

Paleolithic Zooarchaeology in Practice

Edited by

Jonathan A. Haws
Bryan S. Hockett
Jean-Philip Brugal

BAR International Series 1564
2006

This title published by

Archaeopress
Publishers of British Archaeological Reports
Gordon House
276 Banbury Road
Oxford OX2 7ED
England
bar@archaeopress.com
www.archaeopress.com

BAR S1564

Paleolithic Zooarchaeology in Practice

© the individual authors 2006

ISBN 1 84171 994 3

Printed in England by The Basingstoke Press

All BAR titles are available from:

Hadrian Books Ltd
122 Banbury Road
Oxford
OX2 7BP
England
bar@hadrianbooks.co.uk

The current BAR catalogue with details of all titles in print, prices and means of payment is available free from Hadrian Books or may be downloaded from www.archaeopress.com

THE ROLE OF WOOLLY RHINOCEROS AND WOOLLY MAMMOTH IN PALAEOLITHIC ECONOMIES AT VOGELHERD CAVE, GERMANY

Laura B. Niven

Institut für Ur- und Frühgeschichte, Universität Tübingen

The Swabian Jura region of southern Germany contains a series of cave sites located in the vast karst systems of the Lone and Ach Valleys (Figure 1) that were occupied throughout the Middle and Upper Palaeolithic. Archaeological research has been conducted in this region since the mid-late 1800s and has contributed a great deal to our understanding of the Palaeolithic. The scientific significance of this region comes not only from the number of sites with dense Paleolithic deposits but from especially rich artefact and faunal assemblages. For example, many small figurines carved from mammoth ivory were recovered from Aurignacian deposits at Vogelherd, Geissenklösterle, and Hohlenstein-Stadel representing the earliest artwork in Europe. These sites also yielded extensive stone and organic tool inventories as well as large archaeofaunas. Other notable finds include remains of early *Homo sapiens sapiens* from Vogelherd known as the Stetten fossils (Czarnetski 1983; Churchill and Smith 2000); and early dates of 35-40 ka BP for Aurignacian deposits from Geissenklösterle (Richter et al. 2000; Conard and Bolus, in press).

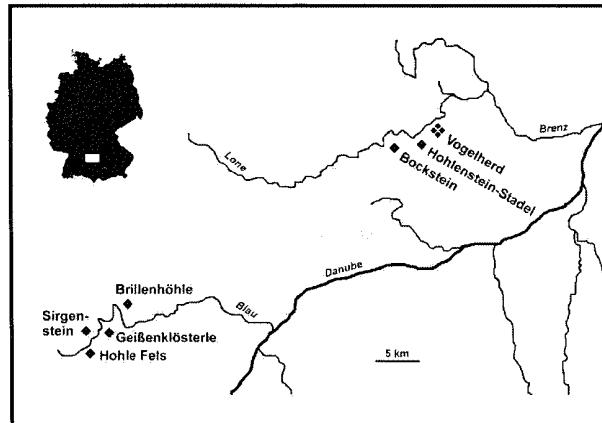


Figure 1: Map of sites mentioned in the text.

Vogelherd is also notable for a large archaeofauna, particularly in the Aurignacian deposit. This paper will focus on the megaherbivore remains from the Middle Palaeolithic and Aurignacian horizons at Vogelherd, which include woolly rhinoceros and woolly mammoth. These taxa are common in Palaeolithic deposits from cave sites in southern Germany but are especially abundant in Vogelherd, a detail that might be a factor of human economic choices, ecology of the taxa, or site taphonomy. A minimum number of 28 individual mammoths in the Aurignacian horizon distinguish Vogelherd not only in the region but as one of the key mammoth localities in Eurasia (Niven 2001). Age profiles and skeletal element representation suggest that multiple factors were involved in the acquisition and

transport of both megaherbivore species at Vogelherd. The exceptional assemblages of rhinoceros and mammoth at the site provide a unique opportunity to evaluate the role of these species in prehistoric economies.

VOGELHERD CAVE

Vogelherd is situated 18 m above the Lone Valley floor and contains entrances to the south, southwest, and north. Passages in the cave run from 15 m – 25 m in length and are at most seven meters wide. Excavations conducted by Gustav Riek in 1931 (Riek 1934) documented seven cultural horizons spanning the Neolithic to the Middle Palaeolithic. The horizons most relevant to this discussion are the Middle Palaeolithic (Riek's Layer VII) and the Aurignacian (Riek's Layers IV and V). Although Riek designated two separate Aurignacian layers, refitting of lithics and bones between Layers IV and V suggests that mixing occurred between them and therefore the faunal remains from both are discussed as one assemblage here. No absolute dates are available for the Middle Palaeolithic deposit but the Aurignacian layers have yielded dates ranging from 29-36 ka BP (Hahn 1993; Conard and Bolus, in press). The wealth of material in the Aurignacian deposit in particular suggests that the site was used intensively during this period, probably in the contexts of multiple occupations.

A large archaeofauna was recovered from Vogelherd, most of which comes from the dense Aurignacian deposit. The Aurignacian faunal assemblage is still being analysed at the time of this writing but consists of ~ 17,000 pieces and is to date the largest of the Swabian Jura cave site faunas from this time period. Provenience information is primarily limited to find horizon only, except for some descriptions of "bone piles" (mammoth) in the Aurignacian. Bone preservation in this deposit ranges from good to substantially weathered. Exact numbers of each taxon are not yet available since this archaeofauna is still being analyzed, but species representation in the Aurignacian includes *Lepus* sp., *Vulpes* sp., *Meles meles*, *Gulo gulo*, *Canis lupus*, *Crocuta spelaea*, *Felis spelaea*, *Felis silvestris*, *Ursus spelaeus*, *Mammuthus primigenius*, *Equus ferus*, *Coelodonta antiquitatis*, *Bos/Bison*, *Rupicapra rupicapra*, *Megaloceros giganteus*, *Cervus elaphus*, *Rangifer tarandus*, and *Sus scrofa*.

In the Middle Palaeolithic Layer VII, 518 specimens were recovered from a limited area in the south cave entrance. Represented taxa include *Vulpes* sp., *Canis lupus*, *Crocuta spelaea*, *Felis spelaea*, *Mammuthus*

Table 1. Skeletal element representation for woolly rhinoceros (*Coelodonta antiquitatis*) in the Middle Palaeolithic and Aurignacian deposits at Vogelherd.

| Element | VII - Middle Palaeolithic | | | IV-V - Aurignacian | | |
|--------------------|---------------------------|-----|-----|--------------------|-----|-----|
| | NISP | MNE | MNI | NISP | MNE | MNI |
| Cranium | | | | | | |
| - occipital cond. | - | - | - | 2 | 2 | 1 |
| - max molars | 22 | 18 | 10 | 18 | 16 | 7 |
| Mandible | | | | | | |
| - mand molars | 8 | 6 | 3 | 29 | 28 | 12 |
| Tooth fragments | 5 | - | - | - | - | - |
| Hyoid | - | - | - | - | - | - |
| Scapula | 1 | 1 | 1 | 4 | 1 | 1 |
| Humerus | 5 | 2 | 2 | 1 | 1 | 1 |
| Radius | 2 | 2 | 1 | 1 | 1 | 1 |
| Ulna | 3 | 3 | 3 | 3 | 3 | 3 |
| Carpals | - | - | - | 3 | 3 | 3 |
| Metacarpal I - III | - | - | - | 3 | 2 | 2 |
| Os Coxae | - | - | - | - | - | - |
| Femur | 1 | 1 | 1 | - | - | - |
| Tibia | 4 | 3 | 3 | 3 | 3 | 2 |
| Fibula | - | - | - | - | - | - |
| Astragalus | 1 | 1 | 1 | - | - | - |
| Calcaneous | 2 | 2 | 1 | 3 | 3 | 3 |
| Tarsals | - | - | - | 2 | 2 | 1 |
| Metatarsal I - III | - | - | - | 3 | 3 | 3 |
| Longbone Fragment | 3 | - | - | - | - | - |
| Sesamoid | - | - | - | 3 | 3 | 1 |
| Phalanx I | - | - | - | 2 | 2 | 1 |
| Phalanx II | - | - | - | 3 | 3 | 1 |
| Phalanx III | - | - | - | 1 | 1 | 1 |
| Vertebrae | - | - | - | - | - | - |
| Ribs | - | - | - | 2 | 2 | 1 |
| Sacrum | - | - | - | - | - | - |
| | 57 | 39 | 10 | 86 | 79 | 12 |

primigenius, *Equus ferus*, *Coelodonta antiquitatis*, *Bos/Bison*, *Megaloceros giganteus*, *Cervus elaphus*, and *Rangifer tarandus*. Much of this archaeofauna is substantially weathered or rolled, probably through geological processes. In addition to the fauna, a small lithic assemblage was also recovered from this layer.

