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THE LARGE VERTEBRATES FROM PICKEN'S HOLE, SOMERSET

by

KATHARINE SCOTT

ABSTRACT

Picken's Hole (NGR ST 3964 5500) is a mainly collapsed limestone cave on the northern slope of a ridge of the Mendip Hills near Compton Bishop, Somerset. It is one of a small series of caves at about 50 m AOD in a ridge of carboniferous limestone. At the time of its excavation in the 1960s, the accessible cave consisted of a short passage 1-1.5 m across opening onto a roughly level platform about 6 m across at the foot of a low cliff. Today the site is almost invisible as the result of weathering of the limestone and the growth of vegetation but it is unlikely ever to have been more than a small shelter.

It is an important site in a number of respects. It was excavated with great attention to documentation. Several horizons were identified and although few artefacts were found, abundant vertebrate remains were recovered. Those from two levels in particular warranted the detailed study presented here. They present a rare occurrence of two large assemblages of bones believed to have been brought to the site at different periods of the Late Pleistocene principally by two different predators. The earlier accumulation is ascribed to wolves and the later to hyaenas.

SUMMARY OF EXCAVATION AND STRATIGRAPHY

The history of excavation at the site and stratigraphic details are discussed elsewhere in this volume (ApSimon, Mullan and Smart pp 239-244 and ApSimon and Smart pp 245-249). In summary, six major subdivisions of the deposits were recognised (Figure 1):

Unit 1 - post-Pleistocene soil containing a variety of modern debris
Unit 2 - clayey breccia containing neither artefacts nor faunal remains
Unit 3 - sandy loam with abundant large vertebrate remains
Unit 4 - limestone breccia in a matrix of coarse sand containing a small assemblage of bones
Unit 5 - reddish brown clay loam with abundant large vertebrate remains
Unit 6 - cemented and sandy breccia containing neither archaeological material nor large vertebrate remains.

With the exception of a small quantity of surface material (Unit 1), which is of Holocene origin, and the sterile Unit 2 below it, most of the excavated animal remains and artefacts are of Late Pleistocene age. Radiocarbon dates indicate a Middle Devensian (last glacial) age for the material in Unit 3 thus making it equivalent in time to Marine Oxygen Isotope Stage 3, MIS 3 (c.60-26 ka). Attempts to date bones from the bone-bearing horizon, Unit 5, have proved unsuccessful, but this stratigraphically earlier fauna is believed to predate MIS 3. On biostratigraphic grounds it is assigned to an interstadial, possibly equated with MIS 5a.

As Units 3, 4 and 5 contain the Pleistocene large vertebrates, discussion will now centre on these levels. Unit 3 was noted to have five sub-units or contexts but the fauna is homogeneous suggesting accumulation during more or less the same climatic conditions. It is typical of other sites of Middle Devensian Age having spotted hyaena, lion, arctic fox, wolf,

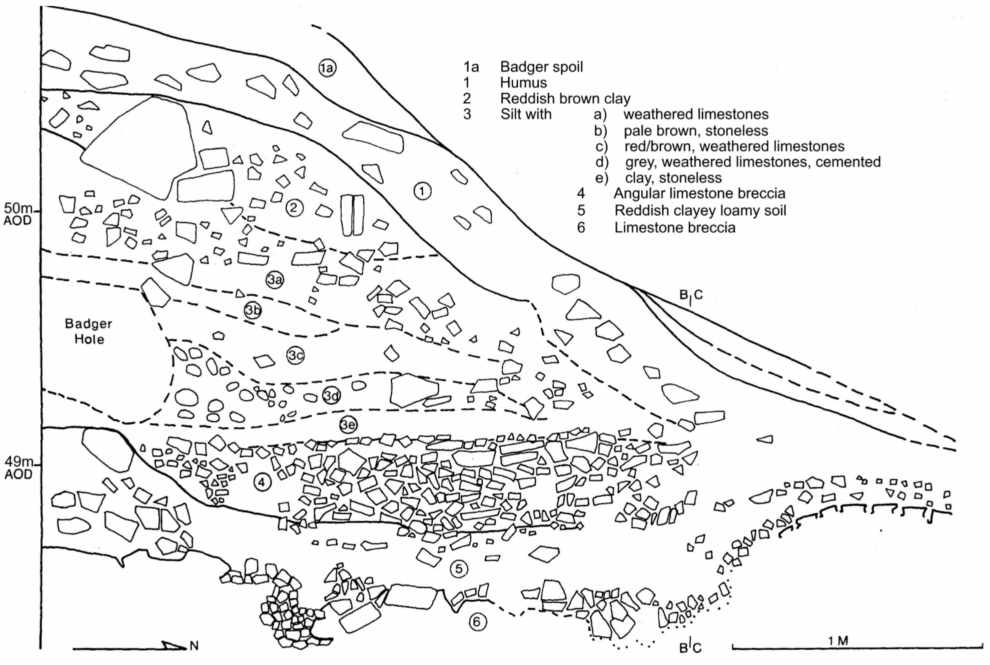

Figure 1. *Section through the deposits at Picken's Hole.*
Redrawn from ApSimon, ***pers. comm.***

bear, woolly mammoth, woolly rhinoceros, horse, reindeer, giant deer and bison. The abundance of spotted hyaena remains, the high degree of chewing of the majority of the bones, and the fact that the cave passage was too small to have been anything other than an animal den suggest that the hyaena was the principal accumulator of the Unit 3 assemblage. Human presence is evident from a number of artefacts (see Wragg Sykes, pp 315-338). Of the artefacts ApSimon (1986) suggests that "The small quantity of material, the striking of a number of flakes from but a single flint core, the restricted distribution of the artefacts, and the absence of other signs of occupation, are consistent with this having been nothing more than a single brief visit of a few hours, or a day or two." There are no cut-marks visible on the bones from this level. Dates on bones from this unit ranging between c. 27,000 and 46,000 BP concur with a Middle Devensian (MIS 3) age (see Mullan, pp 261-266 for details).

The species represented in Unit 4 are wolf, red fox, reindeer, giant deer and bison. There are no radiocarbon dates for this horizon. The absence of spotted hyaena, woolly rhino and horse indicates that Unit 4 predates the open steppe tundra conditions typical of MIS 3 and is more akin to the underlying Unit 5. ApSimon, (*pers comm.)* considered the Unit 4 fauna to be the last survivors of the Unit 5 fauna in a changing environment. However, giant deer, represented by a single metacarpal, would more typically be associated with the overlying Middle Devensian assemblage (Unit 3) and points to the likelihood that a certain amount of admixture of material is inevitable where the site is an animal den.

Although four subdivisions of Unit 5 were distinguished on the basis of colour changes in the red clay loam, the bones and teeth were regarded as one assemblage by the excavators. There were neither artefacts nor any other signs of human presence in Unit 5. The large vertebrate species from Unit 5 are bear, wolf, red fox, reindeer and bison. Many of the bones are gnawed but to a lesser extent than those in Unit 3. This is attributed to wolves. In a preliminary study of this material Stuart (1982, 1983) recorded red deer in addition to the species listed above. However, the small number of red deer bones attributed to Unit 5 were concentrated in a pocket of matrix at the western limit of the excavation. It is now clear that, although this accumulation was excavated at the same depth as Unit 5, there was no stratigraphic continuity between Unit 5 and the matrix containing the red deer (ApSimon *pers. comm.*)

Several bone samples from Unit 5 were submitted for radiocarbon dating (Mullan, pp 261-266), but the dates of c.25,000 B.P. and c.27,000 B.P. are younger than those from the overlying Unit 3 and are clearly anomalous.

The Units 3 and 5 assemblages were studied with a view to ascertaining species and body-part representation, the age at death of predators and prey, and the extent of damage to bones (cut-marks, tooth punctures, signs of gnawing). There are several reasons for making such a detailed study. In the first instance, the range of species is indicative of the prevailing climate and environment at the time of their accumulation. As the site was evidently not a natural trap or fissure into which bones were washed, the range of species and the condition of the bones should also enable one to identify the agent(s) of accumulation. Some animals might have been brought to the site as food; others may have died while occupying the shelter. Many of the clues lie in the bones themselves but, in order to interpret the data, reference is also made to ethological studies available for the living counterparts of the represented species with various questions in mind. To what extent do the carnivores represented make use of dens? What factors might govern prey selection? Are meat-bearing bones brought back to the dens?

SPECIES AND SKELETAL REPRESENTATION AT PICKEN'S HOLE

A list of vertebrate species identified in Units 3, 4 and 5 is provided in Table 1. The details of all the skeletal elements for each species are given in Tables 4-15 (Appendix 1).

Clearly the two main Units (3 and 5) have quite different vertebrate faunas. The tenet of this paper is that these differences are due to a combination of two factors. The two levels were possibly separated in time by thousands of years and accumulated under very different environmental conditions. This in turn not only determined what ungulates were locally available to be brought to the site by predators but also determined which predators would be present. Unit 3 is considered to represent a mid-Devensian hyaena den and Unit 5 is thought to have been accumulated primarily by wolves, probably during an early Devensian. The large vertebrates from Unit 4 have the characteristics of the Unit 5 material, but it is a very small assemblage and will not form part of the main discussion.

Table 1. *The large vertebrates from Picken's Hole. Numbers shown are the number of identified specimens for each species. For details of skeletal elements and minimum numbers of individuals represented see Appendix 1 Tables 4-15.*

	Unit 5 MIS 5a	**Unit 5/4**	**Unit 4**	**Unit 3** MIS 3
Carnivora				
Vulpes lagopus, arctic fox	-	-	-	37
Vulpes vulpes, red (common) fox	157	20	262	-
Canis lupus, wolf	92	-	7	13
Ursus arctos, brown bear	57	-	-	3
Crocuta crocuta, spotted hyaena	-	-	-	234
Panthera leo spelaea, lion	-	-	-	3
Proboscidea				
Mammuthus primigenius, woolly mammoth	-	-	-	30
Perissodactyla				
Equus ferus, horse	-	-	-	161
Coelodonta antiquitatis, woolly rhinoceros	-	-	-	160
Artiodactyla				
Megaloceros giganteus, giant deer	-	-	1	4
Cervus elaphus, red deer	-	-	-	47
Rangifer tarandus, reindeer	584	56	18	184
Bison priscus, bison	223	-	14	48

CLIMATE, ENVIRONMENT AND CHRONOLOGY OF UNIT 3 AND UNIT 5

Unit 3

Woolly rhino and horse predominate in a fauna comprised of large grazers. Spotted hyaena is more frequently represented than any other species. The predominance of these three is indicative of the highly productive environment that was evidently typical of much of southern Britain during the mid-Devensian. Sites with comparable faunas are collectively assigned to the Pin Hole mammal assemblage-zone (Currant and Jacobi, 2011) and include Coygan Cave (Scott, 1986; Aldhouse-Green *et al.* 1995), Tornewton Cave (Sutcliffe and Zeuner, 1962), Wookey Hole Hyaena Den (Currant and Jacobi, 1997), Pin Hole Cave (Currant and Jacobi, 2001), Robin Hood Cave (Jacobi and Grûn, 2003) and Sutton Courtenay (Eeles and Scott *in prep.*). Radiocarbon dates range between c.30,000 and >50,000 BP (Jacobi *et al.* 2006) but the limitations of radiocarbon beyond 50, 000 years make it likely that these mid-Devensian vertebrate faunas range further back in time, perhaps to c.60,000 years BP, thus spanning all of MIS 3 (Currant and Jacobi, 2011).

The fauna from Unit 3 at Picken's Hole and from the other above-mentioned sites indicate abundant grassland with a virtual absence of trees: a steppe environment. This particular habitat, commonly referred to in the literature as the 'Mammoth Steppe', characterised a vast expanse of Eurasia during the Late Pleistocene and supported a far greater diversity of very large herbivores than would be possible anywhere today: mammoths, woolly rhinos, horses, bison, reindeer, and giant deer, plus dependant lions, hyaenas, sabre-toothed cats and others (Guthrie. 1982; Haynes, 2001). Currant and Jacobi (1997) state that it is difficult to interpret the environmental significance of the range of British mid-Devensian large herbivores because they are indicative of a highly productive environment that, in many ways, is more reminiscent of interglacial than cold stage conditions. However, a clue to this apparent anomaly surely lies in the detailed stable-isotope record for MIS 3. This indicates that the period around 59 ka BP to 44 ka BP was relatively warm and stable (Barron, *et al.* 2003) which then gradually deteriorated into a period of climatic instability throughout the rest of the stage with alternating periods of intense cold and milder conditions, some of perhaps only a few decades duration (Dansgaard, *et al.* 1993). If animals (and humans) remained in Britain throughout the climatic fluctuations of MIS 3 then perhaps, as suggested by Currant and Jacobi *op.cit.*, they coped with the highly variable conditions by being pre-adapted to extreme seasonal temperature ranges and predominantly arid environments.

