Aspects of the Palaeoecology of Large Predators, including Man, during the British Upper Pleistocene, with particular emphasis on Predator-Prey Relationships

VOLUME I

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SUMMARY

This thesis discusses aspects of the palaeoecology of large predators, including man, during the Upper Pleistocene in Britain, with particular emphasis on predator-prey relationships. Upper Pleistocene is here taken as the Ipswichian (last) interglacial and the Devensian (last) glaciation. In addition to man, the term large predator includes lion, hyaena, wolf, leopard, bear, lynx and wolverine.

The primary aim is to predict features of past predator and prey behaviour by integrating the results of modern ethological observations on similar or analogous species with the published evidence of Upper Pleistocene environments deduced from botanical, sedimentological and geomorphological investigations, and thus to extract information on trends in predator ecology and predator-prey relationships between the Ipswichian and Devensian. The study also examines the possibility that interpretations of human activity in Upper Pleistocene Britain have been founded largely on material accumulated by hyaenas, and discusses the value of examining past human behaviour from an ecological perspective in which man is regarded as one predator among many.

The predictions of past behaviour are tested on vertebrate remains recovered from Upper Pleistocene deposits and now available in numerous museum collections. Much of the material derives from hyaena-accumulated bone assemblages in caves, and holds a potential wealth of information on the behaviour of this species and its predatory and scavenging activities. It is argued that the broad scope of the enquiry overcomes the shortcomings of this material which result from inadequate standards of recovery, recording and curation.

The major conclusions reached in the study are:

1. That man and large mammals were seasonal occupants of Devensian Britain, on the evidence of reindeer antler remains, bear specimens in hyaena-accumulated assemblages and an analysis of tooth wear in horses.

2. That Ipswichian hyaenas found conditions more arduous than their Devensian counterparts, and may have died out at the end of Zone II of the interglacial, on the evidence of hyaena mortalities and the extent of bone consumption in hyaena-accumulated assemblages of the period.

3. That Devensian hyaenas did not tend to kill horses but instead scavenged their remains, most probably from lion kills, in view of the evidence for sexual parity in samples of horse teeth.

4. That much of the vertebrate material associated with Upper Palaeolithic industries and taken to show evidence of human economic activities is indeed the result of hyaena bone-accumulation, on the basis of comparisons with modern hyaena behaviour, and therefore inadmissable.

5. That an integration of present results with those from Europe and other parts of the world suggests that the importance of man as a member of the Pleistocene fauna may have been overemphasised.

"The paleontologist, indeed, generally comes much too late to find anything but bones. Instead he finds something denied to the neontologist: the time element..."

(Kurtén 1953: 5)

CHAPTER 1. Introduction

This study discusses aspects of the palaeoecology of large predators, including man, during the Upper Pleistocene in Britain, with particular emphasis on predator-prey relationships. The primary aim is to produce fresh insight into features of a palaeoecosystem which has received relatively little attention, beyond description, by the integration of palaeontological data with the results of modern ethological observations on species similar or analagous to those living in the past.

A second aim is to point to and correct the misleading impression of human activity in Upper Pleistocene Britain which has resulted from the misinterpretation of predator-accumulated bone as the work of man. This aspect of the study is discussed in Chapter 5.3 (p 117), when the evidence of human activity is reviewed in the light of an analysis of the bone debris.

A third aim is to discover whether the ecological similarities between predators and man can actually offer significant insight into aspects of later human prehistory. Man is considered in this study as a part of the large predator community and an attempt will be made to examine his likely past behaviour from a more ecological perspective, similar to that adopted for the other community members, rather than from the more usual artefact-orientated standpoint of the prehistorian. For this purpose, the availability of a technology appropriate to the exploitation of Upper Pleistocene game is taken as given, and an attempt simply made to evaluate past patterns of predation-related human behaviour as an exercise in palaeoethological reconstruction which parallels that applied to the other predators. This kind of approach may be capable of pointing to features of past human behaviour which are of considerable general interest and wide relevance, and receives further discussion in Chapter 6.2.

For present purposes, the term large predator covers man, lion, hyaena, wolf, leopard, bear, lynx and wolverine. Hyaena refers to the genus *Crocuta*, including the modern spotted form of East and South Africa, *C. crocuta*, and the fossil form, *C. crocuta spelaea*, and the distinction between these two species will be apparent from the context of discussion. Scientific names of all modern and fossil species mentioned in the study are given in Appendix 1. The Upper Pleistocene is taken to cover the last interglacial and glacial periods that are generally recognised in this country as the Ipswichian and Devensian respectively (Mitchell *et al* 1973). A full discussion of British Upper Pleistocene chronology is given in Chapter 3.

Following an initial discussion of material and methods in Chapter 2 and a review of environment, chronology and site setting in Chapter 3, the remainder of the study falls into two main parts. The first part, Chapter 4, presents a summary of the ethological data on the modern representatives, or in some cases analogues, of the Pleistocene large mammals, with the aim of establishing the likely behaviour of the fossil species. The scope includes morphology, feeding and reproductive behaviour, as well as appropriate predatory and anti-predator responses. The intention is not to present an exhaustive statement of all aspects of behaviour, but to extract and combine the information most relevant to a reconstruction of former predator-prey relationships. The chapter concludes with a series of predictions about the evidence most likely to be found in British Upper Pleistocene deposits.

Considerable emphasis is given to the hyaena, but this should be seen in perspective. The best modern predator ageing data, as well as the bulk of the British fossil predator evidence, relates to this species, but these points should not be taken to imply that the hyaena was the best or the most important predator among its contemporaries in this country. It should become apparent that a simple count of species specimens in an assemblage may give rather misleading results unless a wider view of accumulation processes is taken.

The second part, Chapters 5 and 6, examines the available material in the light of the predictions made in Chapter 4 and discusses interpretations. Chapter 5 presents a species-by-species account of the results of measurement and examination, together with an assessment of the evidence for human activity, and considers bone accumulation, faunal changes and the distinctive features of faunal assemblages from Ipswichian and Devensian deposits. Chapter 6 presents and discusses the major conclusions arrived at. These are dealt with in two ways: firstly with specific reference to Upper Pleistocene Britain and secondly, the wider relevance of this study. In this latter section, attention is drawn to the implications of predator studies for our views of the importance and activities of man during the Pleistocene. The third and final part of the chapter assesses the approach adopted in the study and suggests points of emphasis for further research.

1.1 The Nature and Limitations of the data

In presenting a reconstruction of predator palaeoecology, it is necessary to assess the extent to which the nature of the data may prevent such a goal from being realised.

The study considers museum collections of material from three major classes of depositional context. Firstly, most of the specimens derive from Upper Pleistocene cave deposits, and represent bone assemblages which accumulated through the activity of predators. Since many features of predator behaviour are related to prey capture (Schaller 1972; Kruuk 1972), and find reflection in the prey composition, it is clear that a study which encompasses past predator-prey interactions may profit from an analysis of food debris.

Hyaenas are particularly important in this study, both as accumulators of bone and as one of the best represented species in cave deposits. As will be shown, these animals both kill and scavenge with equal ability, and their food debris can potentially reveal not only their own predation strategy but also that of other carnivores from whom they may have appropriated carcases. The bones of the hyaenas themselves afford important evidence of population age structure and lifestyle.

A second class of evidence, also from cave deposits, is that accumulated through natural trapping of animals which fell into openings and pot-holes. Carnivore remains may occur in some numbers, presumably reflecting the attraction of carcases already trapped. In this case the information on predator-prey interactions is much less direct, although high proportions of predators may point to hunger and the need to scavenge, but considerable value attaches to the rather more complete bones often found in these deposits. Hyaenas are less likely to dominate the carnivore component of the assemblage in trap deposits.

The third class of evidence is from open-air sites. These tend to be of water-lain material, such as river gravels, and pose a number of problems for the vertebrate palaeontologist interested in predation strategies. The context of inclusion may be difficult to establish, and the relationship between ungulates and predators is not readily apparent. Carnivore remains are also infrequent in such deposits, possibly because of their relatively small size compared with those of the large-boned herbivores which usually dominate such assemblages and because of the low frequency of the order in the total vertebrate biomass. Occasional marks of chewing on bones may be the only evidence of predator presence actually preserved in such sites.