Thorough collection of most if not all faunal material during excavation is indicated by the amount of small or unidentifiable bone fragments, specimens that were often discarded in early archaeological fieldwork. However, considering that the excavation of Vogelherd was conducted in just three months without sediment screening, it is possible that some smaller material was not collected by Riek and his team. Despite the rich archaeofauna having been recovered from Vogelherd, analysis of the bone assemblage is limited to one paleontological study by Ullrich Lehmann (1954). Therefore, an archaeozoological study of the faunal

material is currently being conducted by the author in an attempt to elucidate patterns of faunal exploitation by prehistoric humans in the Swabian Jura.

THE WOOLLY RHINOCEROS ASSEMBLAGES

All Vogelherd rhinoceros specimens were identified to *Coelodonta antiquitatis* based on the distinctive tooth morphology of this species (Guérin 1980). The assemblages are predominated by molars but bone is also present (Table 1). The teeth were aged using a combination of tooth eruption, wear patterns, and crown heights, which were then compared to published data from both known-age samples of African black rhinoceros (Goddard 1970; Hitchins 1978; du Toit 1986). Absolute ages were not the goal, instead this methodology was applied in order to estimate the age of the individuals with appropriately wide age ranges to

allow for differences among the genera. Numerous studies of both modern and fossil rhinoceros show similar tooth development among the genera, with tooth eruption subject to less variation than tooth wear. Fortunately, a large proportion of the Vogelherd rhinoceros molars from both deposits are not yet in wear and could be aged with more confidence than older individuals. Similar methodologies were applied to other Pleistocene rhinoceros assemblages including Hofstade, Belgium (Germonpré 1993), Taubach, Germany (Bratlund 1999a), Biache-Saint-Vaast, France (Auguste 1992), and Le Cotte de Saint-Brelade, Jersey Islands (Scott 1986).

The ageing study and interpretations of age distributions of the Vogelherd rhinoceroses are based on both biology and behavior of modern African rhinoceros. Age profiles are divided into five age groups; these groups are not all of equal year amounts, since several major life changes occur in the first three to four years of life. Incorporating life histories and behavior specific to rhinoceros seemed most appropriate to understanding the age distributions of the archaeological assemblage. Group I (0 – 3 years) consists of infancy to the weaning period (~24 months) and independence of calves from their mothers at ca. 2.0 – 3.5 years (Owen-Smith 1988:136-139); Group II (4 – 11 years) includes these newly independent juveniles, subadults (4 – 11 years, depending on sex), and individuals reaching sexual maturity at ca. seven years (females) (Owen-Smith 1988:143-144); Groups III – V are of seven-year increments and include fully adult animals until estimated age of death at ~35 years.

Layer VII: Middle Palaeolithic. A total of 57 rhinoceros specimens come from Layer VII. The entire archaeofauna from this layer is characterized as severely damaged by carnivores. Extensive carnivore gnawing is exhibited on all the rhinoceros bone, with every long bone shaft reduced to a midshaft cylinder and showing scooping of cancellous bone, deep tooth scoring, and ragged break edges typical of hyaena damage (Zapfe 1939; Sutcliffe 1970). Considering the thickness of rhinoceros cortical bone (up to 2 cm), it is clear that hyaenas were the only creature powerful enough to cause such damage and presence of hyaena remains in the deposit (NISP = 7, MNI = 4) speaks to their involvement in the entire bone assemblage (Stiner 1994). Remains of wolf (NISP = 9, MNI = 4) and lion (NISP = 2, MNI = 1) also suggest these animals' participation and some of the gnawing damage appears to have been caused by other bone chewers than hyaenas. The extent of gnawing on much of the Layer VII bone (all taxa) implies a "kennel pattern" (Haynes 1982) by either wolves and/or hyaenas, although the absence of juvenile teeth from either of these carnivores does not support this argument. Seventy-nine percent (91% of rhinoceros bone NISP) of the Layer VII bone exhibits carnivore gnawing, suggesting that the assemblage was accumulated primarily by these animals as opposed to hominids, however it is worth briefly discussing other criteria in this argument.

The Middle Palaeolithic archaeofauna from Vogelherd is comprised of 20% (MNI) carnivores and 80% herbivores. One criterion for carnivore accumulated assemblages is that $\geq 20\%$ of the total MNI is carnivores (Cruz-Uribe 1991; Pickering 2002), a factor derived from studies of modern hyaena assemblages. A lack of anthropogenic modifications on the rhinoceros and other Layer VII bone also argues against hominid accumulation, however it is possible that hominids were responsible for some of the spiral breakage on horse and bovid long bones. Weathering of the bone might also account for a lack of surface modifications such as cut marks. If the absence of anthropomorphic modifications is not just a taphonomic factor, then overall the rhinoceros assemblage does not fit Blumenschine's (1988) suggested criteria for a hominid accumulation; the lack of modifications also prohibits recognition of whether hominids had first access to the bones, which they subsequently discarded and were subjected to carnivore ravaging later (Blumenschine 1988, 1995). The amount and location of gnawing marks is usually used to distinguish the sequence of carnivores and hominid access to a carcass (Blumenschine 1988, 1995; Selvaggio 1994, 1998; Capaldo 1998) but this is often a more complicated issue than we think (see Lupo and O'Connell 2002). For example, marrow in rhinoceros long bones is distributed throughout trabecular and cancellous bone as opposed to being concentrated in cavities. This factor might have made these elements unattractive for marrow exploitation by hominids and therefore we should not expect breakage of these elements nor rule out hominid activity based solely on presence or absence of breakage typical of marrow extraction. Whether or not hominids did accumulate the rhinoceros bone, the spongy nature of the long bones would have made them appealing to carnivores even if they had been earlier defleshed by hominids and the extensive tooth marks on this assemblage might obscure first access by hominids. In general, the spongy nature of rhinoceros limb bones (note: as well as proboscidean) must be taken into account before assuming that hominids did not utilize them for food but overall, the taphonomic evidence points to carnivores as the primary bone collectors in the Vogelherd Middle Palaeolithic layer.