An alternative theory, proposed here, is that these mammals were only in Britain intermittently, during the milder episodes, and therefore never had to make major adaptations to extremely cold conditions. Of the extant species represented in the mid-Devensian sites (e.g. reindeer) some are evidently adapted to the harsh environments of modern day periglacial regions but, equally, they can live at more temperate latitudes. In fact, it is likely that the Late Pleistocene offered a far more optimal habitat with less pressure from human encroachment than they experience in the marginal areas where they survive today. Exactly what environments are represented by the Devensian cave faunas may never be fully known as so little other biological material (vegetation, molluscs, and insects) is known from these sites. It is interesting to note however, that at recent excavations of 'open' mid-Devensian sites (Sutton Courtenay and Lynford) mammoths, woolly rhinos and other large grazers have been found with artefacts and in association with insects and molluscs of distinctly temperate habitats (Eeles *pers. comm.*; Coope (in Boismier *et al.* 2003).

The likelihood of these large herbivores being in Britain during the mild rather than the very cold episodes of MIS 3 is even more credible if one takes into account their dietary requirements. Although southern Britain during the Middle Devensian was marginal to northerly, glaciated regions, it was clearly unlike any existing periglacial zone. This fact is crucial to our understanding and interpretation of animal and human behaviour and adaptation in the Late Pleistocene. Today, the periglacial regions are characterised by acidic boreal soils, summers are short, winters are long and extreme, and precipitation in the form of snow is heavy. Most importantly, the heavy winter snowfall not only buries possible forage for months at a time but it melts in the spring over the frozen ground causing much of the region to become impenetrable bog. Thus soil temperatures remain low, even in the summer, which in turn affects plant growth strategies. The outcome is a low size, low quality herbage quite unsuitable to sustain high ungulate biomass. As noted above, Guthrie (1982) suggests that the Mammoth Steppe supported a far greater diversity of very large herbivores during the Late Pleistocene than would be possible anywhere today, suggesting a productive environment. Winters might have been cold, even in the milder episodes, but this need not have adversely affected such well-insulated species as mammoth and woolly rhino with their dense subcutaneous fat layer and thick fur. The limiting factor would have been the availability or otherwise of abundant grazing. Vegetation and soil analyses from Late Pleistocene deposits indicate that the flora was rich and the soil fertile which in turn suggest that the plant-growing season was long, and that the resulting fodder for the herbivores was high in nutrients and available energy. Most importantly, although the annual seasonal cycle might have been characterised by cold winters, it is likely that there was little snowfall, with wind preventing snow from settling to any great extent. Not having been buried under snow for many months, summer soils would have been generally warm and dry. Today, the rains of the steppe tundra region peak in the late summer, which is too late for optimum plant productivity. In order to maximise the benefit to growing plants needed to support the range of large herbivores evident during MIS 3, most of the annual moisture is likely to have fallen as rain in the spring, and to a lesser extent in the summer. For many years, analogies have been made between the Last Ice Age and modern periglacial landscapes creating a vision of mammoths clearing snow with their tusks to reach grazing and people in thick furs making shelter in snow covered or glaciated landscapes. Instead, for the valleys around the Mendip Hills for much of the mid-Devensian, perhaps we should envisage an early spring with abundant herbs, giving rise to additional, luxurious summer growth with medium and tall herbaceous plants available late into the autumn, an ideal environment for large herds of horse, woolly rhino and mammoth.

Unit 5

The total absence of the large grazers (mammoth, woolly rhinoceros and horse) from Unit 5 with herbivores represented by only two species (reindeer and bison) is indicative of a somewhat different environment from that of Unit 3. Likewise, the list of carnivores is restricted by comparison with Unit 3. Wolf, bear and common fox are present but hyaena and lion are absent.

The ubiquity of bison in British Pleistocene assemblages attributed to both glacial and interglacial stages indicates that bison tolerated a wide range of climatic conditions. In Pleistocene studies, reindeer are generally regarded as indicative of cool or cold climate and are frequently associated with open terrain, cold-stage species such as woolly rhino, mammoth and horse.

However, the association of reindeer and bison without the mammoths, woolly rhinos and horses is typical of numerous British sites believed to pre-date MIS 3 and to reflect interstadial conditions equivalent to MIS 5a. Currant and Jacobi (2001, 2011) assign 21 British faunal assemblages to this period (designated the Banwell Bone Cave mammal assemblage-zone).

Among these are Willments's Pit, Isleworth, and Cassington in Oxfordshire. At both locations, the reindeer/bison fauna is associated with vegetation and molluscs indicative of a cool temperate environment equated with MIS 5a (Coope and Angus 1975; Maddy *et al.* 1998). The fauna from Cassington Pit and from another Oxfordshire site (Tuckwells Pit, Abingdon) were both analysed by the author (Scott and Buckingham *in prep.*). Both have a reindeer/bison/wolf/bear fauna (such as at Picken's Hole Unit 5) and both are associated with a rich molluscan and beetle fauna and abundant vegetation indicative of a temperate, predominantly treeless environment (Coope, Keen, Farmer, *pers. comm.*). Preliminary OSL dates (Rhodes *pers. comm.*) from these horizons range from c.90, 000 – 78, 000 BP, indicative of equivalence to MIS 5a and Currant and Jacobi's Banwell Bone Cave mammal assemblage-zone.

It could be mooted that the reindeer/bison fauna of Unit 5 might represent a cool temperate interval at any time during the Devensian and therefore be much later than MIS 5a. Two factors argue against this. Firstly, faunas identical to that from Pin Hole mammal assemblage-zone (woolly mammoth, woolly rhino, horse) have been observed to overlie the reindeer/bison faunas of the Banwell Bone Cave mammal assemblae-zone at many British sites. No reversal of this sequence has ever been observed (Currant and Jacobi, 2011). Secondly, if the bones from Unit 5 were of mid-Devensian or later age, they would have been within the same range for radiocarbon dating as the material from Unit 3. In the light of the above evidence, it is concluded that the particular association in Unit 5 of reindeer and bison remains accompanied by remains of wolf and bear, places this unit within the interstadial equated with MIS 5a.

THE ROLE OF VARIOUS PREDATORS IN THE ACCUMULATION OF THE BONES FROM UNITS 3 AND 5

One of the aims of studying these faunas was to define characteristics of the various assemblages that might distinguish which predators were responsible for the accumulations. Any of the predators listed in Table 2 could have been responsible in some measure for the bones in these horizons, either by bringing food into the caves or by dying there.

Unit 3 has five possible agents of accumulation: humans, wolves, bears, foxes, lions and hyaenas but it is concluded that the assemblage resulted primarily from the denning and feeding activities of the spotted hyaena. It is interesting to compare this material with the assemblage from Unit 5, where wolves are believed to have been the principal bone collectors.

As all those represented at Picken's Hole have close modern counterparts, analogies for the Late Pleistocene material can be found in published studies on the diet, habitat and behaviour of modern day carnivores. From this extensive literature it emerges that there are patterns of behaviour characteristic of various predatory species with respect to dietary preference and degree of bone destruction. These are reflected in the resultant bone residues and it seems from a study of these fossil faunas that close parallels may be drawn between a number of living predators and their fossil counterparts in terms of prey preference and degree of damage inflicted on bones. However, in referring to the ethological literature as a basis for interpreting the Picken's Hole assemblages, one bears in mind that environmental differences might in some measure have resulted in behavioural differences. This is not only with reference to climate and habitat changes but to the effect that modern restrictions on the ranges of both predators and prey might have had on their behaviour compared with that in the Pleistocene. In attempting to identify the agent of accumulation at a fossil site where several predators are evident, one is aware that the activities of the most destructive might have obliterated those of the less destructive. Both these points will be discussed further with reference to the particular predators concerned.

Table 2. *Predator and prey groups represented in the two main units at Picken's Hole.*

	Unit 5	Unit 3
		Human+
Predators	Red fox	Arctic fox
	Wolf	Wolf
	Brown bear	Brown bear
		Spotted hyaena
		Lion
Prey		Mammoth
		Woolly rhino
		Horse
	Reindeer	Reindeer
		Giant deer
		Red deer
	Bison	Bison

+artefacts

ORIGINS OF THE LARGE VERTEBRATES FROM UNIT 3

The role of humans in the Unit 3 assemblage

Although humans are represented by a number of artefacts and some teeth in Unit 3, people may effectively be ruled out as the major contributor to this assemblage. Despite the artefacts at least indicating the presence of humans in the vicinity at the time of accumulation of the bones, there is nothing to indicate more than sporadic visits to the site. The fact that human occupation of the site was evidently limited can most obviously be explained by the structure of the site. Picken's Hole was a shallow overhang extending into a narrow tunnel and would have provided a far better animal den than a human habitation. Perhaps the artefacts were dropped by people who crawled in to investigate or to seek short-term shelter. The human teeth, if indeed from Unit 3, might well represent the remains of hunting or scavenging by one of the other carnivores. Cut marks were not found on any of the Unit 3 bones and almost all had been extensively gnawed.

Wolf, bear, arctic fox, and lion

Wolves (and bears on occasion) predate upon reindeer and bison (Pimlott, 1967; Mech, 1970; Holleman and Stephenson, 1981) and both species use dens for shelter and raising young thus neither of these can be ruled out as contributors to the Unit 3 assemblage. Of the two, the wolf is the more likely as it provisions its young with meat at the den (Burton, 1979). This is not so in the case of bears. They occupy dens during the winter months and Kurtén (1968) suggests that high frequencies of young and old bear remains in Pleistocene cave assemblages represent animals that died during the winter denning up period. The fact that there are only three bear teeth in Unit 3 (two canines and a lower molar) indicates that Picken's Hole was not a preferred bear den site.

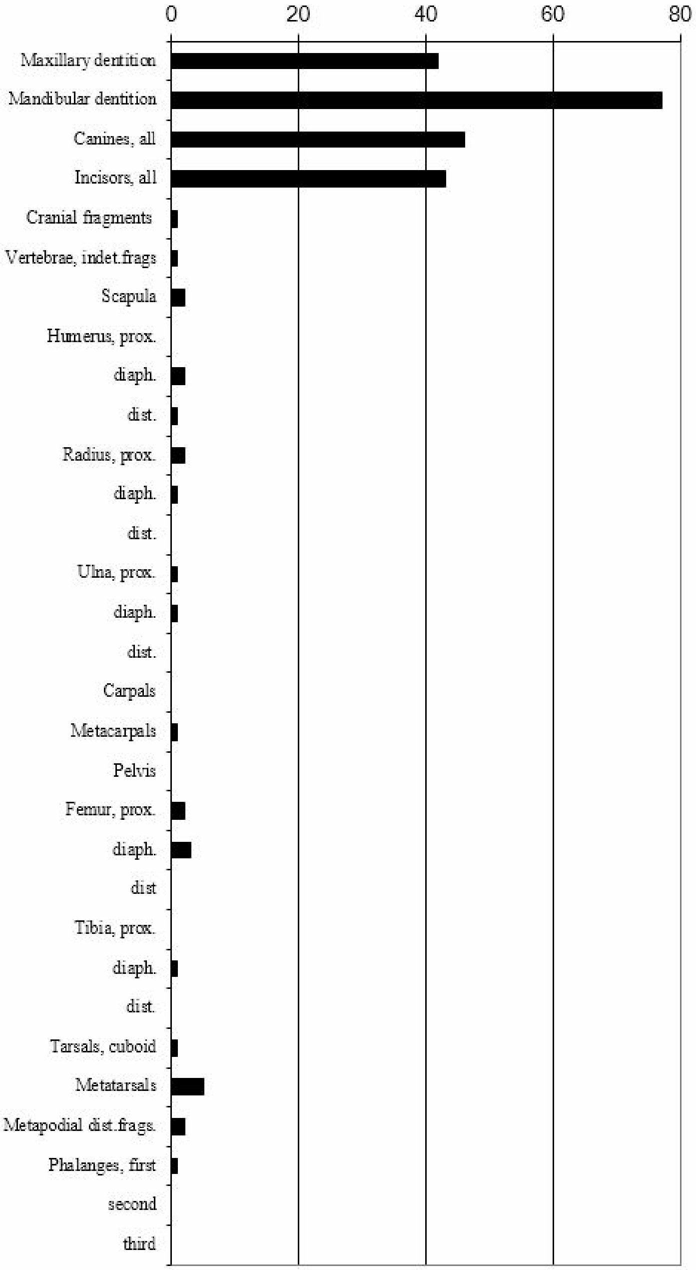

Figure 2. *Hyaena remains from Unit 3.*

The arctic fox in tundra regions today does not hibernate and has been seen hunting at temperatures of -45° C (Burton, 1979). It eats a variety of vegetable and animal foods, the latter of which includes carrion as well as birds, lemmings and other small vertebrates. When there is a surplus of food, caches are made and prey brought back to the den. At Picken's Hole therefore, the arctic fox could have brought in some of the meat-bearing bones and its own remains might represent death at the sites during periods of denning. Alternatively, arctic fox might represent the prey of one of the larger carnivores. Wolves prey upon foxes (Burton, 1979), and southern African hyaenas prey upon jackals (Mills and Mills, 1977), the size equivalent of the arctic fox.

Lion was indeed present during the Middle Devensian but is not commonly represented at British sites of this age. As with the bear, the few remains of lion in Unit 3 could represent an animal that died there, or the food remains of another of the carnivores. If behaviourally similar to their African counterparts, who feed at their kill sites, it is unlikely that the Devensian lions were taking meat-bearing bones into the shelter.