Despite these problems of open-site taphonomy, however, material from such deposits is in no sense ignored in this study. Fluviatile deposits frequently provide evidence of vegetation associated with the faunal remains, in the form of pollen and plant macrofossils, and such evidence may also be an important factor in relative dating, a point discussed further in Chapter 3.2(i) (p 33). Many open-site samples, like those from natural traps, can also offer important evidence of size ranges in species in view of the relative completeness of specimens. Furthermore, both of these latter categories of site produce important evidence of species diversity which may reinforce, or in some cases augment, that accumulated by predators in the process of food selection and consumption. However, the treatment of open-air sites and natural traps differs from that accorded to sites of predator accumulation in one important respect. Since the approach to Pleistocene predator-prey relationships adopted here requires some estimation of body part representation and bone fragmentation in sites of predator activity, discussion of these remains in Chapter 5 is accompanied by full details of the specimens seen and recorded, as given in the various tables referred to in that Chapter. For open-air sites and natural traps, the numbers of bones of each species, their anatomical distribution and their degree of fragmentation are of less relevance to the present enquiry, and the numbers given for many of these sites refer only to specimens examined and recorded for the kind of size estimations referred to above. Since although not relevant to the present study this material would have been of interest for further work, the decision not to include material from certain sites was generally a function of the size of the collection and the time available. Sites where the material for a species was thus partially recorded are indicated in Tables 2-23.

By contrast with the evidence of hyaena-accumulated bone, it is extremely difficult to point to Upper Pleistocene bone-assemblages in caves of this country which have clearly resulted from human activity. Open-air sites, whether settlement camps or hunting stations, are also few in number, and the vertebrate remains scanty. The evidence of human presence in Upper Pleistocene Britain is, in short, extremely sparse, whether measured in terms of actual sites or the food debris and artefacts found within their deposits. The significance of this observation is discussed further in Chapters 5.3 and 6.2, but it should be emphasised that this paucity of occupation evidence is important for palaeoecological reconstruction whether concern centres on man or on predators in general, and does not simply mean that human activities during this period should be overlooked. Genuine absence of any member of the ecological community is well-worth knowing, and is not a limitation of the data.

The early history of interest in British fossil mammals, discussed further below in section 1.2(c) of this chapter, has both advantages and drawbacks for the modern worker. On the one hand, stratigraphic control of recovered objects was often non-existent, and the views current at the time of excavation required none. Without the concept of phases in the Pleistocene, even following acceptance of the earth's antiquity, there was no reason for early workers to assume that some fossil animals were deposited under different environmental circumstances to others. In addition, recording and curation of finds was frequently inadequate by modern standards, and there can be no doubt that much valuable information about fossil material has been lost. These deficiencies will frustrate approaches which seek to examine the fine details of assemblage composition, and raise a number of obstacles to the quantified analysis of the data. On the other hand, the vast amount of material actually recovered over this long period of interest presents the modern-day investigator with a very large body of data which may be profitably examined at a lower resolution. It is possible to show that much of the material comes from deposits of Upper Pleistocene date, and that although lacking precision in many respects the remains represent activity over a sufficient span of time to permit investigation of long-term trends in Upper Pleistocene predator-prey relationships.

Although the sparse distribution of known sites may place limitations on the reconstruction of these trends, the available evidence covers a wide latitude within the country (Maps 1 and 2). A more serious objection that may be raised is the chronological uncertainties over many deposits and the consequent difficulties of inter-site correlation of these trends. This problem is particularly evident in the case of Devensian sites. The matter is discussed more fully in Chapter 3.3(i), but the difficulties clearly increase with the level of required precision. Although any effort to reconstruct palaeoecological systems will inevitably be only partly successful, it would seem more fruitful to attempt broad generalisations which the data can support than simply to reiterate its drawbacks and difficulties.

Perhaps the most important feature of the British Upper Pleistocene faunal evidence is the fact that it relates to two major climatic phases, the last interglacial and glacial phases. It is thus possible to contrast the environments of the two episodes, discussed further in Chapter 3, and to observe changes in the patterns of fossil evidence which may be related to adaptations on the part of the animals in the face of major climatic shifts. It is these broad changes that are the basis of this present investigation, rather than the more subtle and presently obscured events within each of the two phases, and the study thus concentrates on how to extract information on trends in predator ecology and predator-prey relationships between the Ipswichian interglacial and the Devensian glaciation.

1.2 Previous Work

(a) Approaches to Palaeoecology

Athough numerous workers have investigated Pleistocene mammals over the years, most have confined their attentions to identification and phylogenetics, with little emphasis on behaviour and ecology. Many studies have consisted of appended reports to archaeological articles, and even specific examinations of a number of mammal species have been tied to archaeological material and questions of human behaviour (for instance Delpech 1972, 1975; de Lumley 1976). As one of the most prolific writers on African Pleistocene mammals, Klein (1979: 2) has recently stated that insight into past human ecology is the main aim of his work, although his studies have at times encompassed wider aspects (Klein 1974).

For the archaeologist the mammals of the Pleistocene are viewed only as the food of palaeolithic man, a perspective well demonstrated in the latest work on the British Upper Palaeolithic (Campbell 1977).

Archaeological reports on French material also carry this emphasis, while seeking further evidence of ever finer climatic and chronological sequences in addition (Bordes and Prat 1965; Bordes *et al* 1972; de Lumley 1976; Bouchud 1975). The animals seem to be regarded as neither of intrinsic interest nor of value in the search for wider palaeoecological understanding, and few of these studies take adequate account of factors such as species behaviour in their interpretations.

Although Guthrie (1967, 1968) has made some attempt to reconstruct the palaeoecology of large mammals of Late Pleistocene Alaska, the major studies of fossil populations and their behaviour have been those of Kurtén (1953, 1954, 1955a, 1957a, 1958, 1963, 1968a, 1969a, 1969b), most notably on the bears and the hyaenas. These latter works were, however, in the main presented before the results of modern-day ethological studies became available.

(b) Predator Ethology and Human Prehistory

Over a decade ago, Schaller and Lowther (1969) argued that workers in the field of early hominid behaviour could derive great insight into the selective forces which shaped human society by examining the activities of ecologically similar species such as the social carnivores. They drew attention to the advantages which accrue from hunting socially, such as increased success, ability to tackle larger prey, fuller use of kills, division of labour within the society and the ability to win more disputes over food, and concluded by suggesting that further analysis be made of the relative importance of primate- and carnivore-related aspects of human social systems.

Since that time, further references to the possible value of such approaches have been made by Schaller (1972), in his detailed study of the Serengeti lions, and by Kruuk (1972) in his work on hyaenas. A few workers, such as King (1976a, 1976b) and Thompson (1976) have taken up the challenge and sought to produce models of early hominid society by applying the results of predator ethology, but little effort has been made to consider these results in the context of Middle and Upper Pleistocene human groups. Only Dart (1956) and Ardrey (1961, 1966, 1970, 1976) have attempted to apply predator parallels to later prehistoric society, and to modern social behaviour, but their efforts have produced strong criticisms about partial and inaccurate use of the evidence (Boylan 1972; Brace 1978; Leakey and Lewin 1977).

(c) Previous Work on British Pleistocene Mammals

The heyday of previous studies on fossil mammals in Britain was during the last century and the earlier part of the present one. Buckland (1823) published his report on the Kirkdale Cave hyaena den, together with a review of the evidence which he felt supported the biblical flood theory, and provided the first detailed account of such a deposit. Falconer (Murchison 1868) made a number of important studies and instigated the excavation of the Brixham Cave, but his untimely death robbed the subject of his expertise at a point when the best discoveries were just about to be made. Dawkins (1862, 1863a, 1863b, 1865, 1866, 1867, 1868, 1871, 1874, 1875, 1876, 1877, 1880) then began a series of publications on material recovered in a number of excavations, and attempted various syntheses of the evidence for man and the fauna. His discoveries included the important sites of Wookey Hole Hyaena Den and the caves at Creswell.

Vertebrate remains recovered during this time were summarised in a series of monographs published by the Palaeontographical Society on British Pleistocene mammals. Covering a wide range of species, they include the cats (Dawkins and Sanford 1866-72), the hyaena (Reynolds 1902), the bears (Reynolds 1906) and the canids (Reynolds 1909). Sanford (1867) issued a catalogue of felid remains from Mendip sites held in the Taunton Museum, one which was clearly intended to be the first of a series on fossil remains from the area, and which dealt with the important material recovered by people such as Beard and Williams who excavated a number of caves in the early part of the century (Rutter 1829).