The post-cranial rhinoceros bone assemblage is small in this layer and is represented solely by limb elements. Excluding the astragalus and calcaneous, tarsals, carpals, foot, and axial bone are not present, elements that would certainly have been destroyed through carnivore feeding and/or diagenesis. According to surveys of Pleistocene hyaena dens and mixed bone assemblages (hominids and hyaenas), such bone frequencies of rhinoceros are found at both types of sites (Brugal et al. 1997; Fosse 1999). In addition, tooth NISPs for rhinoceros are often $> 50\%$ in both site types; Vogelherd Layer VII teeth make up 61% of rhinoceros NISP. In other words, the skeletal element frequency from the small Middle Palaeolithic assemblage at Vogelherd offers no clarification of hominid role in this accumulation and no meaningful conclusions can be

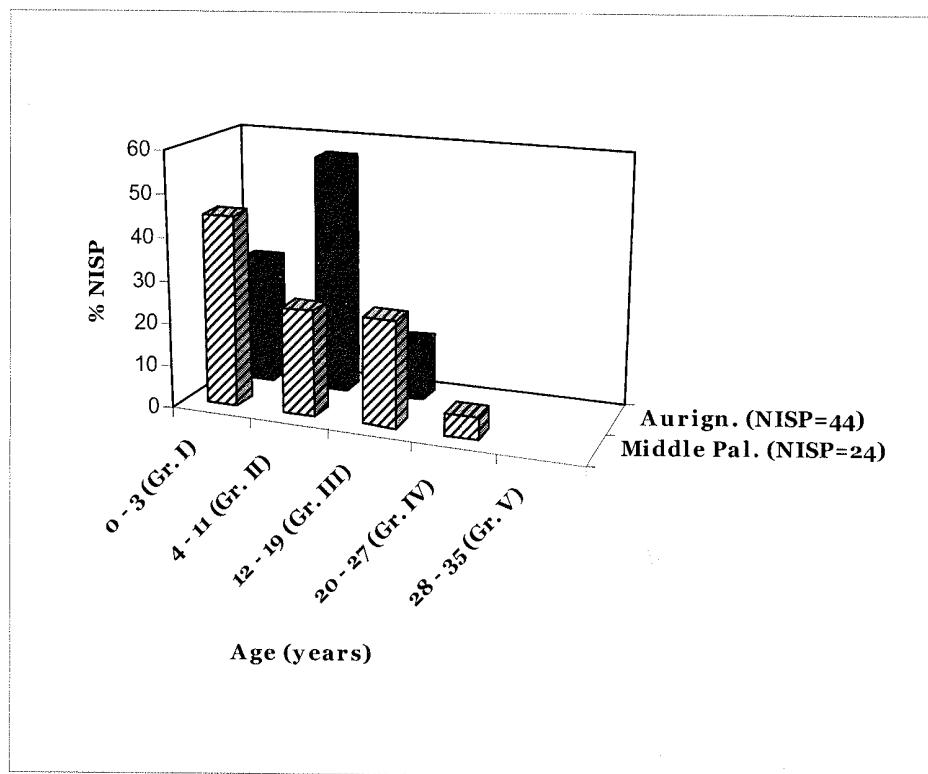


Figure 2. Age representation for woolly rhinoceros in the Middle Palaeolithic and Aurignacian deposits at Vogelherd.

made about skeletal element representation of rhinoceros in this layer except that bone is underrepresented in comparison to the teeth, with the highest bone MNI estimate being three (ulna, tibia).

Age profiles should not be used to identify the cause of death (e.g., Kurtén 1953; Stiner 1994) and often raise more questions than they answer, but they can be used in conjunction with other lines of evidence to recognize patterns of predation by various agents. The age profile for rhinoceros in Layer VII (Figure 2) is based on a molar assemblage consisting of 24 isolated specimens, representing a minimum of 10 individuals (MNI). The highest proportion of individuals is found in Group I with smaller numbers in Groups II-IV and no individuals in Group V. Based on the archaeological and taphonomic evidence, this age profile might reflect predation by carnivores, scavenging by carnivores of natural or hominid-procured rhinoceros, or hunting by hominids.

There is no doubt that large carnivores chewed on the rhinoceros bone in this deposit and it is quite possible they were the cause of death for at least some of the individuals. This proposition is based on published data on the hunting behavior of modern counterparts of the three large carnivores represented at Vogelherd: cave hyaena (*Crocuta spelaea*), wolf (*Canis lupus*),

and cave lion (*Felis spelaea*). Cave bears (*Ursus spelaeus*) could have gnawed on the bone similar to

extant ursids (Haynes 1980, 1982) but are not candidates as predators of rhinoceros.

The infantile rhinoceroses (Group I) would be vulnerable to predation by large carnivores, as this age class of both rhinoceros and other large herbivores is often preyed upon by extant hyaena (Kruuk 1972; Kingdon 1979; Owen-Smith 1988; Berger and Cunningham 1994), lion (Owen-Smith 1988; Kingdon 1979; Brain et al. 1999) and wolf (Mech 1970; Haynes 1980; Carbyn et al. 1993). Fossil assemblages of large herbivores also show a similar pattern of prey choice by large carnivores and the proportion of juveniles goes up according to body weight (e.g., Rawn-Schatzinger 1992; Daeschler 1996; Palmqvist et al. 1996; Navarro and Palmqvist 1999; Lister 2001). Group II individuals would have been newly independent from their mothers and also vulnerable to predation, alone or in pairs (Owen-Smith 1988). Groups III and IV would have been less likely to fall prey to carnivores or die from illness or injury but could have perished from any one of these factors. The big carnivores (fossil and extant) did/do occasionally prey on unencumbered and healthy adult large game, for example from solitary species or single animals excluded from a herd (Schaller 1972; Kingdon 1979; Guthrie 1990). If Pleistocene rhinoceroses were similar to modern ones in terms of herd structure, the young adult and adult age groups would have included solitary animals and small groups or pairs (Owen-Smith 1988; Kingdon 1979). In addition to predation, adults would also have

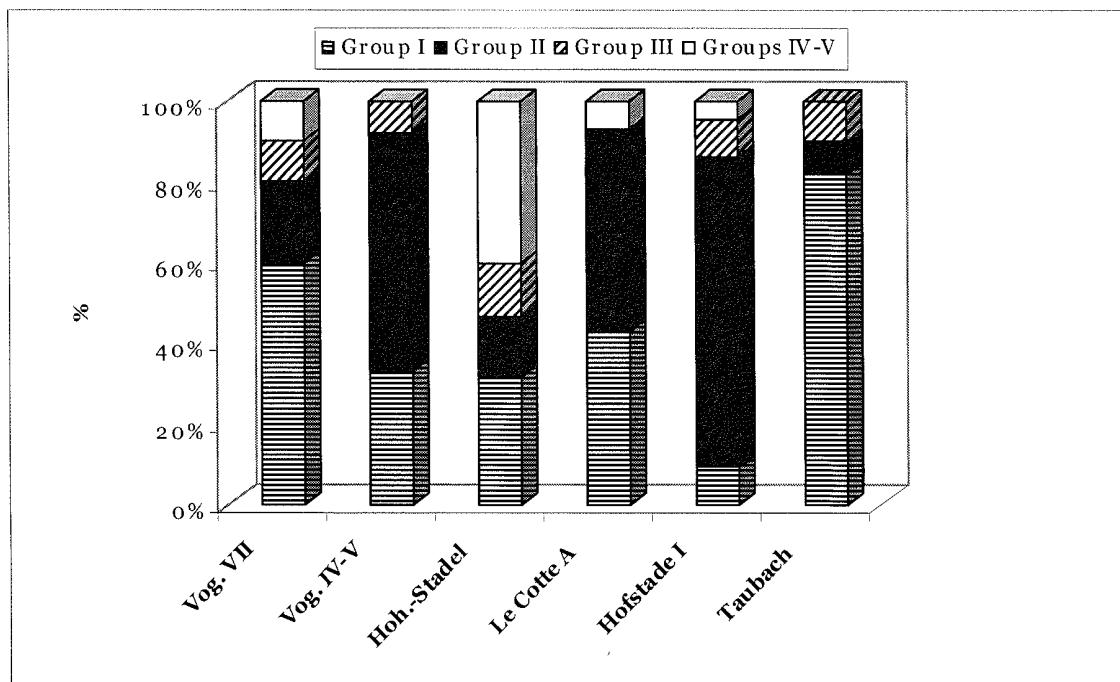


Figure 3. Comparison of rhinoceros age representation from selected Pleistocene assemblages as expressed in %MNI (except Hohlenstein-Stadel %NISP). Data from Gamble (1999:314, Table 7 - Hohlenstein-Stadel), Scott (1986:133, Figure 13.15 - Le Cotte A), Germonpré (1993:290, Table 13 - Hofstade I), and Bratlund (1999a:100, Table 13 - Taubach).

been vulnerable to death from severe ecological conditions such as drought or cold as well as natural causes. Adult rhinoceroses are reflected in the age profile from the paleontological locality of Hofstade I, Belgium (Figure 3), which was interpreted by Germonpré (1993) as showing death from extreme winters and/or drought. Modern studies of African rhinoceros that died from drought also show substantial frequencies of young adult and adult individuals (Goddard 1970; Dunham 1985). Scavenging of carcass parts from such death events of adult rhinoceroses is also possible, as any of the large carnivores would have been capable of transporting these parts into the cave.