The spotted hyaena

The most abundantly represented carnivore at the site is the spotted hyaena. Its own remains are believed to represent the deaths of hyaenas while occupying the cave. Hyaena coprolites commonly occur at sites where hyaena remains are numerous but they are absent from the Picken's Hole assemblage studied. One of two possibilities might account for the evident absence of hyaena coprolites at this site. Although the bone-rich faeces of extant hyaenas are very distinctive, they are not necessarily preserved in such a distinctive form in fossil hyaena dens. At the Upper Pleistocene cave of Bois Roche, for example, while individual coprolites were not evident, fine mesh screening revealed that all layers were rich in rounded, millimetre-sized coprolite fragments (Villa *et al.* 2010). The authors suggest that *in situ* fragmentation and destruction of coprolites might have been due to the humidity of the cave environment and intensive trampling by the hyena cubs (as indicated by the rounded fracture edges).

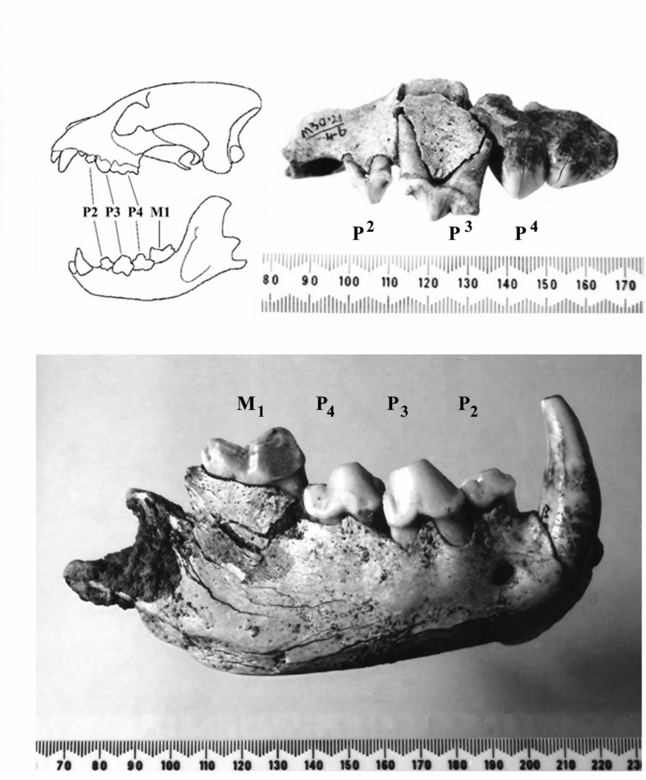

Figure 3. *Top left: diagram of hyaena skull showing upper and lower dentition. Top right: part of left maxilla of young hyaena from Unit 3 showing P2, P3 in place and P4 erupting. Bottom: Right mandible of adult hyaena from Unit 3.*

Alternatively, coprolites never were part of the deposit. Spotted hyaenas, like many gregarious mammals, habitually defecate in specific areas, named latrines, occasionally forming large accumulations. However, these tend not to be in occupied dens but in fringe areas, near rivers, roads, and paths (Pineda *et al.* 2017). Undoubtedly, coprolites are known from cave deposits but perhaps hyaenas occupying a shelter as small as Picken's Hole made use of latrine sites elsewhere.

Figure 4. *Reindeer teeth from Unit 3. Top row: upper teeth, the last of which has been eroded by the hyaena's gastric juices. Bottom row: lower teeth with 4th and 5th eroded*

Figure 5. *Bison astragli from Unit 3: first three gnawed and acid eroded, compared with last, which is only slightly gnawed.*

The extensive gnawing evident on the bones of prey species indicate that this was a den to which food was brought by the hyaenas..

As regards the hyaena remains themselves, it is apparent from Figure 2 that teeth greatly outnumber post-cranial remains. Deciduous and permanent dentition are both present and many teeth are in virtually complete mandibles or maxillae (Figure 3). On the basis of degree of wear of the teeth, it is possible to determine that the Unit 3 hyaenas fall principally into two age groups – very young (under a year old) and old. Few prime age adults are represented (Scott, 1986). These more vulnerable individuals very likely died in the den and were eaten by other members of the clan as their remains have been chewed in a way that is characteristic of hyaena gnawing. As a rule, present-day spotted hyaenas do not prey upon others of their species, although they will kill members of other clans if their young are threatened. They do, however, eat dead members of their own clans (Kruuk, 1972). As regards the remains of all the prey species, the extensive damage to most of the bones (illustrated, for example, in Figures 4 - 8) resembles that caused by modern spotted hyaenas and was almost certainly caused by this animal. Furthermore, there were a great many acid-worn bones and teeth that had either been partly digested and regurgitated, or passed right through the predators' digestive systems. Some of these chewed and acid-worn specimens are illustrated in Figures 4 and 5.

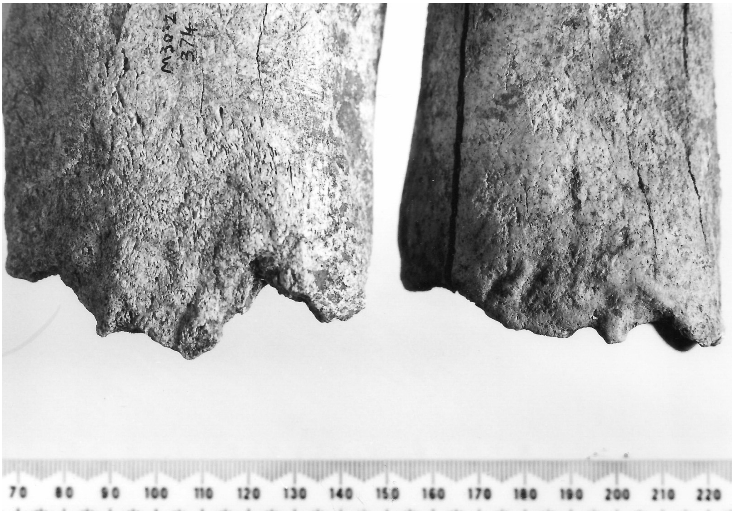

Figure 6. *Woolly rhinoceros limb bones from Unit 3 showing distinctive hyaena gnawing.*

The African spotted hyaena is tolerant of other species sharing its den, such as the porcupine (Mills and Mills, 1977) and the warthog (Deane, 1962). Den-sharing may have characterised the Devensian hyaenas, or the dens may have been occupied successively by the various carnivores listed, so that it is inevitable that some of the prey will be of various and indeterminate origin. However, the sheer size of some of the prey species in Unit 3 probably precludes all but the spotted hyaena as the accumulator of these remains.

Of all the carnivores represented in Unit 3, at the present day, only the spotted hyaena is observed to carry such heavy objects as elephant and rhinoceros limbs and jaws over considerable distances. The counterparts of these species, mammoth and woolly rhino, are represented in Unit 3, the woolly rhino especially so. Some of the giant deer elements would have been very heavy and probably represent hyaena activity too. Horse remains are common and believed also to represent the prey of hyaenas. I have noticed, while examining collections of bones from other deposits of Devensian age, that wherever hyaena is common, horse and woolly rhino are always common (Figure 9). The dominance of woolly rhinoceros and horse is also recorded as typical for some hyaena bone assemblages in Germany (Diedrich, 2012; 2015). However, Fourvel *et al.* (2012, 2014) record a number of French hyaena assemblages where horse is almost invariably the most commonly represented prey species associated with high numbers of large bovid or red deer. On this point it is interesting to note observations on the feeding behaviour of the African spotted hyaena.

A wide variety of large herbivores are available to the hyaena and on these it preys actively, either by scavenging or hunting. Prey selection, however, is apparently not determined by preference on the part of the hyaena for particular species, but is a reflection rather of the actual abundance of a prey species in relation to other ungulates (Kruuk, 1972; Hill, 1978; Houston, 1979; Bertram, 1979; Lansing, *et al.* 2009). From a palaeoecological point of view, it is interesting to speculate that the predominance of woolly rhino and horse at Devensian 'hyaena dens' might reflect particularly high frequencies of these species relative to other herbivores in Britain at that time. Guthrie (1982) and Olivier (1982) point out that the proboscideans and perissodactyls (mammoth, horse and woolly rhino in Devensian Britain) would have been better adapted physiologically to exist on a lower quality, higher fibre diet than the rest of the ungulate community of the Northern Hemisphere during the Late Pleistocene. Thus, although the presence of bison, reindeer and red deer in Unit 3 indicates that there must have been a diversity of herbaceous plant forms to suit a range of herbivores, the overwhelming predominance of horse and woolly rhino noted at a number of British cave sites is probably indicative of extensive grassland of a type highly suitable to these species making them thus more frequently available to the hyaenas.

Figure 7. *Typical damage to woolly rhinoceros limb bones after hyaena gnawing. Epiphyses are almost always destroyed leaving the shaft with much pitting and scoring.*

Although prey availability will have played a major role in determining what the Devensian hyaenas brought into the dens, studies of the living spotted hyaena suggest that another factor, the feeding behaviour of hyaenas, might be equally important in determining what occurs in these dens. Presently, a spotted hyaena den assemblage is largely determined by the ability of the bone to survive the destructive feeding behaviour of this animal. Hyaenas eat voraciously, crush bones with their enormously powerful jaws and, in many instances, have been observed to consume everything but the stomach contents and horns of an ungulate in a remarkably short space of time. Kruuk (1972) watched a hyaena eat every trace of a gazelle fawn in less than two minutes. Even such large animals as giraffe and young elephant have all but disappeared when several hyaenas have been feeding on their carcasses for a few hours (Douglas-Hamilton and Douglas-Hamilton, 1975; Brain, 1981; Lansing, *et al.* 2009). Smaller skeletal elements may be swallowed and even the largest bones, if not crushed, are often considerably reduced in size (as illustrated, for example, in Figures 4 and 5).

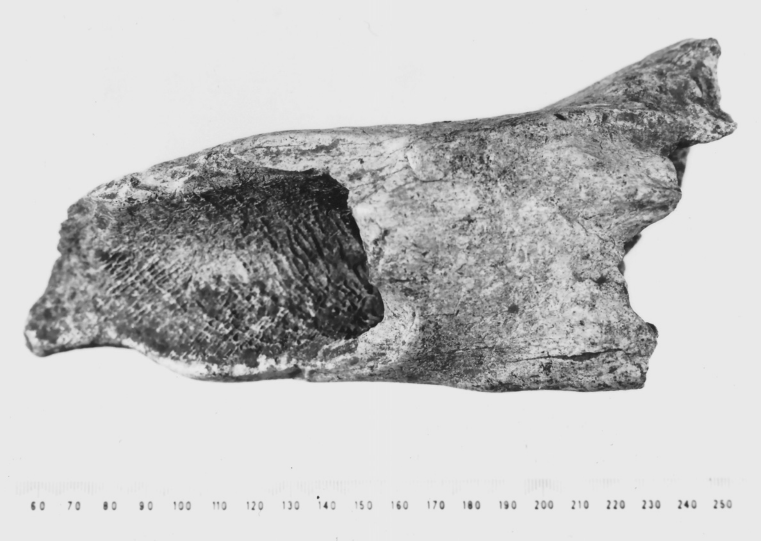

Figure 8. *Typical damage to a bison limb bone after hyaena gnawing. Epiphyses are almost always destroyed leaving the shaft with much pitting and scoring.*

In general, living spotted hyaenas feed on a carcass at the scene of death of the animal. The extent to which a carcass is disarticulated so that parts can be carried away depends upon a variety of factors. These include the degree of competition, the place of the hyaena in the social hierarchy of the clan, the degree of disturbance by, or proximity to, humans, and the quantity of food available at the time (Kruuk, 1972; Brain, 1981; Lansing, *et al.* 2009). Although there are records of hyaenas taking parts of carcasses back to dens where they have cubs (van Lawick-Goodall and van Lawick-Goodall, 1970; Kruuk, 1972; Hill, 1980), as a rule, hyaenas do not provision their young with meat. Most bones at hyaena dens represent food taken to the lair by older cubs looking for seclusion and wanting to avoid competition from the adults (Kruuk 1972; Bertram 1979).

At British sites where the spotted hyaena is believed to have been the main contributor to the bone assemblages, the quantities of fossils are often great. At the present day, spotted hyaenas accumulate bones at their dens (Sutcliffe, 1970; Kruuk, 1972; Mills and Mills, 1977; Hill, 1983) but the bones tend to accumulate around the entrance area and in nothing like the concentrations that characterize the British sites. Two principal reasons may account for these differences. Firstly, it is possible that the Devensian climate encouraged greater den use than is the case in Africa today but, more probably, the type of den will dictate the quantity of material that can be accumulated in it. Where there are caves or rocky crevices available to hyaenas in Africa they make use of them but, for the most part, they occupy burrows previously dug by other animals. The likelihood that these burrows will collapse or fill with sediment after a limited period, and before enormous quantities of bones have had time to accumulate, is therefore great. Caves, on the other hand, such as those in Britain, remained to be used and filled over a considerably longer period. Whether or not older cubs (as observed now) accumulated the majority of bones in the British dens is again something that cannot be known, but the size and weight of various of the skeletal elements, particularly with attached meat, suggests similar behaviour, as discussed below.

HYAENAS AND THEIR PREY: WHAT SURVIVES AT THE DEN

Table 2 shows the presence of seven species of herbivore in Unit 3; all potential prey for the hyaenas. The frequencies of the skeletal elements by which these species are represented are illustrated in Figure 11. As there were only two bones of giant deer, this species is omitted.