These works naturally suffered from inadequate knowledge of ethology, particularly so in the case of the predators, and such descriptions of lifestyle as may be found in them bear a heavy overlay of Victorian value judgement and anthropocentrism. The hyaena receives little sympathy while the virtues of the lion are extolled. On the other hand, while Dawkins and Sanford (1866-72) attempted to give some background to the description of cave lion remains, the works of Reynolds in particular are rather dry, with scant discussion beyond an anatomical description of the species on the basis of a few specimens assumed to be typical. While an attempt to reconstruct ethology and ecology would have been ill-advised through lack of chronological and behavioural understanding, rather fuller use and discussion of quantities and contextual information at their disposal, and now in many cases lost, would have been invaluable.

More recently, a number of important contributions have been made by Sutcliffe (1955, 1957, 1960, 1969, 1970; Sutcliffe and Zeuner 1962), including excavations at the Ipswichian sites of Joint Mitnor and Tornewton, the former a trap deposit and the latter a living site of hyaenas. He has also discussed the adaptations of British hyaenas, although he now considers (Sutcliffe pers. comm.) that his treatment may have been a little premature, and has provided vital comparative information on hyaena bone accumulating activity in East Africa which is of direct relevance to British Pleistocene studies. Perhaps his most important recent contribution has been to studies on British Pleistocene rodents (Sutcliffe and Kowalski 1976), during the course of which he has brought attention to bear on the problems of chronology in the Upper Pleistocene.

During the course of his investigations of Pleistocene predators, Kurtén (1956, 1963, 1969a) made a series of measurements on collections of British hyaenas, paying particular attention to changes in size and morphology between Ipswichian and Devensian times. The data collected for this present study have extended those obtained by Kurten, and the work considers palaeoecology in more detail, but his results and approach have provided much of the impetus.

The absence of stratigraphic details and in many cases lack of information on the recovery of many collections in British museums has hardly encouraged further enquiry. One of the latest workers to attempt any significant synthesis is Stuart (1974, 1976, 1977) who was careful to use only the best dated and stratified materials in his studies of British Pleistocene vertebrate history. As a result, while he was successful in his aim of sketching a broad outline of mammalian arrivals and disappearances, together with some description of environment, the stance adopted inevitably meant passing over a large proportion of the total evidence.

Most recently, Grigson (1978) has attempted a survey of the Late Pleistocene ungulates of Britain, in an effort to establish species presence for the Late Glacial chronozones. As she also found, the lack of detail in the data confound such efforts at finer resolution, particularly when seeking to separate faunas of the Late Glacial from those of the immediately preceding period, and like Stuart she felt it necessary to omit many sites from consideration.

(d) Archaeology

Interest in human presence in Britain during the Pleistocene has as long a history as the investigation of the other mammals. Many of the earliest investigators had as much interest in geology and the vertebrate fauna as they had in man, and often laboured under the impression that man and extinct animals were not contemporaries. Only with the excavation of the Brixham Cave in 1859 (Busk 1872) did the coexistance become generally accepted. Dawkins (1880) produced one of the earliest syntheses of the evidence for human presence in Britain, having himself provided clear evidence for the antiquity of man at the Wookey Hole Hyaena Den (Dawkins 1862, 1863a, 1863b).

Since Dawkins wrote, few major syntheses have appeared. The Lower Palaeolithic is poorly covered, with the exception of the work of Wymer (1968), although Roe (1968) has provided a gazeteer of Lower and Middle Palaeolithic sites. Garrod (1926) summarised the evidence for Upper Palaeolithic occupation known at that time, and this has recently been revised by Campbell (1971, 1977). Mellars (1974) and Megaw and Simpson (1979) included much of Campbell's review in their own recent syntheses, but as a result incorporated the shortcomings of Campbell's economic interpretations which are discussed further in Chapter 5.3 (P 117) of this present study.

CHAPTER 2. Materials and Methods

2.1 Introduction

This study has involved firsthand examination of faunal material from British Ipswichian and Devensian sites. As was pointed out in the introduction, the stratigraphic details relating to any one deposit are often imprecise, although there can be no doubt about which of the two major periods are being dealt with in view of the great differences discussed further in Chapter 3. While such imprecision may inhibit the study of changes within each period, it remains possible to see broad changes over the total timespan of the Upper Pleistocene by observing the shifts in population parameters.

Probably the best summary of osteometry currently available is that published by von den Dreisch (1976), the result of several years' experience by the Munich workers. Two important drawbacks to this guide, however, are that it does not deal with a number of species likely to be found in Pleistocene contexts and that it tends to assume that whole bones will be found. In addition, it gives little attention to teeth and their measurements, and these are often a considerable proportion of any Pleistocene sample.

To overcome these problems, I decided to adopt a measurement scheme for predators proposed by Professor Björn Kurtén of Helsinki University in private discussion. This scheme has the merit of providing direct comparison with Kurtén's own extensive data on these animals, while being broadly applicable to other species. It provides for detailed measurement of isolated teeth and essential measurements of length and robusticity in long bones.

For horse, measurements on the teeth and the astragalus were recorded in a manner suggested by Dr. François Prat, the eminent French palaeontologist, who has made detailed studies of French populations of this animal.

2.2 Identification

The analyses carried out in the course of this study have involved identification of Pleistocene vertebrate remains, since most museum collections are inadequately sorted either by species or by anatomical part. First-hand experience of identification was gained initially during undergraduate practicals at Sheffield, where an introduction was given to domestic fauna recognition. This was augmented by a two-month visit to the Institut du Quaternaire at Bordeaux University as a postgraduate. While there, experience in the identification of Pleistocene fauna was gained under the guidance of Dr. François Prat. Copies of his teaching notes were presented to me at the end of the visit, and these and the thoroughness of his tuition have been an invaluable aid to the study. A week spent with Professor Björn Kurtén in Helsinki provided final details of the identification of predator remains, particularly those of the hyaena.

On the spot identifications were carried out with reference to comparative specimens where available, and to comprehensive notes and diagrams taken from authorities such as Prat and Kurtén and compiled in a bone atlas in the absence of such material.

Two particular points of identification are worth note. <u>Bison</u> remains were separated from those of <u>Bos</u> using criteria established by Olsen (1960) for distinguishing all parts of the post-cranial skeleton of the two species. Separation points are given by Olsen in descriptive and diagrammatic form which may be readily applied to fossil material. Male and female cast reindeer antler were distinguished using criteria established by Bouchud (1966) and reiterated by Sturdy (1975). The essential differences between cast antlers of male and female reindeer are illustrated in Figure 67.

2.3 Measurement Techniques

Measurements up to 150 mm were made with engineering vernier callipers capable of reading to 0.01 mm. Unless stated to the contrary, such measurements were recorded to the nearest 0.1 mm. Longer measurements were taken using either a steel tape or a measuring board, and recorded to the nearest 1 mm.

To gauge the accuracy of results obtained using the callipers, a series of replicate measurements of length and breadth of a hyaena tooth were made over a number of days. The results were as follows:

	Length	Breadth
Mean ± Standard Error	24.53±0.009	14.05±0.010
Standard deviation	0.047	0.057
Variance	0.002	0.003
Coefficient of variation	0.190	0.407
Range	24.5-24.6	13.9-14.1
Number of specimens	30	

These results suggest an acceptable level of accuracy, and any posited interpopulation variations are likely to be considerably greater, in circumstances of fossil data, than the inaccuracies indicated by the above Standard Errors.

2.4 Measurements Taken

(i) Long bones
1. Greatest length
2. Proximal breadth
3. Proximal anteroposterior diameter
4. Minimum transverse breadth of shaft
5. Maximum distal breadth
6. Transverse breadth of distal articulation in humerus
7. Functional length of ulna from coronoid process to distal end
8. Inner diameter of ulna sigmoid notch
9. Transverse breadth of femoral neck
10. Diameter of femoral head
11. Distal anteroposterior diameter of tibia.

(ii) Metapodia
1. Greatest length
2. Proximal breadth
3. Minimum transverse breadth of shaft
4. Maximum distal breadth

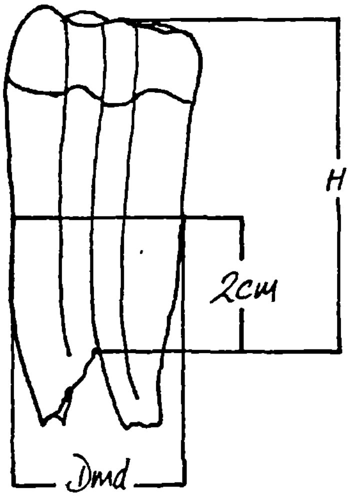
(iii) Skulls
1. Basal length (prosthion-basion)
2. Rostral breadth
3. Palatal length
4. Muzzle breadth
5. Zygomatic breadth
6. Condyle breadth
7. Interorbital breadth
8. Postorbital process
9. Postorbital constriction
10. Height, basion-saggital crest.