It is also probable that large carnivores scavenged rhinoceros bones on the landscape and/or those left by hominid predators. The very young and solitary young adult/adult rhinoceros reflected in the Vogelherd age profile would have been vulnerable to predation by hominids as well as carnivores, as these age groups would pose less of a hunting challenge than adults. Perhaps they were targeted around a source of water or minerals, a scenario suggested by Bratlund (1999a) for some of the rhinoceros procurement at Taubach. In some cases, adult prey might have been hunted by hominids as an adaptation to their predator competition (large carnivores), who singled out infantile and very old animals (Stiner 1994; Gamble 1999). It is plausible that hominids hunted a range of age groups depending on the situation.

A similar rhinoceros age profile is seen at the Swabian Jura site of Hohlenstein-Stadel, which also shows what looks to be an overlap of hominid and large carnivore use of the cave during the Middle Palaeolithic (Gamble 1979, 1999). The woolly rhinoceros age representation at Hohlenstein-Stadel is similar to Vogelherd, with a higher proportion of infantile animals but quite different in its nearly equal number of the next three age groups (Figure 3). Like Vogelherd Layer VII, the Hohlenstein-Stadel age representation could reflect a combination of activities and the presence Group III and IV individuals at the two sites does not necessarily reflect hunting of these age classes by hominids. However Stiner (1994) and Gamble's (1999) suggestions that adult game made up the hominid niche deserves consideration and is also supported by other rhinoceros assemblages with strong evidence for hominid procurement.

Despite a great deal of skepticism over the hunting abilities of Neandertals, there is ample evidence of these hominids hunting rhinoceros. Using modern rhinoceros as an analog, it could be proposed that Pleistocene rhinoceroses were often found solitary or in small groups and pairs, which would have presented less of a hunting challenge than a herd species such as proboscideans. Although some extant rhinoceros can be aggressive towards predators (see review in Bratlund 1999a), it has poor long-distance eyesight (Kingdon 1979) and would therefore be vulnerable when alone.

The best example of Neandertal rhinoceros hunting is seen at the interglacial site of Taubach, Germany (Bratlund 1999a, 1999b), where it looks as if most of the 76 woodland rhinoceroses (*Stephanorhinus kirchbergensis*) were procured by Neandertals. The age profile shows predominantly Group I and Group II animals with a few individuals from Group III+ (Bratlund 1999a:100). Cutmarked bone is common and carnivore modification present but not extensive. Interglacial rhinoceros (*Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*) assemblages from Biache-Saint-Vaast, France (Auguste 1992) also suggest Neandertal hunting but of adult animals (MNI = 8). Cut marks were documented on some of the bone (Auguste 1992:64, Table 12). The woolly rhinoceros and woolly mammoth bonebeds at Le Cotte de Saint-Brelade, Jersey Islands were deposited in a glacial phase before the last Interglacial presumably as the result of hominid activity (Scott 1986). Most of the rhinoceroses fall into age Groups I and II with a few individuals from Group IV (Scott 1986:133, Figure 13.15). Although we have no carcass with embedded weapon such as the straight-tusked elephant and spear at Lehringen, Germany (Thieme and Veil 1985), the argument for Neandertal hunting of rhinoceros is supported by butchery traces on multiple rhinoceros assemblages. It is beyond the scope of this paper to discuss whether or not Neandertals were capable of hunting large mammals regularly, however a large body of research on Middle Palaeolithic stone artifacts as projectiles (Shea 1993; Shea et al. 2001) and archaeofaunas (e.g., Jaubert et al. 1990; Hoffecker et al. 1991; Gaudzinski 1995; Gaudzinski and Turner 1999; Gaudzinski and Roebroeks 2000) has shown the answer to be “yes”. Additionally, isotopic signatures reflecting highly carnivorous Neandertal diets (Bocherens et al. 1999, 2001; Richards et al. 2000) are adequate support to put this debate to rest.

Layers IV-V: Aurignacian. A total of 86 rhinoceros specimens was recovered from Layers IV-V (Table 1). Isolated teeth are the most frequent element but a small bone assemblage is present. An MNI of 12 is based on mandibular molars. In contrast to the Middle Palaeolithic rhinoceros remains, carnivore gnawing is minimal on the Aurignacian rhinoceros assemblage, exhibited on just 17% of the specimens. No modifications attributed to humans were documented. Skeletal elements are more equally represented in this assemblage although bone counts are still low when compared to teeth. The Aurignacian archaeofauna is large and association with hearth features and rich artefact assemblage points to accumulation primarily by humans, probably in the contexts of repeated occupations. Large carnivores were present as well and no doubt contributed to this assemblage, but they were clearly not as major players in the Aurignacian deposit as they were in the Middle Palaeolithic. Nonetheless, the role of humans in the rhinoceros assemblage is ambiguous considering the lack of butchery traces.

Skeletal bone is similarly lacking in the Aurignacian deposit, representing a maximum bone MNI of three from several elements. The small sample size and probable palimpsest nature of this deposit demand cautious interpretations of element frequency and carcass utilization. One such cautious proposal is that complete carcasses or carcass portions were transported to the site. Presence of carpals, tarsals, and sesamoids attest to transport of limb segments, a pattern that was also detected in the equid and bovid assemblages from the Aurignacian deposit in Vogelherd. Bone frequency from Layers IV-V fits both hyaena and mixed hyaena-hominid assemblages (Brugal et al. 1997; Fosse 1999) but is also similar to the probable hunted assemblage from Taubach (Bratlund 1999a). Overall, some hints of interesting patterns can be discerned from the small Aurignacian rhinoceros assemblage but they must be regarded tentatively, considering the complicated formation history of the deposit.

The age profile for the Aurignacian rhinoceros remains reflects individuals from age groups I-III and no animals from the older adult groups (Figure 2). As discussed in the above summary of the Middle Palaeolithic rhinoceros age profile from Vogelherd, the Group II and III individuals would have been susceptible to predation by carnivores or humans. The best-represented age group in the Aurignacian assemblage is Group II (4-11 years), which includes newly solitary or small groups and paired rhinoceroses. It is possible that Aurignacian groups opportunistically procured single rhinoceroses of this age group or cow-calf pairs of Groups I and II.

To summarize, the woolly rhinoceros assemblages from the Middle Palaeolithic and Aurignacian deposits at Vogelherd provide interesting information yet ambiguous pictures of the role of this species in the site. The heavily carnivore modified nature of the Middle Palaeolithic rhinoceros remains clearly shows the role of large carnivores in the assemblage but prohibits any conclusions regarding the role of hominids. Alternating use of the cave by carnivores and hominids might be reflected in the assemblage, similar to other Middle Palaeolithic caves in Eurasia (e.g., Gamble 1999; Enloe et al. 2000; and see Table 1 in Fosse 1999:74). The slightly larger Aurignacian rhinoceros assemblage offers more insights on skeletal element frequencies and reflects a higher proportion of Group II individuals, the age class most likely to be preyed upon by human groups. Although carnivore modification is minimal on the Aurignacian assemblage, a dearth of anthropogenic modifications and the complicated formation history of the deposit prohibit making any confident conclusions regarding human contribution to the rhinoceros assemblage. In spite of studies of extant hyenas and their food remains as well as descriptions of Pleistocene hyaena dens (Villa and Bartram 1996; Brugal et al. 1997; Bartram and Villa 1998; Fosse 1999; Tournepiche and Couture 1999) that have contributed vastly to our understanding of this bone collector, defining the roles of

Table 2. Skeletal element representation for woolly mammoth (*Mammuthus primigenius*) in the Middle Palaeolithic and Aurignacian at Vogelherd.

