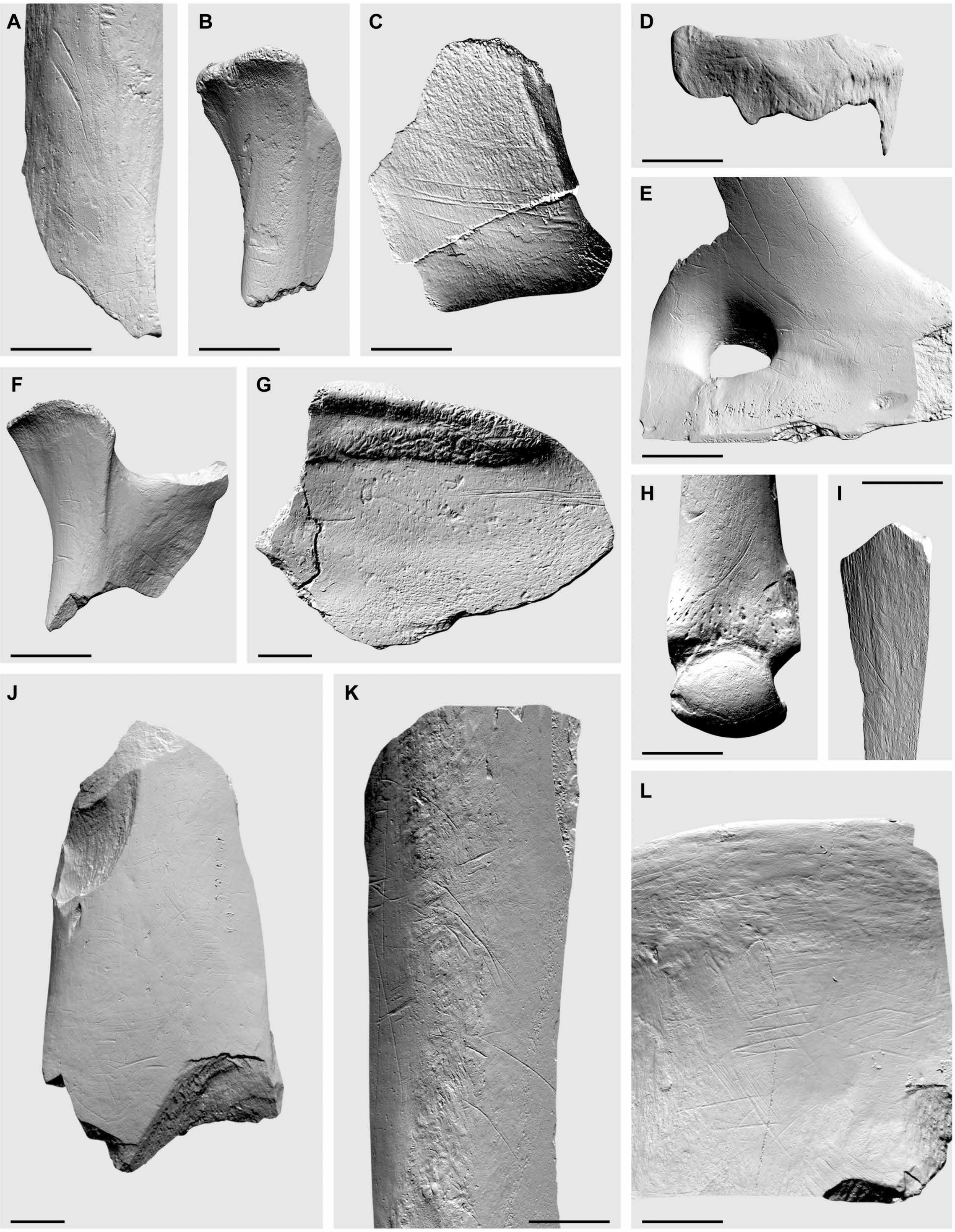


Fig. 7. Examples of cut marks in the NN2/2B faunal assemblage. Images obtained through three-dimensional microscans (LIM ToolScan R360), texture-free mode. (**A**) *Equus* sp., Tibia dex. (no. 14474). (**B**) Cervid, *Dama* size, Mandible dex. (no. 14632). (**C**) *Equus* sp., second lumbar vertebral spine (no. 22339). (**D**) Cervid, *Dama-Cervus* size, Phalange 2 (no. 15111). (**E**) Cervid, *Capreolus-Dama* size, Sacrum, (no. 31868). (**F**) Cervid, *Dama* size, Mandible dex. (no. 11154). (**G**) *Equus* sp., Maxilla dex. (no. 15471). (**H**) *Ursus* cf. *arctos*, Metatarsus II dex. (no. 4046). (**I**) *B. primigenius*, Tibia sin. (no. 10121). (**J**) *B. primigenius*, Humerus dex. (no. 9412). (**K**) *Equus* sp., Tibia dex. (no. 14474). (**L**) *Equus* sp., Scapula dex (no. 31934). Scale bar 1 cm.

Fig. 8. Examples of hammerstone-induced impact damage on long bones from NN2/2B. (**A**) *B. primigenius*, Tibia dex., impacts from posteromedial (no. 4892). (**B**) *B. primigenius*, Humerus sin., impacts from posteromedial (no. 4283). (**C**) *B. primigenius*, Tibia dex., impact from anterolateral (no. 8437). (**D**) *Equus* sp., Humerus sin., impacts from posterolateral (no. 21758).