(iv) Teeth
1. Length at cingulum
2. Breadth at cingulum (maximum or breadth of blade for carnassial).

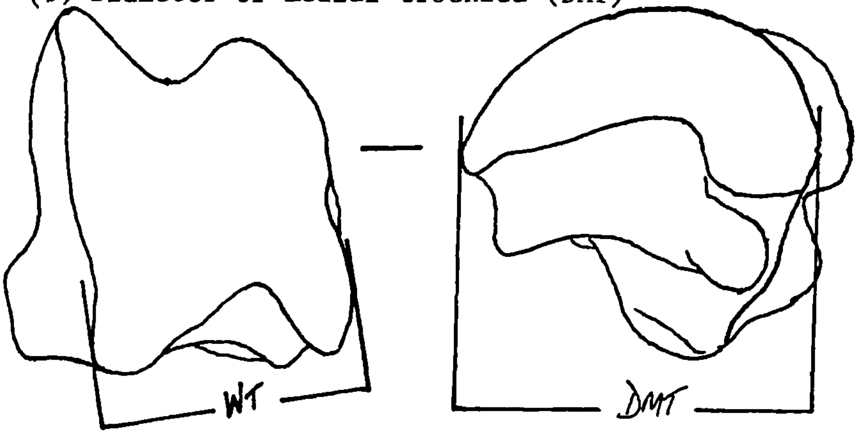
The above measurements were taken and recorded as appropriate to the species under examination and the extent of fragmentation. The following special measurements were taken:

1. Horse

(i) Upper and lower premolars and molars
   (a) Height of the crown (H)
   (b) Mesio-distal diameter (Dmd)
   measured 2 cm above
   root bifurcation

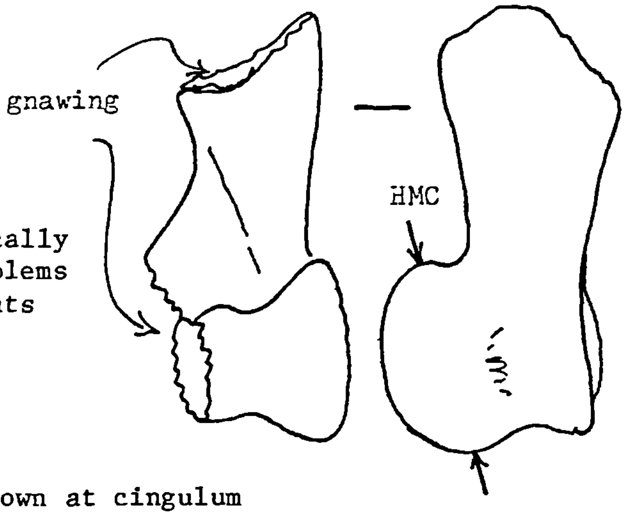


(ii) Astragalus
(a) Width of tibial articulation (WT)
(b) Diameter of medial trochlea (DMT)



These horse measurements were selected on the advice of Prat, and permit comparison with his own measurements of horse remains from various French Pleistocene sites.

2. Rhinoceros
(i) Humerus
Height of medial condyle (HMC)
This measurement was specifically selected to overcome the problems of hyaena gnawing at the points indicated, permitting at least one measurement to be obtained on most specimens.



(ii) Upper molar 3
1. Length of buccal surface of crown at cingulum
2. Length of lingual surface of crown at cingulum
4. Height of buccal surface from cingulum.

The purpose of all measurements was to obtain indications of size variation, sexual dimorphism, age and seasonality within and between populations as appropriate to the individual species. The manner in which specific measurements bear on these aspects of study is dealt with in the relevant sections of Chapter 5.

2.5 Assessment of Age at death

The problem of age assessment, although mentioned briefly above, deserves further consideration. Clearly, in any study where interactions between predators and prey are a central aspect, age at death figures for the various populations are a factor of major importance. Since teeth are frequently found in fossil deposits, much of the work on age determination has concentrated on them. As Harris (1978) points out, tooth attrition is in fact one of the oldest known techniques for age determination, being widely known as a factor in judging the worth of a horse.

(i) Hyaena

In the case of fossil hyaena, teeth are well represented in all deposits where the animals appear. In his East African work, Kruuk (1972) used teeth as an age indicator, and compared the age ranges of the Serengeti and Ngorongoro hyaena populations on that basis. Since he was dealing with individual animals each with a complete dentition, rather than the mixture of fragments commonly found by the palaeontologist, he used only one tooth, the lower premolar 3, in his aging estimates (Kruuk 1972: 33). This tooth, one of the large conical bone crushers, can be easily placed in one of a number of wear categories from I (unworn) to V, as shown in Figure 1. Since many of the samples consisted of isolated teeth, and it seemed worthwhile to have as full a record as possible, it was necessary to obtain some measure of wear on other teeth for a given wear stage on lower premolar 3. As Kruuk did not give this information, a series of modern specimens were examined. Most came from the British Museum collection, but specimens from other collections were added as available, and a full list is given in Table 1. From this body of data, average wear patterns for upper and lower dentitions were derived, shown in Figure 2, permitting individual teeth to be aged. Such wear templates have the additional advantage of permitting the evaluation of complete dentitions, serving as a constant check on the method and a guide to aberrant patterns among a population.

This extension of the East African wear categories to fossil material has been critised by Kruuk (pers. comm.), who has suggested that factors such as relative tooth hardness and the extent of bone chewing may have a considerable effect upon the wear of a predator's teeth. He therefore feels that it is difficult to use his method to obtain age classes for Pleistocene hyaenas of Europe, and to compare populations of that period, and has suggested that tooth sectioning to reveal annual dentine rings is the only way to approach the problem. In that way, of course, each tooth should reveal the true age of the animal at death, and perhaps even season of death. Such a technique would permit a more detailed assessment of hyaena mortalities than could ever be possible using wear criteria. However, a number of points may be raised in reply to this viewpoint.

The evolutionary history of the spotted hyaena, as discussed by Ewer (1973), suggests that this species owes its dental and digestive specialisations to the occupation of an essentially scavenging niche for much of the early period. Thus although relative tooth hardness and extent of bone gnawing may have some effect on the wear rate, the dentition is well adapted to such activity. It is difficult to see why there should be any great difference in tooth hardness between the various Pleistocene populations, and only dietary differences are therefore perhaps worth considering. In effect, a wear stage could be expressed in terms of "gnawing years", and the problem is to decide whether worn teeth point to heavy usage by relatively young animals or to more moderate usage by older ones. Kruuk's work actually provides the best modern-day test to answer this.

As discussed further in Chapter 4.1.1 of this study (p 82), Kruuk found that in the Serengeti hyaenas did more scavenging, often taking only choice pieces from a carcase. In the Ngorongoro Crater, fuller use was made of each food item, skeletal parts included, and the hyaenas there had a harder lifestyle and consumed more bone. Yet it was in the Serengeti that the highest proportion of hyaenas with worn teeth was found, in age groups IV and V, and since they consumed less bone it is a fair interpretation that they were old animals. This would suggest that while both diet and age may play some part in determining the tooth wear of a species, diet may be of less importance.

As Kurtén (1953) has pointed out, longevity in mammalian populations appears to be largely dictated, in practice, by the durability of the teeth. An animal with heavily worn teeth is effectively at the end of its lifespan. Of course it is possible, with special feeding, to enhance that span, and to make it thus dependent on the wear and tear of other bodily parts, particularly so in the case of horses. In that sense diet is certainly important, but the chief virtue of such examples lies in their pointing up the fact that an animal which never masticated would have largely unworn teeth. Special feeds aside, any diet must produce tooth attrition.

It may be illuminating to ask what it would mean in real terms if diet were the major determinant of tooth wear? Since the plains hyaenas have a higher proportion of animals in tooth wear classes IV and V, those animals would have to be considerably older than those of the crater in the same wear classes. Kruuk (1972: 34) quotes 25 as observed age maxima for captive hyaenas, with an average of 12 for quite a large sample. Details are not known, but from observation of zoo feeding practices it is likely that they had a fair proportion of bone in their diets, although perhaps not to the same extent as the crater hyaenas. For Ngorongoro, Kruuk suggests age limits of 6-16 years for wear class IV and 16 years and over for wear class V. These are broad groupings. It should be noted that once class V is reached on lower premolar 3, there is still a reasonable amount of tooth left. Since the tooth is conical, the surface area exposed actually increases considerably with wear, and as Harris (1978) and Spinage (1973) remark, tooth wear generally follows a negative exponential curve, such that the rate tails off with increasing age. Thus if the crater hyaenas reach tooth wear stage V at around 16 years, with several more years of wear left to them, they may closely approach the maximum recorded captivity ages, and in a harsh environment. If the plains hyaenas in wear class V are significantly older, then they must come even closer to, if not actually exceed, the captivity maximum, and that seems fairly unlikely. Bearing in mind that the age classes which Kruuk deduced are broad, and that dietary differences can probably be encompassed quite easily, I would prefer to argue that hyaenas with similar degrees of tooth wear are generally speaking of comparable age.