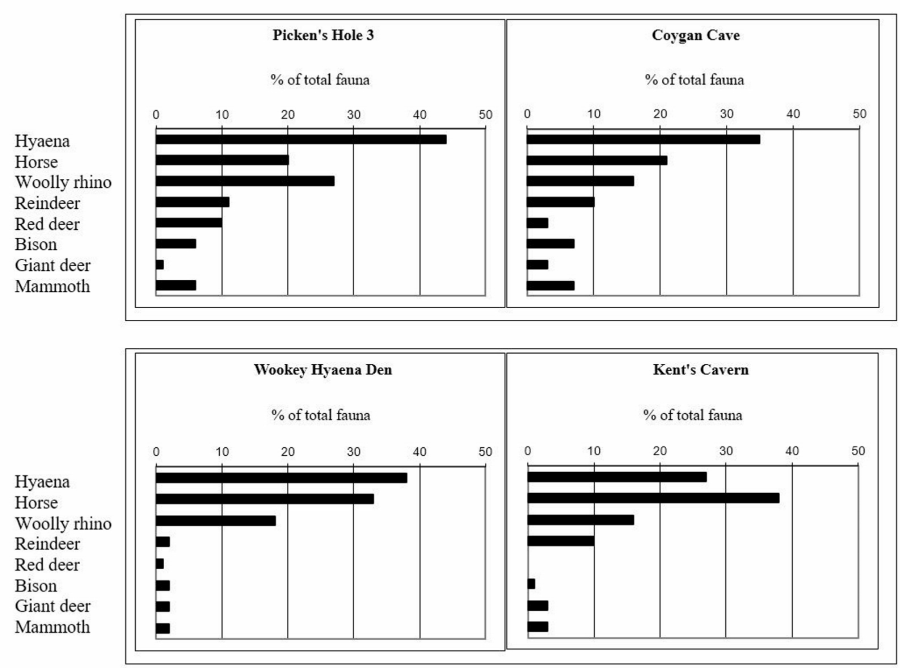

Figure 9. *Large herbivore representation at British cave sites where the spotted hyaena is common (from Scott, 1986).*

The most remarkable feature of these figures is the high number of teeth relative to post-cranial bones. A combination of two factors probably accounts for this disparity: the robusticity (and perhaps inedibility) of teeth versus bones, and the limited ability of the hyaenas to bring in items above a certain weight. The largest animal, the mammoth, is represented by only a few teeth of very young individuals. The virtual absence of the major limb bones of rhino, horse and bison suggests that they were not commonly brought to the den rather than that they were destroyed. All have large, dense bones and, even when gnawed by hyaenas, the central shaft (diaphysis) survives well. Bones at present day hyaena dens generally represent food snatched by immature hyaenas from adults feeding at a kill. In such a situation, it would rarely be possible to disarticulate (and get away with) an entire limb of rhino, bison or horse which would, in any event, be a significant weight. Lower jaws, on the other hand, might be feasible, as would the skulls or partial skulls of young individuals. To some extent, this explanation might account for disparity between the cranial and post-cranial of the red deer. Conversely, the fact that reindeer are the smallest of all the herbivores in Unit 3 might explain the presence of a number of limb bones that possibly came in as one item i.e. attached to bones of the pelvis or shoulder.

The woolly rhino cranial material from Unit 3 provides an interesting illustration of how the age (weight) of prey elements might have determined what sub-adult hyaenas could transport to the den. Woolly rhino teeth are the most numerous and best preserved of the prey species. Although the roots have generally been destroyed by the hyaenas (probably in the process of getting at the pulp cavity in mandibles and maxillae), the teeth are cuboid in shape, dense in structure, and have survived relatively intact. Even deciduous teeth are well represented despite the fact that many of them had evidently been swallowed whole and regurgitated or passed through the hyaena. These teeth are worn smooth and shiny from the action of digestive acids, but are nonetheless identifiable (Figure 10).

Figure 10. *Woolly rhinoceros dentition from Unit 3.*

The numerical frequencies of rhino upper and lower teeth are shown in Figure 12, from which it is apparent that young animals are well represented by deciduous teeth, upper as well as lower. Permanent lower teeth are also very numerous, but not permanent upper teeth. The predominance of juvenile skulls and mandibles is even more apparent when age (mortality) profiles are constructed (Figure 13). The most practical and accurate method of 'ageing' these rhinos is considered to be through the measurement of dental crown height. The detailed methodology is described by the author (Scott, 1986) and is based on the following principals outlined by Klein (1981):

i. that ungulate teeth wear down with age and that the reduction in crown height is roughly constant

ii. that the chronological age of complete crown reduction for a deciduous tooth, when the crown is all but worn away, is the age when it is replaced by a permanent tooth. For a permanent tooth, the chronological age of complete crown reduction is the age past which no individuals survive in the wild. This is known as 'potential ecological longevity'.

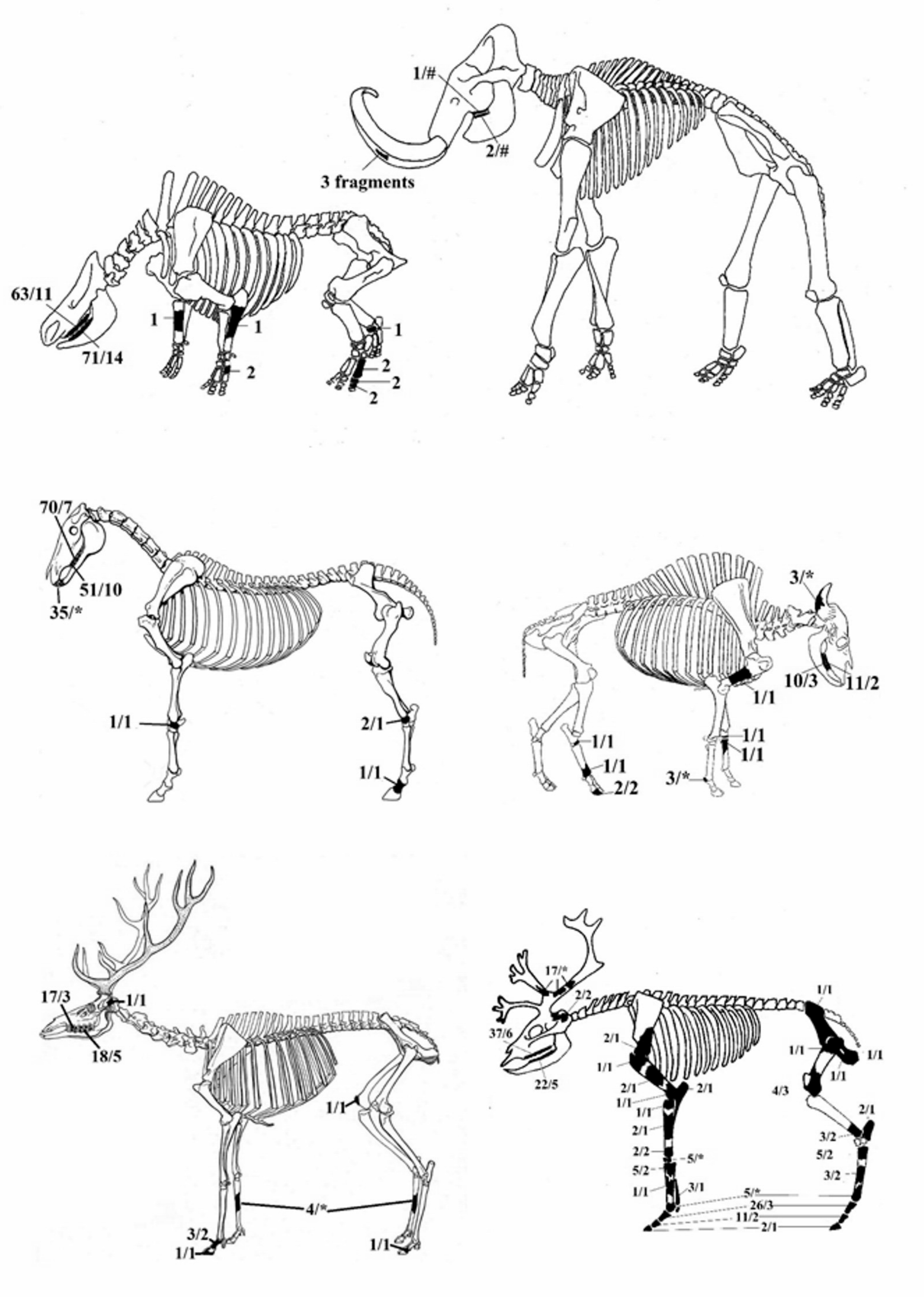

Figure 11. *Skeletal representation of the major prey species from Unit 3 (number of identifiable bones/minimum number of individuals represented).*

iii. that eruption/replacement schedules and potential ecological longevity of an extinct species might be inferred from those of their closest living relatives of similar size and morphology

iv. that the amount of crown height lost per unit time on a deciduous tooth equals the initial unworn crown height divided by the time interval between the age of eruption (usually birth) and the age of replacement by a permanent tooth. The amount of crown height lost on a permanent tooth per unit time equals the initial unworn crown height divided by the time interval between the age of eruption of that tooth and the age at potential ecological longevity

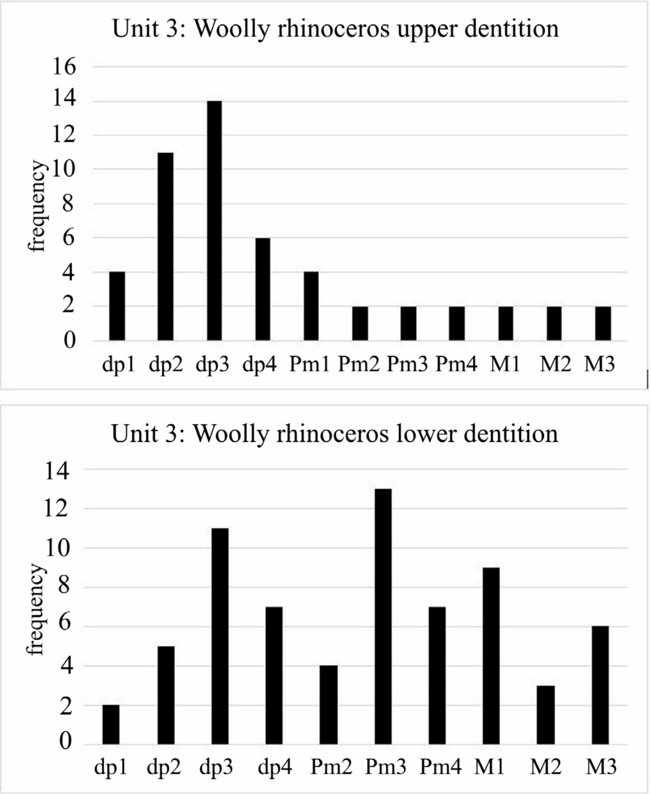

Figure 12. *Numerical frequencies of woolly rhinoceros upper and lower dentition from Unit 3.*

In order to construct an age profile that will include individuals of all ages, crown height must be measured on a category of deciduous teeth and a category of permanent teeth. In order to eliminate the possibility of 'ageing' the same individual twice, it is important to select two teeth that cannot be in wear simultaneously. For the purpose of analysis of the rhinos from Unit 3, dp3 and P3 were selected as they provided the greatest number of measurable specimens. Figures 13a shows the age classes to which the crown height measurements of