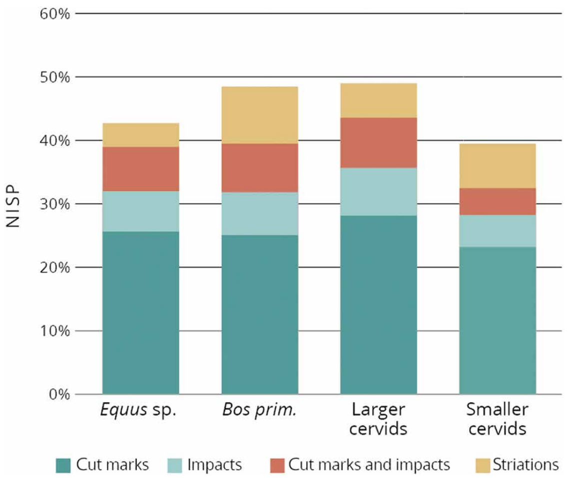


Fig. 9. Frequency (in percentages) of anthropogenic bone surface modifications. Frequency based on NISP, excluding teeth. *Equus* sp. NISP = 2069, *B. primigenius* NISP = 2848, smaller cervids NISP = 999, and larger cervids NISP = 1288.

the archaeological record, as they focus exclusively on long bones. Assemblages such as NN2/2B, which include bones from all anatomical regions and numerous individuals from multiple taxa, present challenges that exceed the scope of those experiments and may introduce biases into quantitative analyses. Nonetheless, some of the characteristic bone fragment morphologies described in grease rendering experiments are also evident in the NN2/2B assemblage (see fig. S36).

We should also note that dedicated bone grease processing was not the only subsistence activity that took place at this location; there is also some evidence that wolves and bears were exploited for their fur, as well as for some butchering of meat and fatty tissues from the rib cages and vertebral columns of ungulates. However, these activities were far less important than the massive extraction of bone fat that clearly constitutes the dominant signal from NN2/2B.