In that case it is possible to use Kruuk's age criteria for comparison of fossil populations. If such criteria could be applied satisfactorily to two modern populations, then I see no reason why they should not be applicable in this study.

Tooth sectioning methods might indeed establish age more precisely, but problems exist as the technique is destructive, and since a number of specimens would have to be sacrificed few museums would be willing to allow such treatment. In the case of some key sites, such as Kirkdale Cave, Joint Mitnor and Barrington, the actual amount of hyaena material is already small, so that results from other sites with large samples would have to be extrapolated to them, and the problems of any differential wear with respect to age would therefore remain.

The requirements of the present study should also be kept in mind. Sacrificing accuracy for speed is a potential pitfall in any undertaking involving a large quantity of data, but the categories employed allow a hyaena to be placed in a juvenile category (I), and four adult categories, which could be termed young (II), young middle age (III), middle age (IV), and senile (V). These seem as adequate to me, as they did to Kruuk, to describe the general parmeters of a death assemblage.

(ii) Age in other species

(a) Horse

In section 2.1 I briefly discussed the use of Prat's system for recording crown height in horse teeth. Although most estimates of horse age tend to be made on incisors (Silver 1969), these occur infrequently in fossil deposits, and it was felt that a measure of attrition in cheek teeth would be more appropriate. Isolated teeth are common for horse as they are for hyaena, so that adequate samples were ensured. In addition to providing an indication of the age ranges of adult horses killed, it was hoped that horse crown heights might shed some light on the problem of seasonal presence during the Devensian glaciation, and these two aspects of the study are discussed further in Chapter 5.9(iv).

(b) Bovidae and cervidae

Crown height of lower molar 3 was measured in some samples of these species, but most samples were too small to permit detailed analysis. In most cases wear categories were assigned instead, but since unlike the hyaena, which has conical teeth, the portion worn from a tooth is not easy to estimate, these were rather less precise. Five categories were recorded as follows in order of age:

1. Unworn (uw)

2. Slightly worn with wear just onto all cusps (sw)

3. Moderately worn with wear up to an (estimated) half of original crown height (mw)

4. Well worn with wear past half height but with cusps still determinable (ww)

5. Very worn with teeth virtually flat (vw)

One problem with age determination in the bovidae and cervidae is that different teeth in the same jaw may show considerably different wear categories, and individual identification of isolated teeth must precede any assessment based on wear data. Identification of isolated teeth presents little problem in horse, but in bovidae and cervidae there are some difficulties.

(c) Rhinoceros

Tooth crown heights discussed above in section 2.4 were used as a guide to age in adult rhinoceros.

(d) Other predators

A scheme of age wear categories similar to those for bovidae and cervidae was adopted. It quickly became apparent that the relatively small sample sizes by comparison with hyaena, together with the lack of similar aging data on wolf and lion in different environments, rendered precision in this matter superfluous.

2.6 Data Analysis

The data analysis has been performed in a number of ways. Teeth of hyaena have been examined for age and size variation using the SPSS package available on the Sheffield computer. This method provides a basic statistical summary of the data, sorts by anatomical part, scatter diagrams and so forth. Horse teeth have been tested for evidence of seasonal wear by a special programme adapted by Dr. N. Fieller of the Department of Probability and Statistics, Sheffield University. This programme searches for evidence of periodicity in tooth attrition, and is described more fully, along with the results, in Chapter 5.9.

In addition to computer-aided studies, long bone and teeth measurements have also been examined by graphical display, utilising techniques of data presentation proposed by Kurtén (1956) and Simpson (1941). Fuller reference to methods will be found in the appropriate sections of Chapter 5. The particular advantage of such techniques lies in their ability to present an impression of bodily proportions and changes in more than one parameter in a single diagram. This permits something of a mulivariate analysis of the data without the complexities of more usual multivariate analysis or necessitating the often unjustified assumptions of data normality which such methods require (Corrucini 1975).

I have resisted the temptation to include every piece of data collected in the course of this study. Only those aspects of modern species behaviour relevant to a palaeontological reconstruction have been considered in the sections on ethology, and in a similar manner only the details of fossil material which appear to offer some insight into fossil population parameters have been reported and commented on. It would be relatively easy to become embroiled in matters of species erection and redefinition, since much research probably remains to be done for a number of British and European Pleistocene groups, but this study would seem to be an inappropriate place for such investigations.

One further aspect of analysis which requires some preliminary discussion and explanation is the estimation of animal numbers in the samples.

2.7 Number Estimation

The problem of number estimation is a recurring one in faunal studies. Virtually every published report on archaeological vertebrate remains, whether from prehistoric or historic sites, gives some discussion to the merits of various techniques. Most focus on the question of whether fragment counts of each species are more satisfactory than estimates of the minimum number of individuals (MNI) for assessing the relative abundances of species. Payne (1972) points to the disparity between number estimates based on each technique, and concludes that the best approach may be simply to determine relative abundance on a number of different parts of the skeleton and to then apply common sense to interpretation, perhaps taking the lowest ratio as nearest the truth and rejecting others as due to differential recovery.

There is no doubt much truth in what Payne says, but it is likely that for most purposes knowing whether say cattle were more important than sheep will be sufficient without having a precise ratio. It is not made clear how Payne would relate the ratios derived by his method to the killed population of animals, and if one cannot do that explicitly, on a mathematical basis, then any accuracy obtained is spurious. If circumstances require a quantification of relative abundance, then a clear basis for the calculation must be established.

In this study, the number of specimens of each species seen is given in Tables 2-23. For most purposes an adequate appreciation of importance may probably be gained directly from these tables, and I make no attempt to display percentages of each species. The significance of these numbers and the difficulties of interpretation are discussed further in Chapters 5.2 and 6. But in the case of hyaena, some evaluation of the relative numbers in each age group is required, beyond that obtainable by ranking. The method adopted here derives from capture-recapture techniques of game estimation, using the 'Petersen" index described by Seber (1973).

Suppose that N represents the total number of animals in a closed population. A sample of these, n1, are captured, tagged and returned to the population. After allowing enough time for mixing, a second sample, n2, is taken at random from the population, and the number of tagged animals in it, m2, noted. Assuming no deaths or recruitment, we have:

$$m2/n2 = n1/N \qquad (1)$$

Therefore $N = (n1 \cdot n2)/m2$ (2)

Now consider a population of killed animals, N. Taking any one body part, the humerus, say, consider a deposited sample to be selected from this population at random, having L left bones, R right bones and P matching pairs. If L is greater than R, then L may be considered analogous to n1 in equation (1), R analogous to n2, P analoguous to m2 and both populations represented by N.

Therefore $N = (L \cdot R)/P$ (3)

If R is greater than L the formula is identical.

A feature of this method of estimation is that it also holds true if the selection of left, right and number of paired bones is made after deposition, in other words by the excavator, and for a number of selection stages. The only requirement is that each selection stage be made randomly.

Casteel (1977) has recently argued than MNI estimates of faunal numbers are to be preferred to the method of formula (3), basing his argument on criticisms of a method put forward by Krantz (1968). Krantz derived the formula

$N = (L + R)/2P$ (4)

where L, R, P and N represent the same sample parameters as in formula (3). In fact the Krantz method is different to the Petersen index approach, seeking as it does to derive an average estimate of N from the ratios of left and right bones to the number of pairs, but the approach is similar, attempting to estimate what is missing on the basis of what is present. Casteel misunderstands Krantz's argument, and shows how one could have a sample with a left, right and pair distribution totally at variance with the known population size. This is unlikely unless the sample has not been drawn at random, since the method depends upon the probability that one will in fact derive a certain distribution related to the population size.