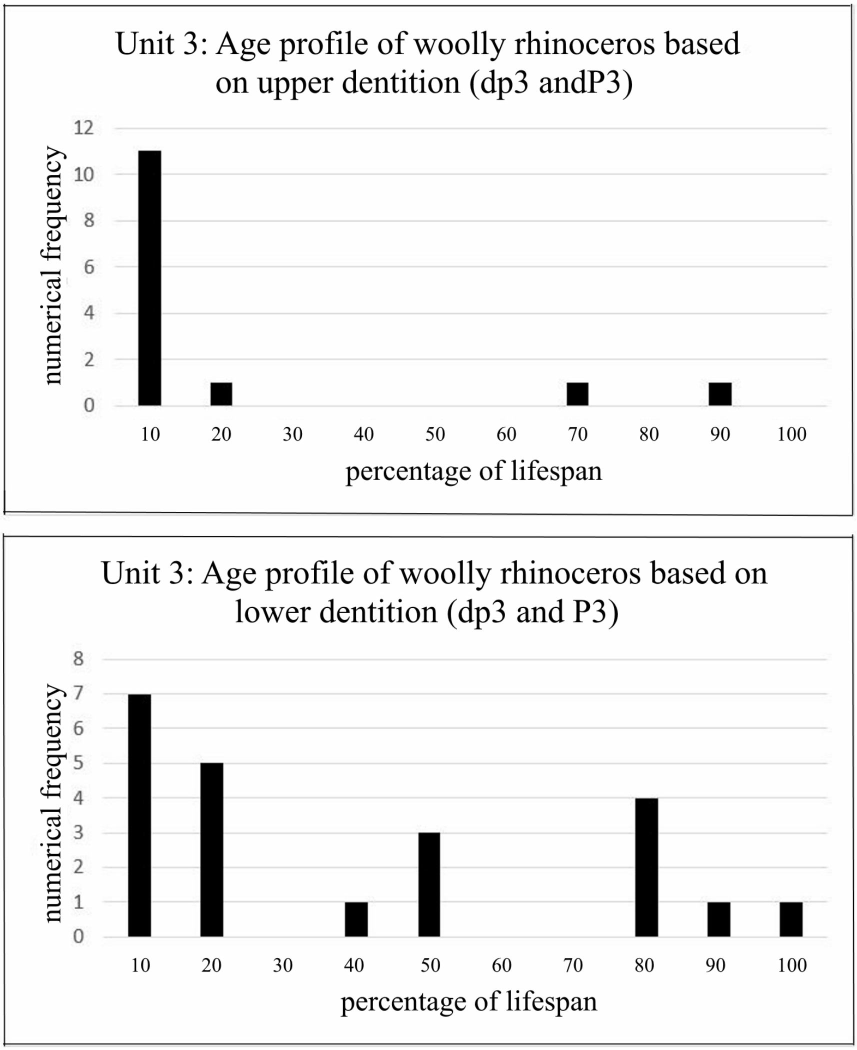

Figure 13. *Age profiles for woolly rhinoceros from Unit 3 based on upper and lower dentition.*

upper teeth are allocated. Each class represents 3 years (10% of potential ecological longevity of 35 years). This is based on data for the black rhinoceros *Diceros bicornis* (Goddard, 1970). The figure emphasises the high percentage of young animals represented by deciduous upper dentition but only two adult teeth (P3). The age profile based on the lower dentition is shown in Figure 13b. Here it is evident that, while there is still a predominance of young animals, a wider age range of rhinos is represented. The most likely explanation for the difference in these age (mortality) profiles is likely to be due to hyaena behaviour. Most of the upper dentition comes from very young animals, the heads of which could probably have been carried or dragged to the dens. Perhaps occasionally part of a maxilla of an older animal was available and brought in too but the weight of adult skulls precluded their transport to the dens. Lower jaws of a wider size/age range were evidently within the carrying capability of the hyaenas.

ORIGINS OF THE LARGE VERTEBRATES FROM UNIT 5

As discussed above with reference to Tables 1 and 2, the differences in species representation between Unit 5 and the hyaena assemblage (Unit 3) are probably primarily due to environmental differences at the time of the accumulation of the bones. Although sufficient grazing must have been available to support the bison at the time of accumulation of Unit 5, the absence of mammoth, woolly rhinoceros and horse suggests the absence of the steppe tundra environment with which these species are generally associated.

As there are no artefacts from Unit 5, nor any other evidence of human presence (such as charcoal or cut-marks on bones), the bones were examined for indications as to which of the three carnivores represented, bear, wolf and fox, might have been responsible for bringing in the reindeer and bison bones. As all three predators are extant, applying the same criteria as discussed for Unit 3, one might compare observations on aspects of their behaviour with respect to prey selection, denning and damage inflicted on bones with observed characteristics of the Unit 5 assemblage.

Table 3. *Dietary information for wolf, red fox and brown bear. Data compiled from Thompson (1952), Pimlott (1967), Mech (1970), Burton (1979), Holleman and Stephenson (1981)*

Carnivore	Animal prey	Plant foods	Hunt or scavenge ?	Transport of meat to den for adult consumption	Provision young with meat at den?
wolf	elk (moose), bison, cattle, reindeer, sheep, cats, hares, rabbits, foxes, bears, badgers, dogs, porcupines, voles, birds, amphibians	fruit	both	Male provides for female with pups	Both parents bring meat to the pups
red fox	rabbits, hares, mice, voles, birds, small carnivores	wide range of vegetable foods	both	dog-fox may provide for vixen with cubs	vixen brings meat to the cubs
brown bear	reindeer, horse, red deer, cattle, elk (moose), insects	grasses, roots, soft fruit, and nuts	both	no	no

The diet of wolves, foxes and bears

Wolves, foxes and brown bears are found today in a wide range of habitats of the Northern Hemisphere and eat an equally wide variety of foods, depending on the particular locality and season. A summary of the dietary preferences of these carnivores is given in Table 3.

Although the wolf's diet is varied, it evidently prefers the hoofed species, in particular reindeer-caribou, elk (moose), white-tailed deer and bison. In North America, the wolves prey principally on white-tailed deer and bison; in Poland, red deer is the main prey with the European bison an important additional resource (Fosse, *et al.* 2012). It is generally accepted that large mammals constitute the basis of the wolf's winter diet while the summer diet is mainly comprised of small mammals, insects, etc., but these smaller species are only resorted to if necessary. This necessity generally arises in the summer because, when the pups are relatively immobile, the adults must remain near the den (Pimlott, 1967; Mech, 1970). However, the summer presence or absence of large ungulates will depend on the seasonal migrations of particular species from year to year. Pimlott (*ibid.*) refers to observations that even after the main movements of caribou have passed by on migration, there are usually stragglers left behind, and the wolves live off these long after the main herds have disappeared. Furthermore, a species such as bison, which is less migratory, forms the staple food of wolves in both summer and winter. Opinions vary as to whether wolves selectively prey upon young, old, and diseased animals, or whether they hunt at random. It seems that, in part, selection depends upon local conditions as much as upon preference. On firm ground a healthy deer can outrun a wolf but in snow, wolves can catch and kill a healthy adult moose or caribou. Although wolves hunt actively, they also scavenge any carrion that is available.

The red fox is both hunter and scavenger. The bulk of its diet consists of small mammals and a variety of birds. Anything larger than a lamb is unlikely to have been hunted, but it will readily scavenge carcasses of larger prey.

Unlike the wolf and red fox, the brown bear is not primarily a meat-eater. However, brown bears do kill such large species as horse, red deer, reindeer (caribou) and elk on occasion, and actively scavenge from carcasses in spring and autumn. Large bears are capable of breaking the limb bones of bison, for example, but this tends to be in years when there have been poor crops of berries, etc. Winter scavenging is also heavy in years when summer and autumn foods are in poor supply (Haynes, 1983).

Considering the above, the reindeer and bison represented in the Unit 5 assemblage might to a greater or lesser extent have been the prey of any of the three predators listed. However, it is important to the interpretation of an assemblage such as this to understand how the den might have been used by each of these three carnivores.

The use of dens by present day wolves, foxes and bears

The adult members of each of these species (bear, wolf and fox) are frequently observed feeding at prey carcasses, but individual adults apparently do not take meat from death sites to dens for later consumption. In spring and early summer, however, a different situation arises in the case of wolves and foxes in that the female finds a den in which to give birth to and rear her young. As indicated in Table 3, parts of carcasses are then brought back to the den. In the case of the red fox, the vixen begins to bring food to the den when the cubs are about a month old and continues to hunt for them until they are independent at about 4 months.

Studies of extant wolves indicate that the use of rock shelters is rare; the occupation of temporary, sandy tunnels being the norm (Fosse, *et al.* 2012). The adult male of both species helps to provision the female while she cares for the very young pups or cubs. In the case of wolves, both parents bring food to the den for the growing pups for 5-6 months. Carcass parts including bones, antlers, and hair are often brought by the animals to the den from a kill site and can be quite abundant (Kowalewski, 2009). As the pups become weaned they may be taken to feed at the site of a nearby kill or to so-called ‘rendezvous sites’ to which adults bring prey.

Den use by the brown bear is quite different. Brown bears are solitary animals, except during the mating season and while the cubs are with the mother. All individuals seek dens at the onset of winter but they do not hibernate as commonly supposed. During the denning period they remain in the den, show a considerable reduction in activity, and depend upon good reserves of fat built up in the autumn to see them through the winter months. The cubs are born in the den at this time (January/February) and emerge from the den with their mother in the spring to accompany her on feeding forays. They are not brought food in the den but are suckled by the she-bear until weaning at about 4 months. As far as adults are concerned, if large prey cannot be consumed at one sitting, the remainder might be cached by burying it under moss and leaves.

In light of the above, it seems that the only contribution by bears to the Unit 5 assemblage might have been by dying in the den during the denning up period. Table 6 (Appendix 1) shows that the bears are far better represented by teeth than by post-cranial bones. Some of these teeth are of mature or old animals but the majority represents immature animals that probably died in the den before they were weaned. The post-cranial bones are few and incomplete with the exception of the dense phalanges. Brain (1981) notes that carnivore epiphyses are less robust than those of ungulates, which would suggest that the bear post-cranial bones (especially those of juveniles) were destroyed, perhaps by the wolves during their subsequent occupation of the site.

Similarly, some of the red fox and wolf remains might represent deaths in the den and some of the foxes might have been prey to wolves. Most of the bones of these two species are highly fragmented. In the case of the wolves, all the post-cranial bones have fused epiphyses and the teeth are generally worn. These might represent the deaths of wolves at the end of their lifespan but adult wolves are frequently killed at their dens by wolves from other packs in disputes over territory (Smith *et al.* 2015). If the cave was used for rearing pups, one might have expected some immature animals to have been represented as well. Their absence may be explained partly by the greater fragility of unfused bones and partly by the fact that wolves eat pups that die in the den.

Of the non-carnivores represented in Unit 5 (hare, vole, and perhaps smaller parts of the carcasses of reindeer) might well have been brought in by the red fox or birds of prey. However, the assemblage is comprised predominantly of the remains of reindeer and bison which, in view of the behavioural observations already cited for the other predators, are attributed to wolves. Moreover, the damage to the reindeer and bison bones is consistent with observations of wolf feeding at the present day. Skeletal representation of these two prey species in Unit 5 is thus discussed below, and the observed pattern of damage to the bone is compared with that from known wolf assemblages. Comparisons are also made with the hyaena assemblage (Unit 3).

REINDEER AND BISON REMAINS IN UNIT 5

Skeletal representation

Reindeer and bison dominate the Unit 5 assemblage. In Figure 22 (Appendix 2) the skeletal representation of these two species is compared. Here a pattern is evident, the underlying cause of which may be attributed to wolf behaviour.

Elements in the categories 'head', 'thorax' and 'feet' are much better represented in both species than other parts of the body. It might be argued that the presentation of the number of bones rather than the number of individuals represented by each body-part gives undue emphasis to vertebrae, ribs and phalanges since there are more of those per skeleton than, for example, humeri. However, observations among living wolves suggest that the Unit 5 wolves will have transported a portion of a carcass consisting of a few articulated bones. Figure 23 illustrates that the skeletal elements being transported to the den differ according to the size of the prey. It would appear that most parts of the body of reindeer were brought in but, as might be expected, the bison is best represented by its smallest bones. Not only would these have been less of a problem to transport than the large limb bones, but the head, vertebrae and lower limbs are more easily disarticulated than are the joints of major limbs (Hill, 1979; Haynes, 1982; Binford, 1981).

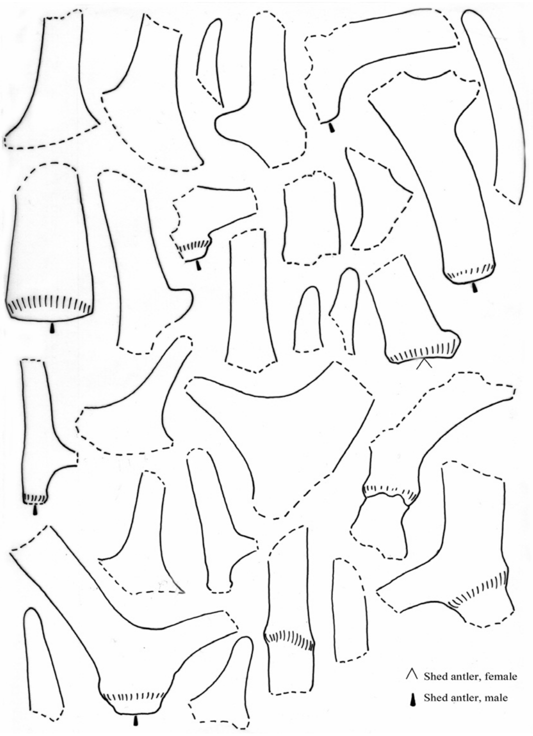

Figure 14. *Outline drawings of typical reindeer antler fragments from Unit 5.*

In Figures 23 and 24 (Appendix 2), body-part representation of the reindeer and bison from Unit 5 is compared with that in the hyaena den assemblage (Unit 3). The representation of reindeer and bison dentition appears similar in all assemblages, but post-cranial representation is different. As might be expected, in view of the greater destructive power of the hyaena, both bison and reindeer limb bones are better represented in wolf assemblages than those accumulated by hyaenas. Ribs and vertebrae of reindeer and bison are scarce in the hyaena assemblage but common, though highly fragmented and gnawed, in Unit 5. Again, this would seem to indicate less destructive chewing of bones by the wolves but, as the spotted hyaena tends to eat ribs and vertebrae at the death location of the prey, it is possible that these elements were taken to the den less frequently than other meat-bearing body-parts.