The assemblage is mainly the result of foragers repeatedly moving parts of carcasses through the Neumark-Nord landscape, from the various locations where animals were killed and initially butchered to the bone processing location described here—a “fat factory” supplied with fat-rich bones of large prey animals "harvested" in the wider landscape. Elsewhere, we documented human movement of skeletal parts through this landscape evidenced by a number of artificial concentrations ($n = 9$) of *P. antiquus* tusks around the NN1 lake, its nearest shore area just 200 m southwest of NN2 (*26*, *55*). One remarkable concentration consisted of nine medium- and large-sized tusks, recorded about 500 m south of NN2, in an area of 10 m by 20 m, without any other associated skeletal material. The NN2/2B assemblage also contained tusk fragments and one complete tusk, a large isolated one in this case, excavated within the fine-grained unit 8 sediments, as were eight shed deer antlers. We do not know why these objects were transported to this location, but whatever the reason, it undoubtedly differed from the "fat focus" dominating the NN2/2B assemblage.

The intense fragmentation of the bones of at least 172 large mammals at NN2/2B fits well with descriptions of marrow and grease production documented in the ethnohistoric record [e.g., (*15*, *16*, *18*, *56*–*58*)]. The NN2/2B assemblage also fits the expectations arising from experimental studies (*17*, *19*) and as inferred from faunal remains recovered from late prehistoric Plains village sites in North America [e.g., (*59*)]. The NN2/2B assemblage testifies to the creation of tens of thousands of small fragments, mainly derived from fat-rich bones, for marrow and grease production, a substantial investment by the site's occupants of both time and effort aimed at retrieving precious lipids from a large number of prey animals. The evidence from NN2/2B constitutes the earliest clear case of intensive grease-rendering yet documented for the Paleolithic.

Our faunal-based interpretation of this NN2 locality as a marrow and grease processing locale also finds support in the presence of the manuports mentioned above (see Supplementary Text and fig. S5), including a percussive toolkit consisting of at least 5 large anvils and 58 hammerstones recovered within the distribution of bones and flint artifacts (*40*). These manuports may have been used for bone fragmentation, beyond their usage on hard contact materials such as during flint tool production, which is evidenced by use-wear analysis (*40*). Use of this toolkit to open green bones would not have left any discernible traces of (macro-) wear, besides occasional impact damage on percussors and anvils when accidentally hit during bone breakage, as documented in the NN2/2B percussive toolkit.

The edge of the NN2 basin would have been a suitable location for grease rendering, as many of the necessary ingredients were readily available at the NN2/2 locality: water, fuel, and hammerstones and anvils obtainable from local outcrops of the Saalian till, which also yielded the flint raw material for the production of sharp-edged tools (*39*).

There is currently no direct evidence for actual boiling of the small bone fragments. However, fire proxies (charcoal, heated bones, and heated lithics) were recovered in abundance within the concentration of faunal remains. Study of microfossils retrieved from calculus has suggested that Neanderthals did boil food items (*60*). Underlining earlier work by Speth (*61*), experiments recently demonstrated that organic perishable containers, e.g., made out of deer skin or birch bark, placed directly on a fire, are capable of heating water sufficiently to process food, with the advantages of wet-cooking beginning at lower, sub-boiling temperatures than thus far acknowledged (*62*).

As mentioned above, this rich assemblage could have resulted from various, multiseasonal import events of fat-rich bones and their subsequent processing for marrow and bone grease, with only a small temporal gap between the kills and the final processing of the bones. The very "tight" spatial distribution of the skeletal elements of the main herbivore groups—bovids, equids, and cervids—is suggestive of a very organized and temporally restricted use of space for the fragmenting and discarding of the thousands of bones, rather than a palimpsest created over an extended period of time by numerous more or less independent import and processing events.

However, how to account for the presence of at least 172 large animals in such a concentrated space and accumulated within a short period? If all of the animals were of just one species, particularly one that could be hunted communally—for example, reindeer or bison—then dozens to hundreds of individuals could have been ambushed or entrapped, killed, and processed in a matter of days or weeks. Ethnohistorically, these massive kills were commonplace [e.g., (*63*, *64*)], and there is also evidence for their occurrence in the Middle Paleolithic (*65*, *66*).