In the light of formulae (2) and (3) and their derivation, it is interesting to consider just what an MNI calculation has to say. Chaplin (1971: 70) claims that it gives "...a direct measure of the number of animals involved and is an abstraction of the true number of animals only within fixed limits." He goes on to emphasise that only verifiable facts are used, and that these therefore provide a sound basis for extrapolation and interpretation. Formulae (2) and (3) suggest otherwise. As used by Chaplin and Casteel, the MNI estimate takes the number of pairs of any bone and adds to it the number of unmatched left plus unmatched right bones. That is the same as taking the total number of left bones and adding to it the number of unmatched right bones, or vice versa. From formula (2), we see that to be equivalent to estimating the number of game in an area by adding the number of untagged game in the second sample to the number of tagged game in the first sample, which is clearly nonsense. Such a method reveals only how many animals have been caught and says nothing about the total population, since there is no direct relationship between those two unless one considers the distribution of tagged specimens. In a precisely similar manner the MNI estimate reveals how many animals are on the table in front of the analyst, nothing less and nothing more.

Of course the Petersen method of calculating faunal numbers depends upon an ability to determine matches. In the case of some body parts, such as mandibles, it is often possible to determine a match by fitting left and right parts together. With other parts, particularly isolated teeth, this is not possible, and size, degree of wear and so on must then be considered. For hyaenas, it was decided to use lower third premolars as the body part for number estimation, whether in the jaw or in isolation. Had all material from each site been in one museum, it would then have been a simple matter of visually comparing specimens, putting together halves of mandibles where possible, and deriving a number for animals in each age group using formula (3). However, most sites have their finds distributed over a number of museums, so that measurements only, as well as the age categories, had to be used.

Each mandible with a third lower molar and each isolated lower third molar was therefore considered, divided into left and right and age class. Where the third premolar was in a jaw, all possible measurements on the other teeth in the jaw, plus measurements of the mandible, were taken into account in determining a match. For isolated teeth, only the individual tooth measurements could be considered. The criterion of matching was that no measurements should differ by more than 0.6 mm between paired elements in an age group, on the basis of observations on modern hyaena dentitions and the occasional find of matching fossil specimens. In the event of a tooth being unmeasurable through wear or breakage, it was assumed to match with any unattached element from the opposite side of the body within the same age class.

CHAPTER 3. The Chronological and Environmental Background

3.1 Introduction.

The aim of this chapter is to present an outline of the chronology and environment of the period under discussion, and to introduce the main faunal elements.

In recent years, it has become increasingly apparent that the sub-division of the Quaternary is extremely complex. Work on deep-sea cores and their oxygen-isotope ratios (Shackleton 1975; Shackleton and Opdyke 1976; Hays *et al* 1976; Mangerud *et al* 1979), loess stratigraphies (Kukla 1975; Fink and Kukla 1976) and fossil beaches (Butzer 1972) all point to a vastly greater number of major climatic fluctuations than have hitherto been assumed, and have firmly closed the door on any lingering notions of a simple sequence based on Alpine stages.

Hays *et al* (1976) claimed close correlations between changes in obliquity and precession of the earth and major climatic changes over the past 500,000 years, thereby providing a timescale for Pleistocene events independent of the events themselves and enabling predictions of climatic shifts to be made. Their work involved the major conceptual leap, absent in previous studies interested in orbital forcing of climatic change, of simply considering the input and output of the system without becoming caught-up in considerations of direct mechanisms or assumed prior knowledge of the number of cycles. The conclusions which they reached have recently been challenged, however, by Kominz and Pisias (1979), who argue that only 25 per cent of the variance in global ice volumes can be attributed to variations in obliquity and precession. In their view, the Pleistocene glacial variations are largely stochastic processes but they also admit that considerable periodicity may be observed.

If deep-sea cores can provide a framework, the problem of relating each stage to the sequence of terrestrial deposits in any one area must still be faced. Work on loess deposits by Kukla (1975) and Fink and Kukla (1976) suggests that this may be a realisable goal in some cases, but as Mangerud et al (1979: 189) point out, correlation of stratigraphic units defined on land with particular stages of the oxygen-isotope record remains a real problem for periods beyond the range of radiocarbon dating. Shackleton (1969) has suggested that oxygen-isotope stage 5e correlates with the Eemian interglacial of the Continent, defined at the type site on the River Eem near Amersfoort in The Netherlands, and argues for a date of 124,000 years, but this point is one of the few generally accepted to have been established.

Bowen (1979a, 1979b) has recently pointed to the dangers of assuming clear correlations between the frequently fragmentary terrestrial record and the apparently complete sequence given by the sea cores. In the absence of direct superimposition, mappable deposits or absolute dates, no "Eemian" deposit actually correlates with oxygen-isotope stage 5e, in the final analysis: any claim to the contrary is supposition at one level or another. This applies with equal force to the correlation of deposits in the British Isles, and it would be folly to rush into an attempt to assign local events to those of either the Continent or the sea core record. We may have to accept that, for the present at least, the cores preserve a record which cannot be matched in most terrestrial deposits.

This would seem to be particularly true in Britain. The recent stratigraphic proposals of the Quaternary Era Sub-Committee of the Geological Society of London (Mitchell et al 1973) found evidence of only two interglacials since the Cromerian, the Hoxnian and the

Ipswichian, which clearly does not accord with the oxygen-isotope record in complexity. However, that is no reason to begin forcing the existing data into a fit, although it certainly gives impetus to further research. It would seem reasonable to equate the Ipswichian with the Eemian, and thus with oxygen-isotope stage 5e, since both appear as the latest interglacials in their respective areas, but one should avoid an assumption of certainty in this. Since the last interglacial and the last glacial are the periods of immediate concern in this study, this correlation may suffice.

3.2 The Ipswichian Interglacial

(i) Chronology

In Britain much of the controversy over Pleistocene stages and their frequency has related to the Ipswichian, but with little emphasis actually being placed on the sea core evidence. Rather, discussion has centred on the number of warm stages to be discerned within this phase on the basis of mammalian assemblages, with Sutcliffe (1975, 1976) and Sutcliffe and Kowalski (1976) arguing that mammalian assemblages assumed to be Ipswichian actually come from two or more warm phases between the last two glacial periods of Mitchell et al. Much of the argument for this theory is based on apparent anomalies in Thames terrace deposits at Ilford and Trafalgar Square, which are claimed by Sutcliffe to lie in separate and therefore non-contemporaneous terraces. Both sites have pollen assigned to the Ipswichian Zone II, as defined by Turner and West (1968), but a markedly different mammalian fauna, in particular presence of hippopotamus and absence of horse at Trafalgar Square contrasting with a lack of hippopotamus and abundant horse at Ilford. Differences in the rhinoceros and mammoth species at the two sites have led Sutcliffe to suggest that Ilford predates Trafalgar Square, and that both represent Zone II of different temperate stages separated by an as yet unrecognised cold stage.

Stuart (1976) has argued against this interpretation on several grounds. Firstly, he suggests that the two sites may not lie on separate terraces, and points to the difficulties of terrace interpretation in the Ilford area. Secondly, he disputes Sutcliffe's identifications of rhinoceros and mammoth to species, and claims that these animals do not support the sequence in deposition between the two sites put forward by Sutcliffe. And thirdly, he points to a good overall correspondence between Ipswichian pollen zones and fauna, and suggests that the horse-less hippopotamus stratum may be a general Ipswichian Zone II phenomenon. In his view, absence of hippopotamus at Ilford may be no more than an artefact of recovery, since the Zone II deposits there were rather localised, and the abundant horse remains actually seem to come from higher levels, within Zone III. Stuart thus agrees that Ilford and Trafalgar Square are faunally distinct, but argues that this stems at least in part from deposition during different zones of a single interglacial.

A further point of dispute between the two authors concerns the position of the Crayford deposits. Sutcliffe (1976) considers the deposits to date from before the Ipswichian Zone II, marking the end of a previous interglacial and perhaps marking the climatic deterioration which led to the formation of the Tornewton Cave Glutton Stratum (Sutcliffe and Zeuner 1962), a deposit generally accepted to be pre-Ipswichian. Stuart, on the other hand, considers that the deposits formed during Zone IV of the Ipswichian, and that the cold elements recovered point to the onset of the Devensian. Again, identification is a feature of the dispute, this time concerning Microtus species. Both Sutcliffe and Currant remain adamant (pers.

comm.) that Crayford is unlikely to be late Ipswichian, pointing to the relatively high levels of the deposit in an area of the Thames basin where such an altitude is generally considered to indicate a pre-Ipswichian date (Map 1).

Clearly the matter is complex, and there is some danger of simply accepting the opinion of the last authority consulted. As West (1976) observed, the only real answer to problems of sequence is better litho- stratigraphy and bio-stratigraphy, in the absence of absolute dates. Until that is achieved there is little point in assuming complexity beyond that demonstrable, unless the assumption can lead to new insight. Returning to the points made above concerning oxygen-isotope stages, it is clear that the terrestrial evidence should not be forced, and neither should one fall into the common trap of disputes such as this and assume that one authority is correct when neither may be. I shall return to a consideration of the problem in Chapter 5.9(i) having presented some of the data collected in this study , and see if this information may shed more light on the matter.