The best represented of all elements at Unit 5 are the reindeer antlers. These are of particular interest. *Rangifer* is the only species of deer in which both males and females produce antlers. These are shed annually and replaced. The newly growing antlers are covered with a furry skin called velvet, which is sloughed off as the antlers harden. Velvet is highly nutritious being comprised of collagen, amino acid, fat, and trace elements for which reason the antlers of dead reindeer are chewed on by a number of animals, including the reindeer themselves. Modern day wolves gnaw the antlers of modern *Rangifer* and *Alces* (reindeer-caribou and elk) when in velvet (Haynes, 1980) leaving very characteristic damage consisting of transverse furrows, short nicks and single grooves. Shed antlers are also gnawed as the distal ends are very rich in protein (Miller *et al.* 2013). At Picken's Hole there are well in excess of a hundred pieces of fairly standard size and most show signs of gnawing. This chewing is characterised by small dents or pitting and scoring rather than by deep tooth marks. A selection of these antler fragments is illustrated in Figures 14 and 15. There are fragments of tine of moderately large antlers and portions of antlers still attached to the frontal bones. Especially noteworthy is the predominance of parts of small antlers and shed antlers, mostly of females and young animals of both sexes. Male reindeer shed their antlers in the autumn but the females and young shed theirs in the late spring. This would have made them available to wolf pups at Picken's Hole just at the point when they were being weaned and looking for nourishing items to chew on. The small tooth marks ('pitting') on the Unit 5 reindeer antlers is attributed here to the wolf pups.

Figure 15. *Typical reindeer antler remains from Unit 5.*

The high number of reindeer antler fragments relative to other parts of the body in Unit 5 is a feature believed by this author to be important in the recognition of wolf-accumulated bones from other late Pleistocene British sites e.g. Inchnadamph Cave (Figure 16) and Tornewton Cave (Scott, 1986). Modern day observations on wolves note that pups gnaw bones and antlers at rendezvous sites and dens. Carcass parts including bones, antlers, and hair are often brought by the animals to the den from a kill site and can be quite abundant, a veritable "bone yard" (Kowalewski, 2009).

Damage to reindeer and bison bones in Unit 5

Two aspects of damage are considered here: the degree of completeness of the bones, and surface damage caused by chewing. Figure 22 shows a high degree of fragmentation of various parts of the skeletons of the reindeer and bison from Unit 5. Various authors describe characteristic damage to bones caused by recent wolves (e.g. Binford, 1981, Haynes, 1983;

Fosse, *et al.* 2012). Typically, shafts of long bones have been split to obtain the marrow and have pitting and scoring on the bone. Epiphyses have frequently been gnawed but this is characterised by pitting and scoring of the epiphyses rather than by their total destruction (Figure 17). The bones from Unit 5 closely resemble published examples of wolf damage to bones as seen, for example, in Figure 18.

The extent and location of damage to the Unit 5 reindeer and bison bones is probably best explained with reference to the manner of feeding of wolves at a carcass. With regard to the disarticulation/destruction of reindeer carcasses, Binford (1981) observes that the most common way in which wolves deal with the forequarters is to eat through the proximal humerus thus separating the scapula, which is then generally dragged away. Haynes (1982) notes that all legs may eventually be detached from the body, though on lightly utilized carcasses only a single limb is separated. The remaining legs at any kill site contain articulated elements, specifically third phalanges still in the hoof sheaths, and often including the metapodial and continuing to the mid-shaft of the tibia, the distal end of the femur, or the distal end of the humerus. Similarly with bison, the section of radius/ulna to hooves is rarely stripped at kill but may be re-visited. This leaves the unmodified leg from the mid-shaft of the humerus down to the foot still in articulation. This might be taken away or dispersed nearby. The hindquarters

Figure 16. *Reindeer antlers from Inchnadamph Cave, Assynt, described as a wolf den (Scott, 1986).*

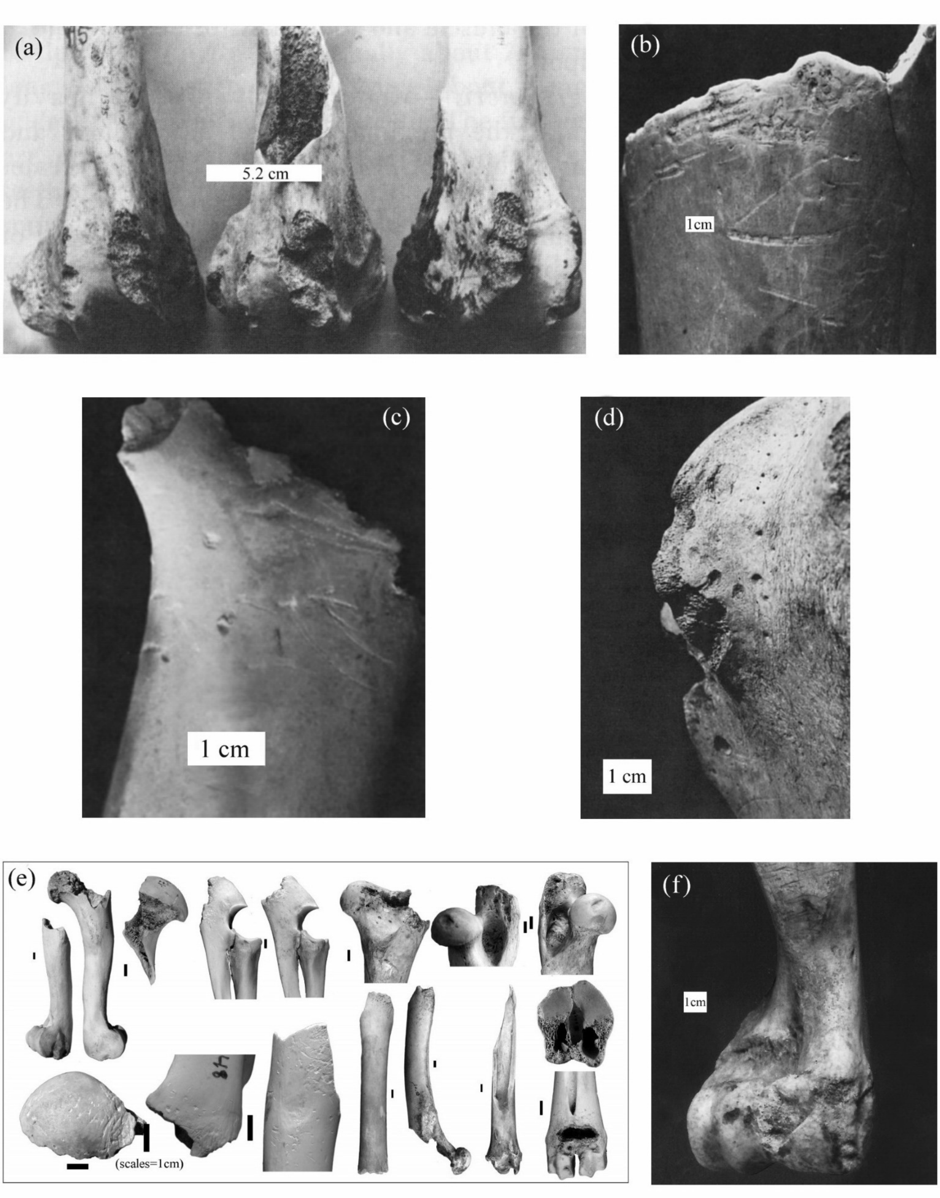

Figure 17. *Damage to bones caused by present day wolves (a) gnawed distal femora of elk and bison; (b) scratch marks on bison femur shaft; (c) scratches and pits on bison humerus shaft; (d) pit impressions on rim of large trochanter of bison femur; (e) bones of red deer gnawed by wolves; (f); humerus of white-tailed deer showing scoring on shaft and gnawing on epiphysis*.

Fig. 17(a) from Haynes 1980; Figs. 17 (b-d) from Haynes 1983; Fig. 17 (e) from Fosse *et al.* 2012; Fig 17(f) by kind permission of Dr J. Mead, University of Maine at Orono.

Figure 18. *Bison bones from Unit 5 showing damage similar to that caused by present day wolves.*

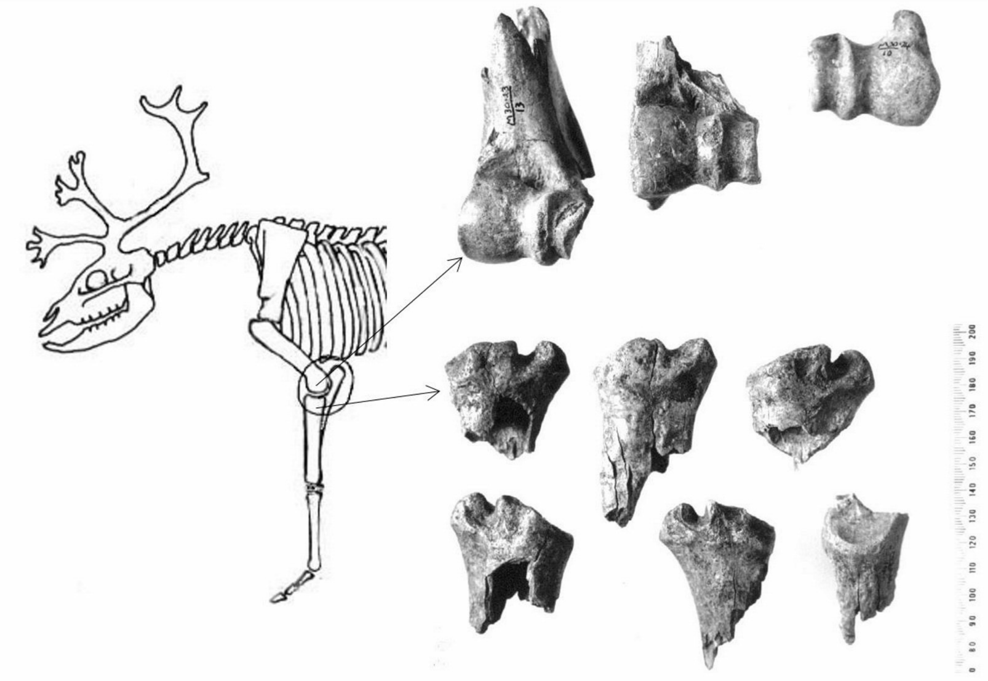

Figure 19. *Humeri and radii of reindeer from Unit 5 showing typical breakage and chewing of the shaft but minor damage to the articular surfaces***.**

are separated from the body by breaking through the proximal femur. This leaves the femur head in the acetabulum (socket) of the pelvis. The rest of the leg might then remain articulated and be taken away or, if broken through the tibia, just the lower leg remains articulated.

As regards the reindeer from Unit 5, the proximal epiphyses of the humerus and femur are the least well-represented parts of these limbs, are fragmentary and chewed, mirroring the damage observed as wolves separate limbs from the body at the shoulder and hip. The distal humeri and femora, on the other hand, are better represented and, although chewing is evident, they are not badly damaged. This is also true of the bones that articulate with them, the proximal radius and ulna and the proximal tibia. A number of the humeri and radii are shown in Figure 19 illustrating typical breakage and chewing of the shaft but minor chewing of the articular surfaces. This would seem to indicate that the fore- and hind limbs were brought to the site still articulated, stripped of meat and tendons and broken mid-shaft for their marrow, but abandoned while still in articulation.

Other joints that appear to have been chewed while still articulated are those of the distal tibia/tarsal joint and the distal metapodial with the phalanges. In other words, the component elements of these joints have been chewed, but are generally unbroken and the articular surfaces infrequently damaged. This suggests that meat was chewed off the lower limbs without necessarily breaking the bones of the feet apart (Figure 20). This is a quite different pattern from that evident in the hyaena assemblage where epiphyses, tarsals and carpals are comparatively rare and the incidence of broken phalanges is much greater. In both types of assemblage, the third phalanx is rare, presumably because it remained embedded in the hoof.

A similar pattern of damage characterises the bison bones from Unit 5 but, as already stated, it seems that only the smaller body-parts were brought to the den. Thus, the best represented elements (lower limbs and feet) show evidence of chewing, but articular surfaces are relatively undamaged, indicating that lower limbs were brought in virtually intact, were then chewed but seldom disarticulated (Figure 21).

For both species, rib and vertebral fragments are common. A high number of vertebral epiphyses showing little damage suggests that articulated sections of the vertebral column were brought to the den. None of the reindeer or bison teeth is in a mandible or maxilla, but as there were a number of fragments of these, it is presumed that the teeth were brought to the site in parts of jaws or skulls.