However, with several different large mammal taxa all well represented in the NN2/2B sample, an alternative (although not mutually exclusive) scenario should be considered. This alternative starts from the observation that for the large amounts of bones excavated, the small size of the concentration and the spatial patterning of fat-rich bone fragments (see above) are very remarkable, certainly given the absence of any archaeologically visible space constraints in the open-air setting of Neumark-Nord. In combination with the almost total absence of carnivore marks, we hypothesize that this remarkable concentration resulted from one or very few import events of animal remains to the location, possibly previously stored in caches all through the surrounding lake landscape or in a large cache close to the NN2/2B location. As demonstrated by the seasonality data (table S15), over the course of the year foragers repeatedly hunted in the Neumark-Nord region, and whenever they succeeded in killing animals beyond their immediate food needs, they may have cached the surplus, including lipid-rich bones. Subsequently, over a comparatively brief period at some undetermined time of year, the caches were emptied, and stored carcass parts were brought to the NN2/2 location for marrow and grease processing.

Caching is an essential component of the hunting way of life, universal among ethnohistorically documented mid- to northern-latitude foragers, who could not survive without cached foods (*67*, *68*) (see Supplementary Text). Caching creates a distinct temporal gap between the time of the death of an animal and its final exploitation through bone processing (see Supplementary Text). Caching would also have created large stores of bones for grease rendering activities, allowing maximum utilization of prey animals. It has been repeatedly argued that bone grease production requires a certain volume of bones to make this labor-intensive processing worthwhile, and, hence, the more bone volume increases—at one location or distributed in the landscape—the more profitable it becomes [e.g., (*69*)]. Caches are archaeologically (almost) invisible, but the Neumark-Nord lake land, which included some deeper lakes such as NN1, could, for instance, have facilitated pond storage as described by Speth (*70*) (see also Supplementary Text). While the existence of such a "caching phase" at Neumark-Nord before the accumulation of fat-rich bones at NN2/2B would provide a good explanation for the characteristics of this remarkable assemblage, given the evidence we currently have at hand, it obviously remains speculation.

While often inferred to be associated with situations of nutritional stress, grease production does also occur in the context of storage practices such as the production of pemmican (*71*). A storage-related use might fit well with the abundance of food resources documented in the warm-temperate Neumark-Nord landscape, rich in animals and plants. With this study's focus on meat and fat, it should be pointed out that the Neumark-Nord environment had a wide range of predictable and readily available plant foods to offer foragers present in the area, and bone-derived lipids might have played a role in their consumption—e.g., added to vegetable stews to make them more nutritious—and/or storage in dried forms.

In addition, carbohydrate sources could have helped fill the calorie deficit that accompanies a diet based heavily on meat. The charred remains of hazelnut (*Corylus avellana*), acorn (*Quercus* sp.), and blackthorn (or sloe plum, *Prunus spinosa*) retrieved during the NN2/2B excavations (*72*) may actually reflect these food items. Many more potential food plants are among the macrobotanically identified remains of more than 190 plant species (*73*) and in the pollen assemblage from the two basins (*33*, *74*). These include carbohydrate sources such as cattail (*Typha* sp.) and reed (*Phragmites australis*), as well as berries and other fruits, e.g., dewberry (*Rubus ceasius*), elderberry (*Sambucus nigra*), and fat hen (*Chenopodium album*), alongside potential green vegetables (*Rumex crispus* and *Urtica dioica*) or plants usable for both their greens and seeds. The notably open (*36*) areas around the basins, with their upland herbs and grasses with representatives of the Triticeae tribe, including the wild relatives of wheat and barley (*33*), would have afforded abundant access to grass seeds, well documented as a regular component of the Neanderthal diet (*75*).

On the scale of the larger Neumark-Nord landscape, interesting patterns emerge for the 300-year period within the Last Interglacial to which we can assign a number of sites, including the one presented here. At NN1, at just a few hundred meters from NN2, we have a series of locations with the remains of extensively exploited straight-tusked elephants, some weighing up to 13 tonnes, of which the (little marrow containing) bones were left intact (*26*). Other sites with skeletal remains of butchered rhino and aurochs, with no evidence for bone marrow exploitation, testify to incomplete exploitation of skeletal remains, as do the only marginally exploited carcasses of fallow deer from NN1 (*38*). These findings make for a contrast with the exhaustive processing of within-bone nutrients documented at NN2, following transport of skeletal parts to this location. Last Interglacial people were obviously doing different things at different places and at different times in this landscape, with the NN2/2 location dedicated to the bone processing activities described here.