For the moment I will concentrate on one aspect of the data on which both Sutcliffe and Stuart seem to agree; that the horse-less hippopotamus stratum at Trafalgar Square is a chronological phenomenon. As Sutcliffe (1976) has pointed out, the assemblage occurs commonly in a number of British caves. He listed Tornewton, Joint Mitnor and Eastern Torrs Caves, Devon; Milton Hill and Durdham Down Caves, Somerset; Victoria Cave, Raygill Fissure and Kirkdale Cave, Yorkshire and Ravenscliffe and probably Bacon Hole, Gower. To this list may be added Robin Hood's Cave, Mother Grundy's Parlour and Hoe Grange, Derbyshire. In fact virtually every cave in the country which has deposits assignable to the Ipswichian has only the horse-less hippopotamus assemblage. Stuart (1976: 224) suggests that horse has never been found in open air sites assigned to Ipswichian Zone II, and that hippopotamus is only known from Zone II and the beginning of Zone III, and it is therefore likely that these cave deposits date to Zone II also (Table 24). The only exceptions to caves with Ipswichian deposits solely of Zone II date would appear to be Bacon Hole and Minchin Hole (Sutcliffe 1976; Sutcliffe and Bowen 1973; Stringer 1975), where other parts of the interglacial sequence do have horse. To these I would add Bleadon Cave in the Mendips, excavated in the early part of last century by William Beard (Barrington and Stanton 1976: 42) and, unfortunately, devoid of stratigraphic data. Sutcliffe and Kowalski (1976: Table 12) have put this deposit in the Devensian cold stage, but as discussed further in Chapter 5.9, I would consider at least part of the deposit to have accumulated during an earlier warm stage which may equate with later Ipswichian.

A further marked feature of the horse-less hippopotamus cave deposits is the inclusion, often in great numbers, of hyaena remains. As will be discussed further in Chapters 4 and 5, the bone-accumulating activities of modern hyaenas, together with the evidence of hyaena bone destruction in the Pleistocene deposits, leaves little doubt that in most cases this animal was the agent of accumulation. Both Sutcliffe (1976) and Stuart (1976) have remarked on the absence of Ilford-type faunas (horse and no hippopotamus) in caves, with Sutcliffe attributing this to the greater age of Ilford assemblages and Stuart suggesting that lack of careful excavation is indicated. Both authors may, however, be mistaken. Although known in numbers only from one Zone II open air site, Barrington, hyaena has also been identified in material from Swanton Morley which may date to Zone II or early Zone III (Phillips 1972; Coxon et al 1980). By constrast the animal is absent from other sites datable to Zones III and IV (Table 24). If hyaenas were only present during Ipswichian Zone II, then only during that period would cave deposits containing bones be likely to have formed, tending to reduce the force of Sutcliffe´s argument. Against Stuart´s suggestion of oversight to explain the lack of horse one can raise the criticism of special pleading. Devensian sites excavated at the same time by the same people under the same conditions are often marked by the abundance of horse specimens, and their absence from the Ipswichian caves would seem to be a genuine feature.

As I shall show in Chapter 5.4 (p135), a good case can be made for a local extinction of the hyaena population towards the end of Zone II. Accumulation of bone deposits being largely confined to this period is therefore probably explained, but this leaves the material from Bacon Hole, Minchin Hole and Bleadon Cave, referred to above, to be explained. Bleadon Cave, judging by the description of Barrington and Stanton (1976: 42), may well have functioned as a trap. The material examined in Taunton Museum certainly suggested this, with cervid remains indicating the presence of most parts of the skeleton, as in the case of the well-attested fissure traps of Joint Mitnor (Sutcliffe 1960) and Hoe Grange (Bemrose and Newton 1905). A single specimen of hyaena in the British Museum (Natural History), a maxillary fragment specimen number 44748, is said to come from the site, but the more extensive collection in Taunton Museum holds no specimens of this species recorded as coming from the cave. As a result, I am not inclined to attach a great deal of weight to the isolated item. Although a quantity of the Taunton collection is unprovenanced, there is every indication that one of the original collectors of material from the site, William Beard, marked origin details on material in his collection, and should therefore have done so with any hyaena remains from Bleadon. The circumstances of deposition at Bacon Hole and Minchin Hole are less clear: since work in these caves is still in progress it may be best to postpone judgement.

Sutcliffe (1976: 5) has suggested that another Mendip site, Hutton Cave, may also be of Ilford type and correspondingly pre-Tornewton Glutton Stratum. Again, I shall discuss this deposit further in Chapter 5.9, but the material seen suggests that rather than predating the Ipswichian Zone II, the fauna may at least in part derive from Devensian times.

Of course if hyaena activity explains the formation of Ipswichian Zone II deposits in a number of caves occupied by this animal, it may still seem odd that trap deposits such as Joint Mitnor, Hoe Grange and Milton Hill had only Zone II material. It may be argued that if they were natural traps, then specimens of Zone III and IV would be expected, including perhaps horse and mammoth. Milton Hill provides little answer to this, being reported in scant detail (Balch 1948: 142-3), but both Joint Mitnor and Hoe Grange appear from published details to have been full deposits, so that no material of Zone III age onwards could have been included. Lest this appear to be special pleading in favour of hyaena activity as an explanation for other deposit formation, it should be borne in mind that Bleadon Cave may afford an example of trap deposits which formed during Zones III or IV, as pointed out above, so that this kind of accumulation need not be confined to Zone II. It may be no more than an unfortunate fact of life that, to date, no trap deposit has been found which spans the Ipswichian.

If the Ipswichian does indeed correlate with the Eemian, and if both are represented by oxygen-isotope stage 5e at 124,000 years (Shackleton 1969, 1975), then any sub-stage of the Ipswichian, such as

Zone II, was itself probably of relatively short duration, as indicated by the faunal estimates of winter and summer temperatures given by Shackleton (1975: Figure 6) and shown in Figure 3 of this study.

(ii) Vegetation and climate

Stuart (1976) and Phillips (1972, 1974) provide useful summaries of the available vegetational and climatic evidence. Most of the sites with pollen are in the east of the country, in river valleys or on the coast (Map 1). Most are of fluviatile context. Table 25 shows the general picture of vegetational succession deduced from the pollen analyses, and suggests a mixed oak forest by the time of Zone II. Most pollen curves show a decrease in herb pollen at this time, followed by a rise in herb frequencies as the forest thinned in Zone III. As Stuart points out, inter-site variation in pollen frequencies is evident, particularly so in Zone II. Since spectra from fluviatile contexts may contain a large component of pollen of local origin, reflecting vegetation very close to the point of deposition, sites close together may show considerable differences between pollen assemblages of similar age.

Stuart also pointed to the work of Turner (1975), who suggested that hippopotamus activity might lead to an overrepresentation of herb pollen at some sites, in view of this animal's habit of grazing on such vegetation and then defecating in the water. In addition, the fauna of Zone II may have been very effective in initiating and maintaining local deforestation.

Deposits assigned to Zone I are generally thin and may suggest a short duration. This view finds some support in Continental pollen diagrams (Stuart 1976: 226).

Zones III and IV show evidence of increasingly open forest, and this picture is in agreement with evidence from terrestrial snails which indicates an absence of woodland taxa. By Zone IV, an open boreal forest is indicated.

The temperature seems to have risen rapidly at the beginning of the interglacial (Phillips 1974), with thermophilous trees and plants appearing in Zone I. For Zone II, plant and animal evidence suggest a very warm period, with summer temperatures 2-3°C warmer than present and a July mean of 19-20°C (Coope 1974; Phillips 1974; Stuart 1976). A mediterranean climate with warm winters has been suggested.

After Zone II, Phillips has suggested an increase in continentality with summer temperatures remaining high.

(iii) Fauna

The fauna of Britain during the Ipswichian is summarised in Table 24. For the purpose of this study, the main concern is with the larger mammals. The carnivores include lion, hyaena, wolf, bear and leopard, although the latter species is not shown in Table 24 since it has not been identified in deposits from any of the sites listed. The prey species comprise hippopotamus, rhinoceros, elephant, giant, red and fallow deer, Bos and bison, horse and a range of small animals, chiefly rodents, which could have provided food for a predator. As Table 24 shows, and as discussed above, hyaena and hippopotamus appear almost entirely confined to Zone II, during which horse is absent, whereas most other species are present throughout. Although steppe rhinoceros and straight-tusked elephant are generally taken as the interglacial representatives of their families , one should also note that mammoth occurs in a number of deposits, and woolly rhinoceros is recorded from Crayford, although they are not recorded from any levels assignable to Zone II. This discussion of the fauna is necessarily brief, since the species will be considered in greater detail in the following chapters.