Figure 20. *Reindeer phalanges showing very little gnawing damage suggesting feet/hooves were largely ignored by the wolves.*

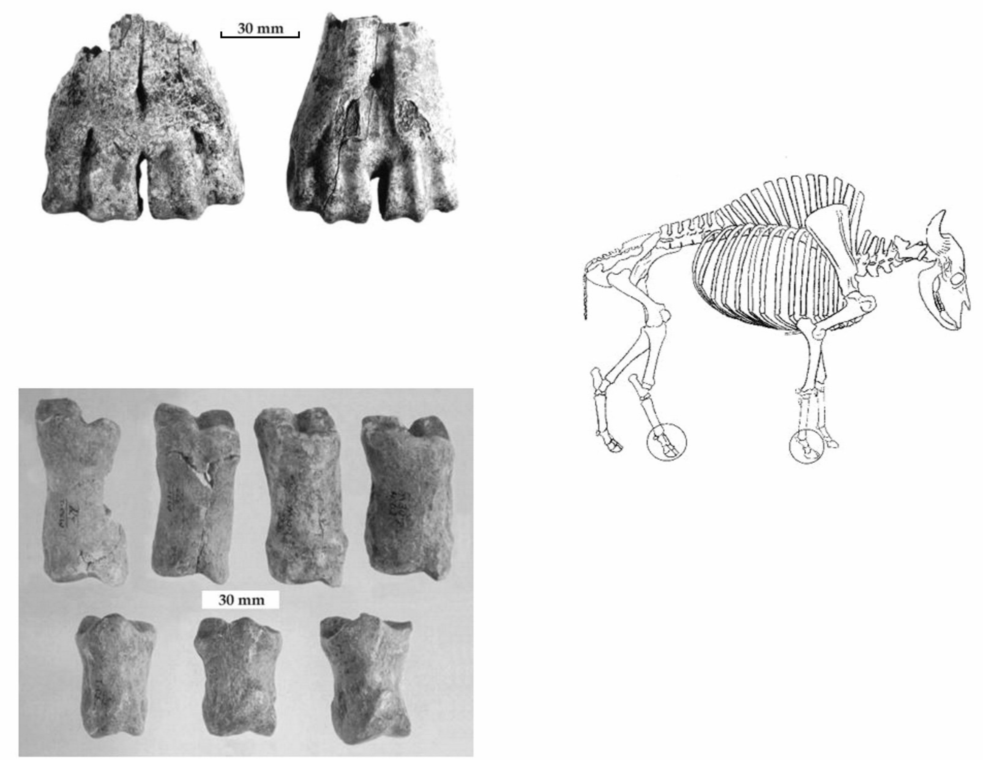

Figure 21. *Bison distal metacarpal (top left) and distal metatarsal (right) and first and second phalanges from Unit 5 showing slight gnawing of the bones but undamaged articulating surfaces. The location of these bones is shown on bison skeleton*.

CONCLUSION

In recent decades there have been many published studies of living carnivores with the purpose of establishing a framework for the interpretation of fossil assemblages. Of those carnivores relevant to the European Pleistocene, attention has focussed particularly on the spotted hyaena. It is a social carnivore, both an opportunistic scavenger and an effective hunter. It eats a wide variety of animals, especially medium to large ungulates, and although it does not provision its young at the den, sub-adult hyaenas in particular transport prey to dens. The spotted hyaena is abundant in the European Pleistocene fossil record and it too evidently brought parts of carcasses of its prey back to dens. In terms of prey species representation and damage to their bones, there are close parallels between modern observations of spotted hyaena behaviour and the many European Pleistocene bone assemblages attributed this predator. The assemblage from Unit 3 at Picken's Hole has all the hallmarks of having been accumulated predominantly by spotted hyaenas.

Wolves are less well known in the European Pleistocene. Modern observations record that wolves usually consume their prey where they are killed or scavenged and that they do not usually transport carcasses to dens. Although males provision females with pups and both parents take prey back to dens for the pups, most authors suggest that this behaviour does not usually generate large bone accumulations. Once the pups are weaned, they tend to congregate at rendezvous sites to which adults bring prey. Although adults and sub-adults gnaw bones at these locations, they are not characterized by large accumulations of bones (Binford, 1981; Fosse, *et al*. 2012; Sala, *et al.* 2014; Sala and Arsuaga, 2016). These are general observations but it is also apparent that there is some variability in bone samples that result from the activities of and consumption by wolves. This variability is recognized as the result of a combination of factors e.g. the seasonal availability of prey, the amount of consumption time spent at a carcass, the degree on inter-carnivore competition

Picken's Hole Unit 5 is thus an important assemblage. With reference to identifying the agent of accumulation of European Pleistocene bones, Fosse, *et al.* (2012) comment that true ungulate bone accumulations made by wolf are suspected in a few cases but are unclear, mainly because of the presence of other carnivore species. As described above, the bones from Unit 5 show all the characteristics of present day prey selection and gnawing of wolves and there is none of the usual possible confusion with the activities of a more destructive carnivore, such as the spotted hyaena. Fortuitously, the Unit 5 assemblage pre-dates the arrival of the spotted hyaena in Britain and there is little evidence in the assemblage of any other carnivore.

Picken's Hole is a particularly interesting and rare site in Britain having two large assemblages of bones believed to have been brought to the site at different periods of the Late Pleistocene. Contemporary studies of wolves and spotted hyaenas support the assertion that the older assemblage (Unit 5) was accumulated by wolves and the younger (Unit 3) by hyaenas. However, it is interesting to note that bones in and around the dens of their modern counterparts are never recorded in the quantities recorded at British fossil sites. While it is possible that wolf behaviour was different in the Pleistocene compared with the present, it is perhaps more likely that the permanence of the British rock shelters compared with the burrows most commonly frequented today meant that they were repeatedly used over a long period of time allowing such large accumulations of prey remains.

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APPENDIX 1.
SKELETAL REPRESENTATION TABLES FOR ALL SPECIES

In the following tables, the numbers in each column indicate the number of identified specimens (NISP). Where there is a second number, this is the minimum number of individuals (MNI) estimated by assessing adults and juveniles, left and right skeletal elements.

Table 4. *Skeletal representation of red and arctic fox at Picken's Hole.*

	red fox Unit 5	**red fox** Unit 5/4	**red fox** Unit 4	**arctic fox** Unit 3
Upper dentition	7/2	-	6/2	-
Lower dentition	13/3	1/1	22/5	6/2
Canines	14	2	21	20
Incisors	1	-	12	3
Vertebrae,				
atlas	1/1	-	-	2/2
axis	3/3	-	-	-
other & frags.	24	5	36	12
Scapula	-	-	1/1	-
Humerus	6/4	1/1	4/2	5/3
Ulna	6/3	-	5/3	2/2
Radius	8/4	-	6/3	2/2
Pelvis	2/2	1/1	2/1	1/1
Femur	5/3	-	3/2	-
Tibia	8/4	-	4/3	3/2
Metapodia	34	8	66	21
Tarsals,				
calcaneum	8/5	1/1	6/3	4/3
astragulus	2/1	-	3/2	-
other	1/1	-	1/1	-
Carpals	-	-	3	1/1
Phalanges,				
first	8	-	26	13
second	2	1	6	1
third	1	-	2	3
Rib fragments	3	-	19	-
indet diaph frags.	-	-	8	-

Table 5. *Skeletal representation of wolf at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Upper dentition	11/3	-	1/1
Lower dentition	13/4	-	1/1
Vertebrae,			
atlas	1/1	-	-
axis	1/1	-	-
lumbar	3/1	-	-
caudal	2/1	-	-
Scapula	5/3	-	1/1
Humerus	2/1	-	1/1
Radius	6/3	-	1/1
Ulna	7/3	-	1/1
Carpals	2/1	-	-
Femur	3/2	-	-
Tibia	3/2	-	-
Tarsals,			
calcaneum	4/2	-	1/1
astragulus	1/1	-	-
other	3/1	-	-
Metapodia, incl. frags.	16	3	-
Phalanges,			
first	5/1	2/1	5/1
second	1/1	2/1	1/1
third	3/1	2/1	-
Rib fragments	+	+	-
vertebral fragments	+	+	-

Table 6. *Skeletal representation of bear at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Upper dentition	4/2	-	1/1
Lower dentition	19/5	-	2/1
Scapula	2/2	-	-
Radius	1/1	-	-
Tibia	1/1	-	-
patella	2/1	-	-
Tarsal	1/1	-	-
Metapodial fragments	11/1	-	-
Phalanges,		-	-
first	4/2		
second	1/1		
third	11/1		

Table 7. *Skeletal representation of lion at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Maxillary dentition	-	-	1/1
Mandibular dentition	-	-	1/1
Phalanx, first	-	-	1/1

Table 8. *Skeletal representation of giant deer at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Upper dentition (P3)	-	-	1/1
Metacarpal, complete	-	-	1/1
Metacarpal, prox.+diaph.	-	-	1/1
Carpal, magnum	-	-	1/1
Tarsal, naviculo-cuboid	-	-	1/1

Table 9. *Skeletal representation of spotted hyaena at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Maxillary dentition	-	-	42/17
Mandibular dentition	-	-	77/22
Canines, all	-	-	46
Incisors, all	-	-	43
Cranial fragments	-	-	1/1
Vertebrae, indet. frags.	-	-	1/1
Scapula	-	-	2/2
Humerus, prox. diaph. dist.	-	-	1/1 1/1 1/1
Radius, prox. diaph. dist.	-	-	1/1 - -
Ulna, prox. diaph. dist	-	-	1/1 1/1 -
Carpals	-	-	-
Metacarpals	-	-	1/1
Pelvis	-	-	-
Femur, prox. diaph. dist.	-	-	2/1 3/2 -
Tibia, prox. diaph. dist.	-	-	- 1/1 -
Tarsals, cuboid	-	-	1/1
Metatarsals	-	-	5/1
Metapodial dist. frags.	-	-	2/*
Phalanges, first second third	-	-	1/1 - -

Table 10. *Skeletal representation of mammoth at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Upper dentition (dp3)	-	-	1/1
Lower dentition, (dp2)	-	-	1/1
(dp3)			1/1
Dental frags, immature	-	-	24
Tusk fragments	-	-	3

Table 11. *Skeletal representation of horse at Picken's Hole.*

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	Unit 5	Unit 4	Unit 3
Maxillary dentition	-	-	70/7
Mandibular dentition	-	-	51/10
Incisors, all	-	-	35
Canines	-	-	1
Carpals	-	-	1/1
Tarsals	-	-	2/1
Phalanx, first	-	-	1/1

Table 12. *Skeletal representation of red deer at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Cranial fragments	-	-	1/1
Maxillary dentition	-	-	17/3
Mandibular dentition	-	-	18/5
Ramus	-	-	1/1
Patella	-	-	1/1
Metapodial frags.	-	-	4/1
Phalanges, first	-	-	3/2
second	-	-	1/1
third	-	-	1/1

Table 13. *Skeletal representation of woolly rhinoceros at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Maxillary dentition	-	-	63/11
Mandibular dentition	-	-	71/14
Mandibular symphysis	-	-	1/1
Dental fragments	-	-	16
Scapula	-	-	-
Humerus, diaphysis	-	-	-
Radius, diaphysis	-	-	1/1
Ulna,			
proximal	-	-	-
diaphysis	-	-	1/1
Metacarpal, proximal	-	-	2/1
Innominate	-	-	-
Femur, diaphysis	-	-	1/1
Tibia,			
diaphysis	-	-	-
diaphysis + distal	-	-	-
Patella	-	-	-
Metatarsal	-	-	2/1
Tarsals,			
astragulus	-	-	1/1
navicular	-	-	-
lateral cuneiform	-	-	-
Phalanges,			
first	-	-	1/1
second	-	-	1/1

Table 14. *Skeletal representation of bison at Picken's Hole.*

	Unit 5	Unit 4	Unit 3
Horn core fragments.	14	-	3
Cranial fragments	17	-	-
Maxiliary dentition	18/4	4/2	11/2
Mandibular dentition	9/3	3/2	10/3
Dental fragments	7	2	11
Vertebrae, atlas	1/1	-	-
axis	1/1	-	-
sacral	1/1	-	-
frags.	12	-	-
Humerus, prox.	-	-	-
diaph.	2/1	-	1/1
dist.	8/3	-	-
Radius	-	-	-
Ulna, prox.	2/2	-	-
diaph.	1/1	-	-
Carpals, magnum	2/1	-	-
unciform	1/1	-	1/1
cuneiform	5/4	-	-
lunate	3/3	-	-
Metacarpal, prox	1/1	-	1/1
diaph.	1/1	-	-
dist.	-	-	3/2
Innominate, ilium	2/1	-	-
acetabulum	5/3	-	-
Femur, prox.	1/1	-	-
diaph.	3/2	-	-
dist.	2/1	-	-
Tibia, prox.	-	-	-
diaph.	1/1	-	-
dist.	4/3	-	-
Tarsals, calcaneum astragulus naviculo-cuboid cuneiform	9/6 9/5 7/4 2/1	- - -	- - 1/1 -
Metatarsal, prox.	7/4	-	-
dist.	-	-	1/1
Metapodial dist. frags.	11	-	-
Sesamoids	5	-	3
Phalanges, first second third	26/4 12/3 1/1	4/2 1/1 -	- 2/2
Rib fragments	9	-	-

Table 15. *Skeletal representation of reindeer at Picken's Hole.*

	Unit 5	Unit 5/4	Unit 4	Unit 3
Antlers incl. frags.	123	3	3	17
Cranial fragments	20	2	-	2/2
Maxillary dentition	21/5	1/1	4/1	37/6
Mandibular dentition	15/4	-	4/2	22/5
Vertebrae,				
atlas	-	-	-	-
axis	3/3	-	-	-
other+frags.	44	5	-	-
Rib fragments	28	17	-	-
Scapula	13/8	1/1	-	2/1
Humerus,				
prox.	4/2	1/1	-	1/1
diaph.	11/5	-	-	2/2
dist.	7/4	1/1	-	1/1
Radius,				
prox.	12/6	1/1	-	1/1
diaph.	2/1	-	1/1	2/2
dist	9/6	1/1	-	2/2
Ulna,				
prox.	9/6	-	-	2/1
dist.	3/2	1/1	-	-
Carpals	22	1/1	-	5
Metacarpal,				
prox.	6/4	2/1	-	5/2
dist	5/2	-	-	1/1
Innominate,				
ilium	8/6	-	-	1/1
ischium	3/2	-	-	1/1
acetabulum	12/7	1/1	-	1/1
pubic symph.	5/3	-	-	-
Femur,				
prox.	2/1	-	-	1/1
diaph.	4/3	-	-	-
dist.	14/6	2/1	-	4/3
Tibia,				
prox.	11/6	-	-	-
diaph.	5/3	-	-	-
dist.	5/4	-	-	3/2