| Element | VII - Middle Palaeolithic | | | IV-V - Aurignacian | | |
|--------------------------|---------------------------|-----|-----|--------------------|-----|-----|
| | NISP | MNE | MNI | NISP | MNE | MNI |
| Cranium | | | | | | |
| - <i>petrous portion</i> | - | - | - | 17 | 17 | 8 |
| - <i>occipital cond.</i> | - | - | - | 9 | 9 | 7 |
| - <i>max molars</i> | 4 | 4 | | 57 | 41 | 28 |
| - <i>other</i> | - | - | - | 319 | - | - |
| Mandible | | | | | | |
| - <i>bone</i> | - | - | - | 13 | 4 | 3 |
| - <i>mand molars</i> | 1 | 1 | 1 | 32 | 30 | 14 |
| Unid. Molars | 4 | - | - | 50 | - | - |
| Hyoid | - | - | - | - | - | - |
| Scapula | - | - | - | 54 | 8 | 8 |
| Humerus | - | - | - | 14 | 6 | 3 |
| Radius | - | - | - | 1 | 1 | 1 |
| Ulna | - | - | - | 9 | 2 | 2 |
| Carpals | - | - | - | 4 | 4 | 2 |
| Os Coxae | - | - | - | 19 | 2 | 1 |
| Femur | - | - | - | 13 | 6 | 4 |
| Tibia | - | - | - | 4 | 2 | 2 |
| Fibula | - | - | - | - | - | - |
| Tarsals | - | - | - | 2 | 2 | 1 |
| Metapodials | - | - | - | - | - | - |
| Longbone Fragment | 2 | - | - | 41 | - | - |
| Sesamoid | - | - | - | - | - | - |
| Phalanges | - | - | - | 5 | 4 | 2 |
| Vertebrae | - | - | - | 12 | 8 | 1 |
| Ribs | 1 | 1 | 1 | 45 | 8 | 1 |
| Sacrum | - | - | - | 1 | 1 | 1 |
| | 12 | 6 | 3 | 721 | 155 | 28 |

carnivores and hominids in bone accumulations, especially in caves, remains a complicated task (Gaudzinski and Turner 1999).

THE WOOLLY MAMMOTH ASSEMBLAGES

Mammoth remains are found in 90% of cave localities in the Swabian Jura of southern Germany (Gamble 1986:313, Table 7.4) although indisputable evidence of mammoth hunting has not yet been found at sites in this region. The specimens from these caves are primarily limited to fragments of teeth, ivory, and bone or in the case of Geissenklösterle, selectively chosen long bone fragments and ribs to be used in tool production (Münzel 2001). Vogelherd is an exception to this pattern and contains a large mammoth assemblage in the Aurignacian deposit. These differences among sites pose intriguing questions about the paleoecology of mammoths as well as their use at these sites.

All mammoth specimens from the Middle Palaeolithic and Aurignacian deposits at Vogelherd were identified as woolly mammoth (*Mammuthus primigenius*) based on tooth morphology (Maglio 1973). Molars make up a large proportion of the mammoth assemblages from Vogelherd and were analyzed in detail for age information. Molars and deciduous tusks were aged using published African and Asian elephant and Siberian mammoth molar data (Laws 1966; Haynes 1991; Kuzmina and Maschenko 1999) and are listed here in equivalent African Elephant Years (AEY; Laws 1966).

Layer VII: Middle Palaeolithic. A total of 13 mammoth specimens were recovered from this layer (Table 2). The ageable tooth sample (NISP = 6, MNI = 3) is too small to be meaningfully illustrated in an age profile but is described briefly: five specimens fall into age Group I (0 – 12 AEY), including three specimens aged at < 1 year; and one molar belongs to Group II or III. Similar to the rhinoceros sample from this layer, juvenile individuals

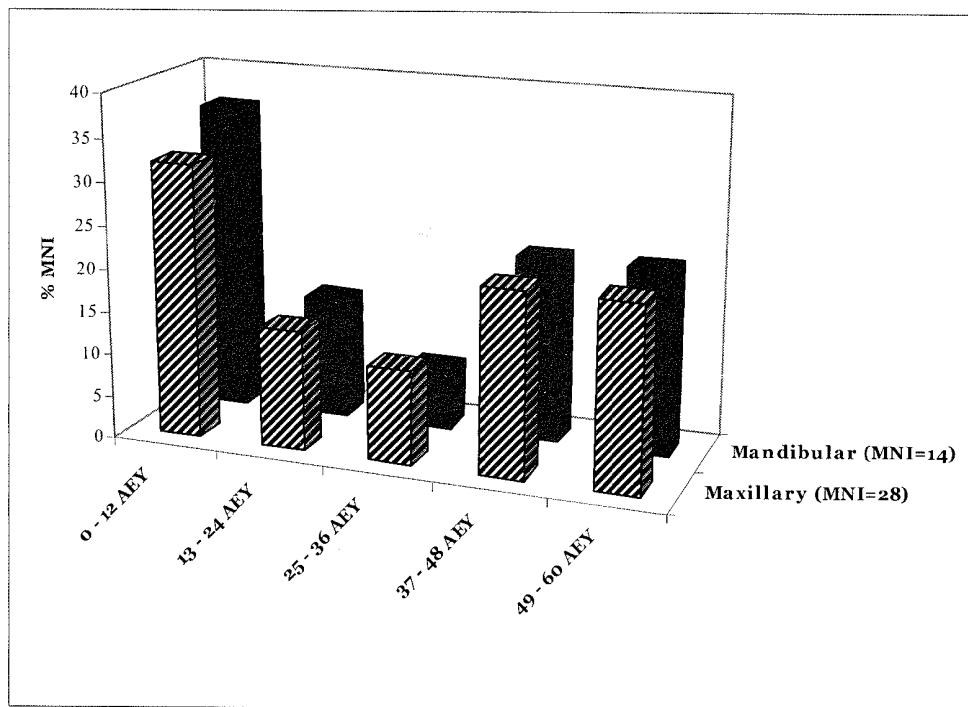


Figure 4. Age representation of woolly mammoth from the Aurignacian deposit at Vogelherd.

are most frequent and could have been the prey of both large carnivores and hominids.

Layers IV-V: Aurignacian. The Aurignacian deposit at Vogelherd contains an extensive mammoth assemblage made up of molars from a minimum of 28 individuals as well as the bone from 12 animals (Table 2). The question of whether mammoths were hunted or collected remains unanswered but age, skeletal element data, and bone preservation suggest a combination of these activities.

All but two molars were isolated; therefore upper and lower molar sets were analyzed separately and respective MNIs were tabulated. The age profile reflects selective deaths of individuals from all age groups, most likely the result of time-averaged, cumulative single mortalities as opposed to one, catastrophic kill (Figure 4). A high proportion of subadults is common in nearly all types of proboscidean death assemblages, as these age groups are more vulnerable to death by predation or natural causes (Haynes 1987). Presence but not predominance of the young adult and adult age groups as seen at Vogelherd is characteristic of selective or non-selective proboscidean death assemblages. Similar to juveniles, old animals are more susceptible to death by predation, disease, and nutritional stress and an age profile showing similar proportions of these age groups might reflect repeated, single mortalities by these causes. The Vogelherd age profile might also reflect opportunistic predation by humans of single animals or small groups from all age classes at sources of water, vegetation, or minerals. Periods of drought or extreme cold would have forced

mammoths to concentrate near water and patches of vegetation and proboscideans' dietary dependence on sodium and calcium is known to drive them to isolated sources (Redmond 1982). Hunting of proboscideans or scavenging of carcasses from natural mortalities at such locations have been proposed at several prehistoric sites in both Eurasia and North America (Abraczinskas 1994; Haynes 1999; Derevianko *et al.* 2000), and such scenarios may be reflected at Vogelherd.