Our analyses demonstrate that Neanderthals were active during multiple seasons within the vicinity of the NN2 area, with animals being killed in all seasons. However, on a broader timescale, Neanderthals were active in this area for at least 2000 years, and their presence is correlated with a period of striking vegetation openness (*36*), probably cocreated by their own activities: fuel collection, trampling, stone procurement, burning, etc. The rich archaeological concentrations documented at NN1 in rescue excavations and recorded in great detail at NN2 result from water-edge activities, with the processing of large prey animals constituting the archaeologically most visible actions. In contrast to the processing locations, campsites proper, if any, were in all probability not situated on the very water edge, but somewhat higher on the slopes, in areas not preserved during subsequent erosion of the Eemian surfaces.

The NN2/2B excavation constitutes a tiny window on a much larger area, in low-resolution documented at NN1, in detail in a small part at NN2, yielding the results described here. It is exceptional preservation rather than exceptional behavior that makes Neumark-Nord a unique site complex in the archaeological record of warm-temperate periods [e.g., (*76*)].

Another implication of this "nonexceptional" character needs to be emphasized: the sheer quantity of herbivores that Neanderthals must have routinely been "harvesting" in this warm-temperate phase. Beyond the remains of minimally 172 large mammals processed at the small locale of NN2/2B alone within a short period, hundreds of herbivores, including straight-tusked elephants, were butchered around the NN1 lake in the early Last Interglacial. Other exposures in the wider area around Neumark-Nord have yielded more coarse-grained evidence of regular exploitation of the same range of prey animals, at sites such as Rabutz, Gröbern, and Taubach (*76*). The last site contained cut-marked remains of 76 rhinos (*77*) and 40 straight-tusked elephants (*76*). Safely assuming that with these sites we are only looking at the tip of the proverbial iceberg [see, e.g., (*78*) for the Eemian record in northwestern France, 700 km to the west of Neumark-Nord], Neanderthal impact on herbivore populations, especially on slowly reproducing taxa, could have been substantial during the Last Interglacial.

The Neumark-Nord evidence underlines that carcass processing usually was not a single event but rather a succession of different practices. The Neumark-Nord data allow us to situate these subsistence activities in a landscape setting, documenting, at various locations, the prey processing chain, from initial butchering to comminution of bones at the grease processing locale presented here. It illustrates in a straightforward way that prey processing activities varied widely within this relatively small area of ~30 ha: from marginal butchering of animals leaving very few cut marks (*38*), single-skeleton locations with some removal of skeletal parts, and extended butchering of very large herbivores, including 13-tonne straight-tusked elephants up to the intensive exploitation of large numbers of fat-rich bones described here. This variation within a small area and within a short period, as well as the accompanying evidence for transport-filtered selection of body parts, calls for great care in making inferences on former subsistence behavior on the basis of a small number of sites or sites from a specific geomorphological setting (e.g., rock shelter sites) only [see (*79*)].

We reiterate that the distinctive sedimentary context of the NN2/2B site was critical in detecting the evidence for bone grease rendering presented in this study. While the zooarchaeological signatures identified at NN2/2B are not unique within the Paleolithic record, this finding suggests that bone grease extraction may have been a more widespread practice, potentially with deeper Pleistocene origins [see (*12*, *21*)]. At present, our data indicate that a labor-intensive focus on extracting within-bone nutrients—comparable to behaviors observed among Upper Paleolithic and (sub)recent hunter-gatherer groups—formed a distinct component of the cultural repertoire of hominins in Europe, 125,000 years ago.