	Unit 5	Unit 5/4	Unit 4	Unit 3
Tarsals,				
calcaneum	17/9	2/1	-	2/1
astragulus	12/6	-	-	-
navico-cuboid	4/3	-	-	-
Metatarsal,				5/2
prox.	8/4	4/1	-	3/2
diaph.	2/1	1/1	-	5
Metapodia, all distal	25	-	-	5
Accessory metapodia	3/1	2/1	-	3/1
Phalanges,				
first	51/5	4/2	5/2	26/3
second	18/2	1/1	1/1	11/2
third	4/2	-	-	2/1
Accessory phalanges,				
first	7/2	-	-	2/1
second	-	-	-	-
third	1/1	-	-	5/1
Sesamoids	6/1	2/1	-	2

APPENDIX 2:
COMPARATIVE REPRESENTATION OF REINDEER AND BISON

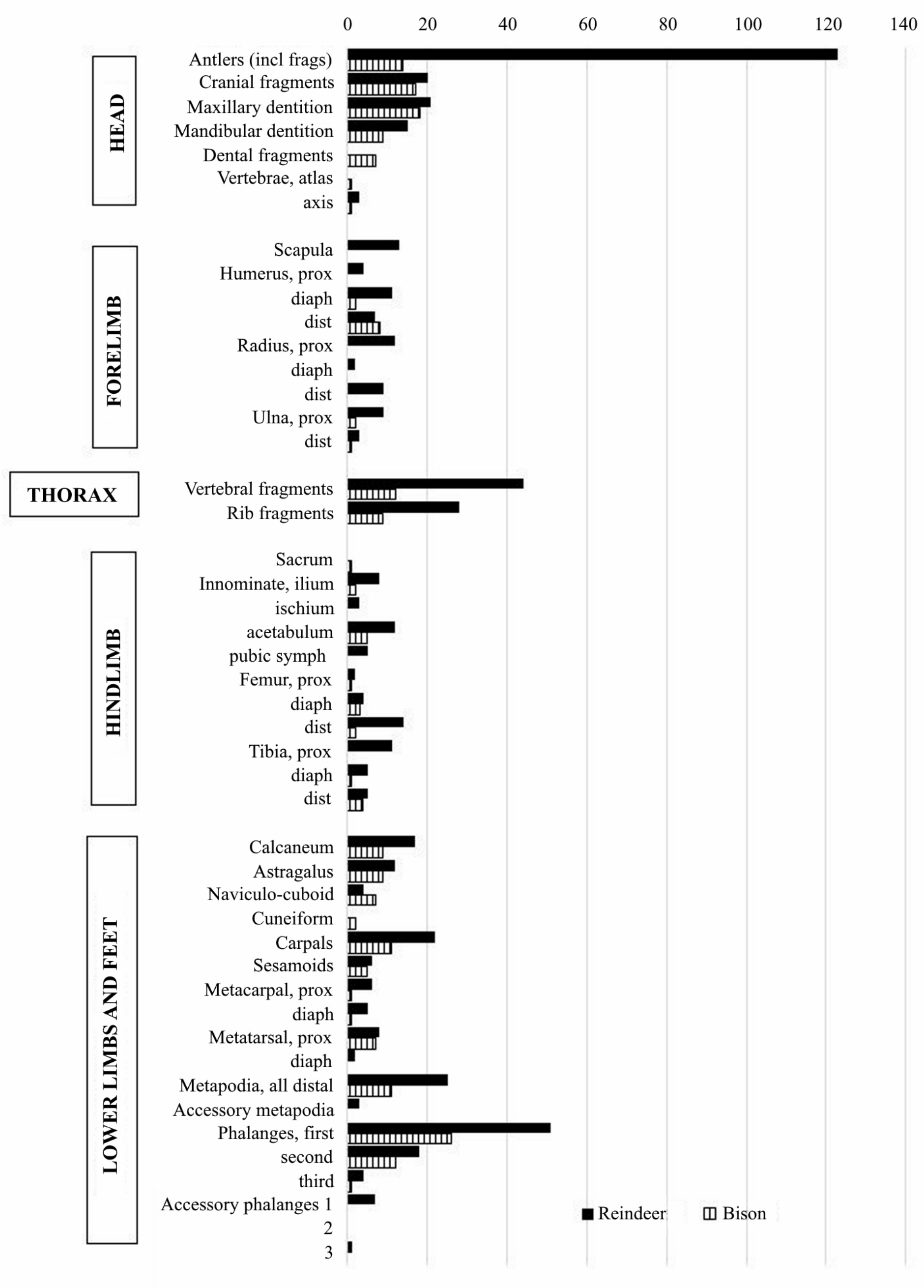

Figure 22. *Skeletal representation of reindeer and bison in Unit 5*.

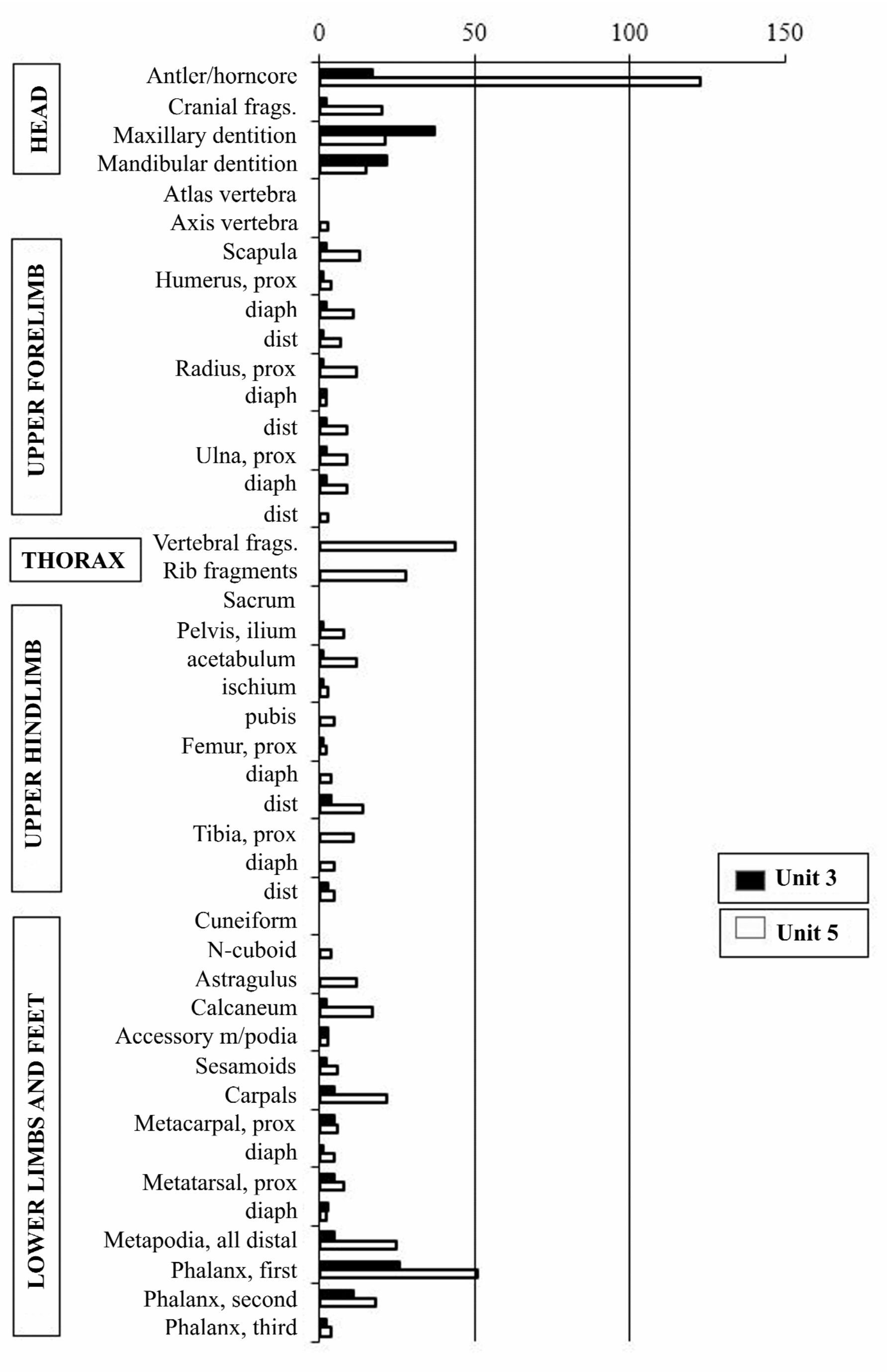

Figure 23. *Comparison of reindeer skeletal elements in Unit 3 and Unit 5*

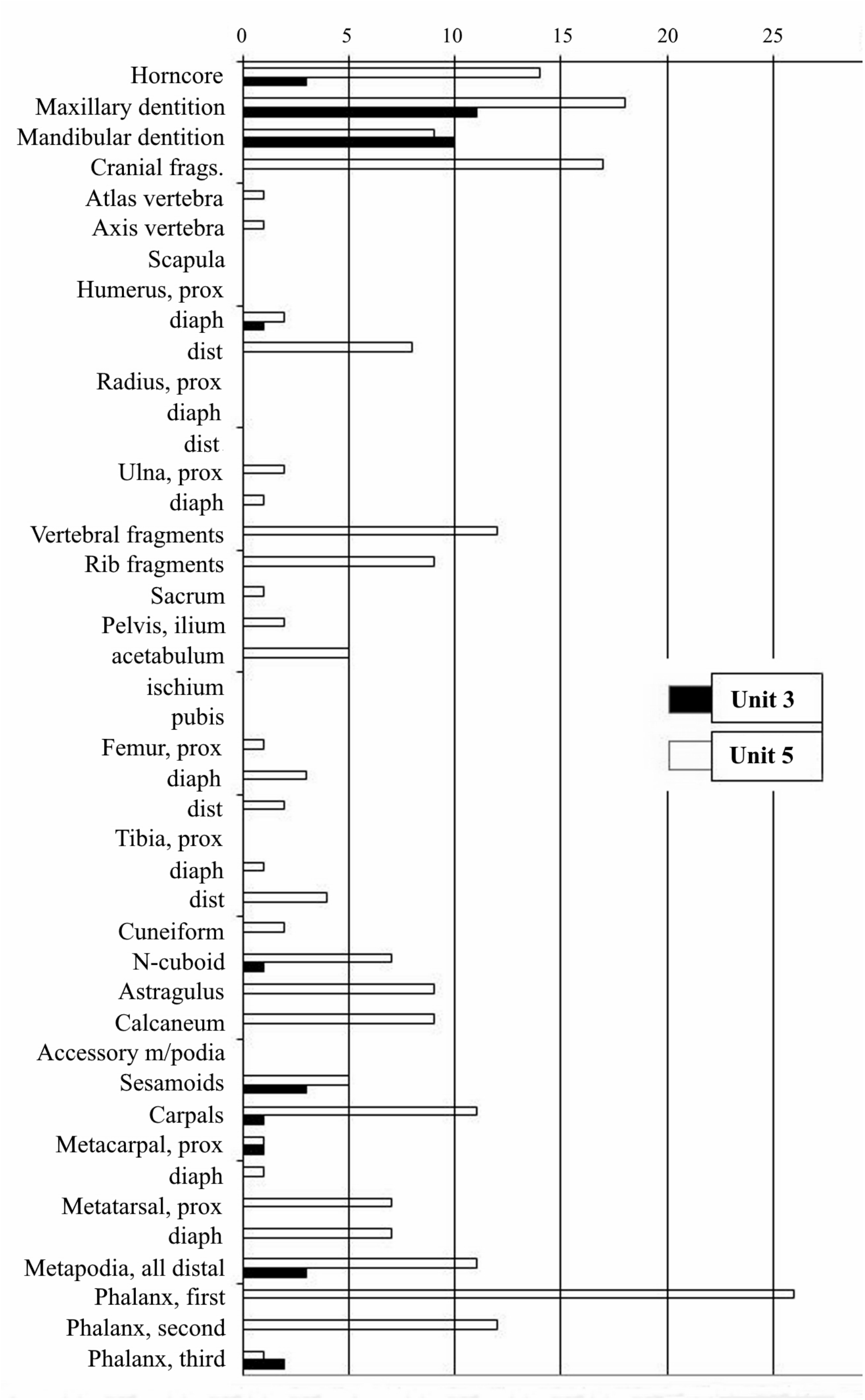

Figure 24. *Comparison of bison skeletal elements in Unit 3 and Unit 5.*

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Katharine Scott
St Cross College
University of Oxford
Oxford, OX1 3LZ
katherine.scott@stx.ox.ac.uk