The mammoth bone assemblage is dominated by cranial portions, which in addition to the molars, points to complete or nearly complete heads being transported to the cave. Tusk portions, scapulae and innomates

are also well-represented, followed by smaller numbers of limb elements. Differential weathering on much of the bone might reflect collecting of already weathered bone on the landscape, similar to what has been proposed at many of the mammoth bone "dwellings" and bone pile sites in central Europe and Russia (Soffer 1993). In the Aurignacian deposit at Vogelherd, a mammoth bone pile containing several tusks, molars, scapulae, one mandible, a "smashed" cranium, and other unidentified bone was documented in the south entrance of the cave (Riek 1934:53-54). According to the excavator Riek (1934:53), the pile was carefully constructed and quite sturdy, which suggests a special use of these elements or the bone pile as a whole. Considering that the cave has three entrances, Aurignacian groups might have used bulky elements such as the crania, mandibles, innomates, and scapulae to construct some sort of barricade or closure. Similar

skeletal element frequencies between Vogelherd and the "dwelling" sites supports the hypothesis that mammoth bone could have been used as a building material at Vogelherd. The bone pile might also have been a store of fuel, as wood would have been scarce on the landscape.

Neither certain evidence of mammoth hunting nor butchery has been found at Vogelherd but mammoth as a source of food cannot be ruled out. Crania might have been an important source of nutrition for human groups in addition to their utilitarian use. Consumption of fat-rich cranial tissues from medium-sized ungulates has been discussed for modern hunter-gatherer groups (Binford 1978, 1984; O'Connell et al. 1988) and proposed for Neandertals as well (Stiner 1994). Reports of modern elephant butchery (Crader 1983; Fisher 1992, 1993) note that crania are usually not transported or extensively butchered, but the number of mammoth crania at Vogelherd requires exploration of possible reasons of their frequency, including their utilization as a nutritional source. Limb portions, also present in the Vogelherd assemblage, would have been a rich source of meat.

There is no question that mammoths were used extensively for other purposes by Upper Palaeolithic groups in the Swabian Jura. The most elegant examples are the small ivory figurines depicting animals (mammoth, horse, lion, bear, bovid) and anthropomorphs from Vogelherd (Aurignacian), Geissenklösterle (Aurignacian, Gravettian), Hohlenstein-Stadel (Aurignacian), and Hohle Fels (Gravettian). Ivory was also used to fashion ornaments, tools, and other objects, while mammoth ribs and long bone flakes served as raw materials for bone points and various tools. Vogelherd is the only regional cave that contained a pile of mammoth remains and vast amounts of bone and complete molars, which possibly reflect a special use for the material. The significantly larger mammoth assemblage at Vogelherd is just one aspect of an exceptionally rich Aurignacian deposit that points to an intensive use of this cave. The Vogelherd mammoths also suggest that fluctuating environmental conditions could have influenced the location and number of mammoths in the local area, provided natural death sites to collect bone, possibilities for opportunistic hunting by Aurignacian groups, or both. Mammoths are represented in various amounts and forms in the Swabian Jura cave sites and in turn provide insight into several aspects of Upper Palaeolithic life in the region.

CONCLUSIONS

Vogelherd cave offers a unique opportunity to evaluate the role of woolly rhinoceros and woolly mammoth in Palaeolithic economies with its large sample of both megaherbivores preserved in the Middle Palaeolithic and Aurignacian deposits. Taphonomic analysis of the rhinoceros and mammoth assemblages indicates that a combination of factors were involved in their acquisition

and transport and that the role of these taxa in the economies of hominid occupants of the cave is not always clear.

Two important questions are raised by these data: 1) why are rhinoceros and mammoth so much more frequent at Vogelherd (especially in the Aurignacian) than at other Swabian Jura sites? and 2) despite their abundance, why is the role of rhinoceros and mammoth in the Palaeolithic economies at Vogelherd much less clear than other well-represented taxa in the assemblages, such as horse and reindeer? To address the first question, the frequency of these taxa might say more about the life histories of the species and paleoecology of the local area than any decisions of human groups, for example periods of higher populations concentrated locally as the result of favorable or unfavorable environmental conditions. This issue is being explored further in the ongoing analysis of the Vogelherd archaeofauna. The mammoth bone pile also points to specific use(s) of the large skeletal elements that could have been related to a number of economic decisions. Excluding the bone pile, the amount of time in which the other mammoth bone or rhinoceros bone was introduced to the cave is not clear and therefore the numbers of these taxa might be in part slightly inflated due to time-averaging. Taphonomic analysis suggests that the rhinoceros and mammoth in this deposit were not always human prey but instead reflect a combination of occasional, opportunistic procurement, collecting of bone on the landscape, and contributions of large carnivores, all of which most likely transpired over time. If some of the animals were indeed human prey, the lack of anthropogenic modifications might be due to several factors, including weathering of bone surfaces and minimal (if any) butchering of carcasses. Spongy rhinoceros and mammoth long bones were probably not worth exploiting for within-bone nutrients, unlike horse and reindeer long bones. In addition, if these megaherbivores were subsistence species, it appears that this was an occasional occurrence at best and were supplemental to more abundant prey such as horse and reindeer. Overall, the Vogelherd data suggest that woolly rhinoceros and woolly mammoth present research challenges unique to their ecology, behavior, and body size but they also raise many intriguing questions about the role of these animals at Vogelherd, especially during the Aurignacian, and the place of the site in the regional settlement system.

ACKNOWLEDGEMENTS

The Vogelherd analysis was partly supported by the Sondersforschungsbereich 275 under the Deutsche Forschungsgemeinschaft; and the Landesgraduiertenförderungsgesetz, Baden-Württemburg. Thanks to the symposium organizers Dr. Bryan Hockett and Jonathan Haws for including me in their session at the 66th Meeting of the Society for American Archaeology (2001). I am very grateful to Dr. Reinhard Ziegler for help identifying the mammoth and rhinoceros molars;

Drs. Bodil Bratlund and Sabine Gaudzinski for providing references; and to Drs. Nicholas Conard, Gary Haynes, Susanne Münzel, Hans-Peter Uerpmann, and Piotr Wojtal for their contributions to this study.

REFERENCES CITED

ABRACZINSKAS, L. M. 1994. The Distribution of Pleistocene Proboscidean Sites in Michigan: A Cooccurrence Analysis of Their Relation to Surface Saline Water. *Michigan Academician* 17: 65-80.

AUGUSTE, P. 1992. Étude Archéozoologique des Grands Mammifères du Site Pléistocène Moyen de Biache-Saint-Vaast (Pas-De-Calais, France): Apports Bio-stratigraphiques et Paleoethnographiques. *L'Anthropologie* 96: 49-70.

BARTRAM, L. E. AND P. VILLA. 1998. The Archaeological Excavation of Prehistoric Hyena Dens: Why Bother? In *Économie Préhistorique: Les Comportements De Subsistance Au Paléolithique*, edited by J.-P. Brugal, L. Meignen and M. Patou-Mathis, pp. 15-29. Editions APDCA, Antibes.

BERGER, J. AND C. CUNNINGHAM. 1994. Active Intervention and Conservation: Africa's Pachyderm Problem. *Science* 263: 1241-1242.

BINFORD, L. R. 1978. *Nunamiut Ethnoarchaeology*. Academic Press, New York.

BINFORD, L.R. 1984. *Faunal Remains from Klasies River Mouth*. Academic Press, New York.

BLUMENSCHINE, R. J. 1988. An Experimental Model of the Timing of Hominid and Carnivore Influence on Archaeological Bone Assemblages. *Journal of Archaeological Science* 15: 483-502.

BLUMENSCHINE, R. 1995. Percussion Marks, Tooth Marks, and Experimental Determinations of the Timing of Hominid and Carnivore Access to Long Bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29: 21-51.

BOCHERENS, H., D. BILLIOU, A. MARIOTTI, M. PATOU-MATHIS, M. OTTE, D. BONJEAN, AND M. TOUSSAINT. 1999. Palaeoenvironmental and Palaeodietary Implications of Isotopic Biogeochemistry of Last Interglacial Neanderthal and Mammal Bones in Scladina Cave (Belgium). *Journal of Archaeological Science* 26: 599-607.