MATERIALS AND METHODS

Materials

For a description of the provenance of the materials analyzed and presented here, we refer to the Supplementary Text.

The NN2/2B faunal assemblage comprises 118,774 bones (fragments) and teeth of a wide variety of large mammals, 19,650 of which were recorded in three dimensions during the 2004–2008 excavations, during which 415 m^2 of the excavated area (491 m^2) yielded faunal remains and lithic artifacts. Ninety percent of all faunal remains are smaller than 50 mm in maximum dimension, and the median bone length is ~20 mm, with the majority of this highly fragmented assemblage recovered during sieving of the archaeology yielding sediments, systematically carried out per individual square meter.

All recovered faunal remains were examined for bone surface modifications. All finds are stored at the Landesamt für Denkmalpflege und Archäologie Sachsen-Anhalt in Halle (Germany).

Methods

Taxonomic determination

Taxonomic identification used the comparative collection at the MONREPOS Archaeological Research Centre and Museum for Human Behavioural Evolution, Neuwied, Germany, supplemented by various anatomical atlases [e.g., (*80*, *81*)]. When species or genus-level identification was not feasible, mammalian specimens were categorized into five live weight–based size classes [Table 1; modified from (*82*, *83*)].

Age determination

Horse teeth were aged via crown height measurements (*84*–*86*) or, when measurements were impossible, by occlusal wear patterns (*86*, *87*). Red deer (*Cervus elaphus*) ages were estimated using a refined quadratic crown height method (*88*, *89*), while large bovid ages were determined using crown height measurements according to Klein and Cruz-Uribe (*90*). Age distributions were visualized using a ternary diagram (juvenile, prime, and old adults) (*91*) (figs. S11 to S13). Bear teeth were aged using the occlusal wear scheme developed by Stiner (*92*, *93*) and adapted by Kindler (*50*).

Species abundance

Species abundance was quantified using the number of identified specimens [NISP (*94*) and MNI (*90*, *95*)].

Skeletal element representation

Skeletal part representation analysis used NISP, MNE, MAU, and standardized %MAU (*69*, *96*). %MAU, the primary unit of analysis, was occasionally grouped by anatomical region for simplification and comparative purposes (*97*). To assess density-mediated survivorship, %MAU was compared with bone mineral density (BMD) data (*49*, *98*), using the BMD2 values provided by (*49*). Skeletal part representation (%MAU) was compared against modern hunter transport decisions (*99*) and meat/marrow utility indices (*12*, *100*).

Bone surface modifications

Bone modifications caused by biotic and abiotic agents were identified using zooarchaeology and taphonomy manuals (*101*, *102*): 20× hand held lenses, a Dino-Lite PRO digital microscope with a magnification up to ×200, and a Leica reflected light microscope with a magnification of up to ×32 were used. Modifications were quantified using NISP and a standardized NISP measure (NISP per element divided by its skeletal frequency).

Bone fragmentation and utility indices

Breakage patterns were recorded and analyzed following (*46*) and (*47*, *103*). For bone mineral density correlation, the values for horses, bovids, and cervids provided by Lam *et al.* (*49*) were used. Utility indices for overall FUI, marrow only (marrow index), and unsaturated marrow (UMI) were taken from Morin (*48*) and Morin and Ready (*12*).

Geographical information system analyses

The primary dataset, encompassing detailed records of archaeological finds, is maintained in the MainFindList Excel sheet. Geospatial information pertinent to selected finds is systematically cataloged in the NMN_All_B_Coordinates file, while lithic artifacts and their detailed attributes are recorded in a Microsoft Access database, NN22 Lithics DB. Geographical information system (GIS) analysis and the initial mapping processes were conducted using QGIS (version 3.16.8-Hannover). Statistical evaluations were performed with IBM SPSS Statistics (version 29.0.1.0). SPSS was used to explore patterns and relationships within the archaeological datasets.

Supplementary Materials

This PDF file includes:

Supplementary Text
Figs. S1 to S36
Tables S1 to S32
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