BOCHERENS, H., D. BILLIOU, A. MARIOTTI, M. TOUSSAINT, M. PATOU-MATHIS, D. BONJEAN, AND M. OTTE. 2001. New Isotopic Evidence for Dietary Habits of Neanderthals from Belgium. *Journal of Human Evolution* 40: 497-505.

BRAIN, C. K., O. FORGE, AND P. ERB. 1999. Lion Predation on Black Rhinoceros (*Diceros Bicornis*) in Etosha National Park. *African Journal of Ecology* 37: 107-109.

BRATLUND, B. 1999a. Taubach Revisited. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz* 46: 67-174.

BRATLUND, B. 1999b. Anthropogenic Factors in the Thanatocoenose of the Last Interglacial Travertines at Taubach (Germany). In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 255-262. Habelt, Bonn.

BRUGAL, J.-P., P. FOSSE, AND J.-L. GUADELLI. 1997. Comparative Study of Bone Assemblages Made by Recent and Pleistocene Hyenids. In *Proceedings of the 1993 Bone Modification Conference, Hot Springs, South Dakota*, edited by L. A. Hannus, L. Rossum and R. P. Winham, pp. 158-187. Occasional Publication No. 1, Archaeology Laboratory, Augustana College, Sioux Falls.

CAPALDO, S. 1998. Simulating the Formation of Dual-Patterned Archaeofaunal Assemblages with Experimental Control Samples. *Journal of Archaeological Science* 25: 311-330.

CARBYN, L. N., S. OOSENBRUG, AND D. W. ANIONS 1993. *Wolves, Bison and the Dynamics Related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park*. Canadian Circumpolar Institute, Edmonton.

CHURCHILL, S. E. AND F. SMITH. 2000. A Modern Human Humerus from the Early Aurignacian of Vogelherdhöhle (Stetten, Germany). *American Journal of Physical Anthropology* 112: 251-273.

CONARD, N. J. AND M. BOLUS. 2003. Dating the Appearance of Modern Humans and Timing of Cultural Innovations in Europe. *Journal of Human Evolution*, 44: 331-371.

CRADER, D. C. 1983. Recent Single-Carcass Bone Scatters and the Problem of "Butchery" Sites in the Archaeological Record. In *Animals and Archaeology: Hunters and Their Prey (I)*, edited by J. Clutton-Brock and C. Grigson, pp. 107-141. British Archaeological Reports Series 163.

CRUZ-URIBE, K. 1991. Distinguishing Hyena from Hominid Bone Accumulations. *Journal of Field Archaeology* 18: 467-486.

CZARNETSKI, A. 1983. Zur Entwicklung Der Menschen in Südwestdeutschland. In *Urgeschichte in Baden-Württemberg*, edited by H.-J. Müller-Beck, pp. 217-240. Konrad Theiss Verlag, Stuttgart.

DAESCHLER, E. B. 1996. Selective Mortality of Mastodons (*Mammut americanum*) from the Port Kennedy Cave (Pleistocene; Irvingtonian), Montgomery County, Pennsylvania. In *Palaeoecology and Palaeo-environments of Late Cenozoic Mammals: Tributes to the Career of C.S. (Rufus) Churcher*, edited by K. M. Stewart and K. L. Seymour, pp. 83-96. University of Toronto Press, Toronto.

DEREVIANKO, A. P., V. ZENIN, S. V. LESHCHINSKIY, AND E. N. MASHCHENKO. 2000. Peculiarities of Mammoth Accumulation at Shestakovo Site in West Siberia. *Archaeology, Ethnology and Anthropology of Eurasia* 3: 42-45.

DU TOIT, R. 1986. Re-Appraisal of Black Rhinoceros Subspecies. *Pachyderm* 6: 5-9.

DUNHAM, K. 1985. Ages of Black Rhinos Killed by Drought and Poaching in Zimbabwe. *Pachyderm* 5: 12-13.

ENLOE, J. G., F. DAVID, AND G. BARYSHNIKOV. 2000. Hyenas and Hunters: Zooarchaeological Investigations at Prolom II Cave, Crimea. *International Journal of Osteoarchaeology* 10: 310-324.

FISHER, J. W. 1992. Observations on the Late Pleistocene Bone Assemblage from the Lamb Spring Site, Colorado. In *Ice Age Hunters of the Rockies*, edited by D. J. Stanford and J. S. Day, pp. 51-81. Denver Museum of Natural History and University Press of Colorado, Boulder.

FISHER, J. W. 1993. Foragers and Farmers: Material Expressions of Interaction at Elephant Processing Sites in the Ituri Forest, Zaire. In *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains*, edited by J. Hudson, pp. 247-262. Southern Illinois University at Carbondale Occasional Paper 21, Carbondale.

FOSSÉ, P. 1999. Cave Occupation During Palaeolithic Times: Man and/or Hyena? In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 73-88. Habelt, Bonn.

GAMBLE, C. 1979. Hunting Strategies in the Central European Palaeolithic. *Proceedings of the Prehistoric Society* 45: 35-52.

GAMBLE, C. 1986. *The Palaeolithic Settlement of Europe*. Cambridge University Press, Cambridge.

GAMBLE, C. 1999. The Hohlenstein-Stadel Revisited. In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 305-324. Habelt, Bonn.

GAUDZINSKI, S. 1995. Wallertheim Revisited: A Re-Analysis of the Fauna from the Middle Palaeolithic Site of Wallertheim (Rheinessen/Germany). *Journal of Archaeological Science* 22: 51-66.

GAUDZINSKI, S. AND W. ROEBROEKS. 1999. Adults Only: Reindeer Hunting at the Middle Palaeolithic Site Salzgitter-Lebenstedt, Northern Germany. *Journal of Human Evolution* 38: 497-521.

GAUDZINSKI, S. AND E. TURNER. 1999. Summarizing the Role of Early Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages. In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 381-393. Habelt, Bonn.

GERMONPRÉ, M. 1993. Taphonomy of Pleistocene Mammal Assemblages in the Flemish Valley, Belgium. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 63: 271-309.

GODDARD, J. 1970. Age Criteria and Vital Statistics of a Black Rhinoceros Population. *East African Wildlife Journal* 8: 105-121.

GUÉRIN, C. 1980. Les Rhinocéros (Mammalia, Perissodactyla) du Miocène Terminal au Pléistocène Supérieur en Europe Occidentale. *Documents des Laboratoires de Géologie* 79: 1-1185.

GUTHRIE, R. D. 1990. *Frozen Fauna of the Mammoth Steppe: The Story of Blue Babe*. University of Chicago Press, Chicago.

HAHN, J. 1993. Urgeschichtliche Forschung der Ostalb. *Karst und Höhle* 1993: 213-224.

HAYNES, G. 1980. Evidence of Carnivore Gnawing on Pleistocene and Recent Mammalian Bones. *Paleobiology* 6 (3): 341-351.

G. HAYNES. 1982. Utilization and Skeletal Disturbances of North American Prey Carcasses. *Arctic* 35 (2): 266-281.

G. HAYNES. 1987. Proboscidean Die-Offs and Die-Outs: Age Profiles of Fossil Collections. *Journal of Archaeological Science* 14: 659-668.

G. HAYNES. 1991. *Mammoths, Mastodonts, and Elephants: Biology, Behavior, and the Fossil Record*. Cambridge University Press, Cambridge.

G. HAYNES. 1999. The Role of Mammoths in Rapid Clovis Dispersal. In *Mammoths and the Mammoth Fauna: Studies of an Extinct Ecosystem*, edited by G. Haynes, J. Klimowicz and J. W. F. Reumer, pp. 9-38. Deinsea, Rotterdam.

HITCHINS, P. M. 1978. Age Determination of the Black Rhinoceros (*Diceros Bicornis* Linn.) in Zululand. *South African Journal of Wildlife Research* 8 (2): 71-80.

HOFFECKER, J., G. BARYSHNIKOV, AND O. POTOPOVA. 1991. Vertebrate Remains from the Mousterian Site of Il'skaya I (Northern Caucasus, USSR): New Analysis and Interpretation. *Journal of Archaeological Science* 18: 113-147.

JAUBERT, J., M. LORBLANCHET, H. LAVILLE, R. SLOTT-MOLLER, A. TURQ, AND J.-P. BRUGAL. 1990. *Les Chasseurs d'aurochs de La Borde : Un Site du Paléolithique Moyen (Livernon, Lot)*. Maison des Sciences de l'Homme, DAF No. 27, Paris.

KINGDON, J. 1979. *East African Mammals: An Atlas of Evolution in Africa*. University of Chicago Press, Chicago.

KRUUK, H. 1972. *The Spotted Hyena: A Study of Predation and Social Behavior*. University of Chicago Press, Chicago.

KURTÉN, B. 1953. *On the Variation and Population Dynamics of Fossil and Recent Mammal Populations*. Acta Zoologica Fennica 76. Helsingforsiae.

KUZMINA, I. E. AND E. N. MASCHENKO. 1999. Age Morphological Changes in the Skull and Skeleton of Mammoth Calves of the Russian Plain. In *Mammoth Calves Mammuthus Primigenius*, edited by I. E. Kuzmina, pp. 51-120. Proceedings of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

LAWS, R. M. 1966. Age Criteria for the African Elephant *Loxodonta A. Africana*. *East African Wildlife Journal* 4: 1-37.

LEHMANN, U. 1954. Die Fauna des "Vogelherds" bei Stetten ob Lontal (Württemberg). *Neues Jahrbuch für Geologie und Paläontologie* 99: 33-146.

LISTER, A. 2001. Age Profile of Mammoths in a Late Pleistocene Hyaena Den at Kent's Cavern, Devon, England. In *Proceedings of the International Conference on Mammoth Site Studies*, edited by D. West, pp. 35-43. University of Kansas Publications in Anthropology Vol. 22, Lawrence.

LUPO, K. D. AND J. F. O'CONNELL. 2002. Cut and Tooth Mark Distributions on Large Animal Bones: Ethnoarchaeological Data from the Hadza and Their Implications for Current Ideas About Early Human Carnivory. *Journal of Archaeological Science* 29: 85-109.

MAGLIO, V. J. 1973. *Origin and Evolution of the Elephantidae*. American Philosophical Society, Philadelphia.

MECH, L. D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*.

MÜNZEL, S. 2001. The Production of Upper Palaeolithic Mammoth Bone Artifacts from Southwestern Germany. In *Le Terra Degli Elefanti - the World of Elephants: Proceedings of the 1st International Congress*, edited by G. Cavarretta, P. Gioia, M. Mussi and M. Palombo, pp. 448-454. CNR, Rome.

NAVARRO, B. M. AND P. PALMQVIST. 1999. Venta Micena (Orce, Granada, Spain): Human Activity in a Hyena Den During the Lower Pleistocene. In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 57-71. Habelt, Bonn.

NIVEN, L. 2001. The Role of Mammoths in Upper Palaeolithic Economies of Southern Germany. In *Le Terra Degli Elefanti - the World of Elephants: Proceedings of the 1st International Congress*, edited by G. Cavarretta, P. Gioia, M. Mussi and M. Palombo, pp. 323-327. CNR, Rome.

O'CONNELL, J. F., K. HAWKES, AND N. BLURTON JONES. 1988. Hadza Hunting, Butchering, and Bone Transport and Their Archaeological Implications. *Journal of Anthropological Research* 44 (2): 113-161.

OWEN-SMITH, R. N. 1988. *Megaherbivores : The Influence of Very Large Body Size on Ecology*. Cambridge University Press, Cambridge.

PALMQVIST, P., B. MARTINEZ-NAVARRO, AND A. ARRIBAS. 1996. Prey Selection by Terrestrial Carnivores in a Lower Pleistocene Community. *Paleobiology* 22 (4): 514-534.

PICKERING, T. R. 2002. Reconsideration of Criteria for Differentiating Faunal Assemblages Accumulated by Hyenas and Hominids. *International Journal of Osteoarchaeology* 12: 127-141.

RAWN-SCHATZINGER, V. 1992. *The Scimitar Cat Homotherium Serum Cope: Osteology, Functional Morphology, and Predatory Behavior*. Illinois State Museum Reports of Investigations, Springfield.

REDMOND, I. 1982. Salt Mining Elephants of Mount Elgon. *Swara* 5: 28-31.

RICHARDS, M., P. PETTIT, E. TRINKAUS, F. SMITH, M. PAUNOVIC, AND I. KARAVANIC. 2000. Neanderthal Diet at Vindija and Neanderthal Predation: The Evidence from Stable Isotopes. *Proceedings of the National Academy of Sciences* 97 (13): 7663-7666.

RICHTER, D., J. WAIBLINGER, W. J. RINK, AND G. A. WAGNER. 2000. Thermoluminescence, Electron Spin Resonance and ^{14}C -Dating of the Late Middle and Early Upper Palaeolithic Site of Geißenklösterle Cave in Southern Germany. *Journal of Archaeological Science* 27: 71-89.

RIEK, G. 1934. *Die Eiszeitjägerstation am Vogelherd im Lontal*. Akademische Verlagsbuchhandlung, Tübingen.

SCHALLER, G. B. 1972. *The Serengeti Lion: a Study of Predator-Prey Relations*. University of Chicago Press, Chicago.

SCOTT, K. 1986. The Large Mammal Fauna. In *Le Cotte St. Brelade, 1961-1978*, edited by P. Callow and J. M. Cornford, pp. 109-137. Geo Books, Norwich.

SELVAGGIO, M. M. 1994. Carnivore Tooth Marks and Stone Tool Butchery Marks on Scavenged Bones: Archaeological Implications. *Journal of Human Evolution* 27: 215-228.

SELVAGGIO, M. M. 1998. Evidence for a Three-Stage Sequence of Hominid and Carnivore Involvement with Long Bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Archaeological Science* 25: 191-202.

SHEA, J. 1993. Lithic Use-Wear Evidence for Hunting by Neandertals and Early Modern Humans from the Levantine Mousterian. In *Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia*, edited by G. L. Peterkin, H. M. Bricker and P. Mellars, pp. 189-187. Archeological Papers of the American Anthropological Association No. 4. American Anthropological Association, Washington, D.C.

SHEA, J., Z. DAVIS, AND K. BROWN. 2001. Experimental Tests of Middle Palaeolithic Spear Points Using a Calibrated Crossbow. *Journal of Archaeological Science* 28: 807-816.

SOFFER, O. 1993. Upper Paleolithic Adaptations in Central and Eastern Europe and Man-Mammoth Interactions. In *From Kostenki to Clovis: Upper Paleolithic-Paleo-Indian Adaptations*, edited by O. Soffer and N. Praslov, pp. 31-49. Plenum Publishers, New York.

STINER, M. 1994. *Honor among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press, Princeton.

SUTCLIFFE, A. J. 1970. Spotted Hyaena: Crusher, Gnawer, Digester and Collector of Bones. *Nature* 227: 1110-1113.

THIEME, H. AND S. VEIL. 1985. Neue Untersuchungen zum Eemzeitlichen Elefanten-Jagdplatz Lehringen, Ldkr. Verden. *Die Kunde* 36: 11-58.

TOURNEPICHE, J.-F. AND C. COUTURE. 1999. The Hyena Den of Rochelot Cave (Charente, France). In *The Role of Humans in the Accumulation of European Lower and Middle Palaeolithic Bone Assemblages*, edited by S. Gaudzinski and E. Turner, pp. 89-101. Habelt, Bonn.

VILLA, P. AND L. E. BARTRAM. 1996. Flaked Bone from a Hyena Den. *Paleo* No 8: 143-159.

ZAPFE, H. 1939. Die Lebensspuren der eiszeitlichen Höhlenhyäne. Die Urgeschichtliche Bedeutung der Lebensspuren knochenfressender Raubtiere. *Palaeobiologica* 7: 111-146.