(iv) Sea level and isolation

Stuart (1976: 241) gave a brief resume of possible British isolation from the Continent during the Ipswichian. On the basis of work by West (1972) and Destombes _et al_ (1975), it seems likely that isolation occurred at least during Zone II and the early part of Zone III, although the problems of determining past sea-levels are considerable. However, while oxygen-isotope data may be difficult, on present evidence, to correlate with terrestrial evidence, they can be of immense help in this area, an aspect which seems to have received remarkably little attention. As Shackleton (1975: 4) emphasises, the deep-sea cores preserve evidence of the amount of ice present, since the ratio of oxygen isotopes reflects the increased salinity resulting from fractional freezing of the lighter isotope, and hence point to the sea level itself. While some of the problems which prevent a simple comparison of isotope ratios, and thus sea levels, are examined in some detail by Shackleton and Opdyke (1976), it is clear that the approach can reveal numbers of high and low sea stand. Thus the data from Atlantic core V23-100 (Parkin and Shackleton 1973; this study Figure 4) suggests that the last sea level equivalent to the present day was that during stage 5e, which would certainly have cut this country off from the Continent.

Of equal importance is the timing of major falls in ocean level, with their implications for faunal migration. In view of the appearance of horse and mammoth in deposits assigned to early Zone III, Stuart (1976: 242) has suggested that these species sought refuge in Scotland during the wooded stages of Zone II, and it is certainly difficult to think of other simple explanations for these phenomena in view of the relatively delayed drop in sea level (Figure 4), making it impossible for them to have migrated from the Continent. The oxygen-isotope record suggests that the period prior to stage 5e was certainly a full glaciation and that conditions towards its end would therefore have been suitable for these species so that they were probably in Britain at the beginning of the Ipswichian.

If Sutcliffe proposes a cold spell interspersed between the deposits at Ilford and Trafalgar Square, then only stage 6 of the oxygen- isotope stratigraphy can be invoked, it would seem. A major glacial advance, lowering the sea to a considerable extent, is in any event implied if the lack of hippopotamus at Ilford and its presence at Trafalgar Square are to be explained by Sutcliffe's scheme, since at some point between the two events conditions had to be suitable for the animal to enter Britain. Although they are good swimmers, it seems inherently unlikely that that these animals would be tempted to cross more than a kilometre or two of cold sea in sufficient numbers to colonise Britain.

3.3 The Devensian Glaciation

(i) Chronology

In contrast to the Ipswichian period, the Devensian attracts considerably less controversy and has a comparatively well-established sequence. This is due in no small part to the availability of radiocarbon dates for much of the timespan, permitting correlation of deposits within Britain and with the Continent and overcoming many of the problems facing the worker on the Ipswichian. Nonetheless, it remains a regrettable fact that many of the mammalian deposits from this period lack a precise date. While this need not, as I shall show, prevent the erection and testing of a model of predator and prey interactions, particularly in comparison with Ipswichian events, this lack of precision does limit the possibility of examining developments within the Devensian.

As Shotton (1977: 109) points out, even radiocarbon cannot at present provide a close chronological definition for the base of the Devensian. Nor can the transition from interglacial to glacial conditions in bio-stratigraphies be easily observed, since Devensian deposits rarely lie on top of Ipswichian ones in a satisfactory manner. The earliest European dates relate to a point which is clearly at some distance from the inception of glacial conditions, being represented by figures of 65-68,000 B.P. at Amersfoort (Shotton 1977: 111). Although these are finite dates, it is important to note that they were obtained by techniques of enrichment, and thus may, as Shotton suggests, be minima. These early dates are summarised in Table 26.

The oxygen-isotope record suggests a quite early date for the inception of cold conditions following stage 5e (Figure 4), pointing to a considerable drop in temperatures by at least 100,000 B.P.. The maximum ice advance appears to have occurred late, however, and is generally put to around 18,000 B.P. (Gates 1976; CLIMAP 1976; West 1977b:295). (Straw (1979; 1980) has argued for two major Devensian ice advances, but Catt (1980) has pointed to a number of difficulties with his scheme. For present purposes I shall align this discussion with West and the term Devensian maximum will refer to the more generally accepted Late Devensian advance at which point conditions appear to have reached their most extreme (see below for discussion of periglacial phenomena p 56 and Table 27)) Fluctuations in oxygen-isotope levels point to considerable climatic variations within the last glacial phase, and must clearly relate in some way to the interstadials deduced from terrestrial deposits. Precisely the same problems of correlation between the two lines of evidence as beset any attempts to integrate deep-sea core evidence are nonetheless apparent, but in view of the new techniques of radiocarbon dating now being developed (Harbottle _et al_ 1979) this difficulty may soon be overcome.

One of the best British sections for the study of earlier material is that of Four Ashes near Wolverhampton (Morgan, A. 1973; Morgan, A. V. 1973; Shotton 1977), the type site of the Devensian, where Ipswichian deposits underlie Early, Middle and Late Devensian layers. However, the only British site with deposits considered likely to equate with those of Amersfoort is Wretton in Norfolk (West _et al_ 1974), although some controversy surrounds this association. These and other Devensian sites are shown on Map 2.

In his recent book on the British Upper Palaeolithic, Campbell (1977) presents a useful tabulation of Devensian radiocarbon dates. A notable feature of these dates is the general paucity of estimates from between around 25,000 b.p. to around 15,000 b.p., particularly evident for determinations made on mammalian remains. If this period marks the height of the ice advance, the absence of mammals is not surprising. However, the most famous specimen to have been dated is the human skeleton from Goat Hole Cave in the Gower Peninsula, the so-called "Red Lady of Paviland" (Buckland 1823), which produced the surprising date of 18,460±340 b.p. on collagen from the leg bones (BN-374; Oakley 1968). More recently, Molleson and Burleigh (1978) have published a date of 27,600±1300 b.p. (BM-1367) obtained on the leg bone of a bovid from the cave (the authors quote the species as _Bos primigenius_, presumably accepting the identification made by

Sollas (1913), but my own investigations of material from the site suggest that the specimen is more likely to have been Bison).

As discussed further in Chapter 5.3 (p 117), Campbell put forward a view of two phases of human occupation associated with Upper Palaeolithic technology, an early phase (EUP) prior to the Devensian maximum and a later phase (LUP) afterwards. Since the tools associated with each phase are distinctive, this sequence of occupation is of some value in establishing relative chronologies for a number of deposits containing artefacts. The excavations at Paviland by Sollas revealed a number of what are now considered to be EUP tools, and the new date for the site may well date that occupation and perhaps the skeleton also.

There is no suggestion of other than human occupation or bone accumulation at Paviland, since the bones show no evidence of gnawing. The one specimen of "hyaena" identified by Sollas is actually a wolf humerus. Paviland therefore holds some information about man and prey species but can tell us little about predator activities and presence.

One of the most potentially useful sites for the study of Devensian occupation of Britain is undoubtedly Kent's Cavern in Torquay. Pengelly (1865-80) recorded the stratigraphy of finds in his diary of the excavation, but never published drawings and sections. Unfortunately, during my visit to Torquay Museum in 1978 the diary, held in the Museum, could not be found, and was assumed to be lost. Only in late 1979 did notice of the sale of one of the volumes of the diary at Sothebys cause a fullscale search of the premises to be made, in the course of which the remaining volumes were found. The circumstances of this incident are unclear, but the effect has been to prevent my use of the excavation records, and I have taken the Kent's Cavern material as simply another Devensian deposit for the purpose of this study.

Campbell (1977: 132) claims his own examination of Pengelly's diaries , together with an examination of the faunal remains held at Torquay, both confirms the accuracy of Pengelly's identifications and leads to certain insights into changing faunal patterns during the Devensian. In particular, he sees evidence of lessened hyaena and woolly rhinoceros during the LUP phase, as well as absence of lion and mammoth. But as with much of Campbell's work, as I shall discuss later, one wonders whether the conclusions really follow from the evidence presented. For example, the total number of specimens used by Campbell in his interpretation of prey species selection by human hunters during LUP times at this site is just 37 teeth. One must question the wisdom of using only teeth to interpret such activity and of quoting percentages to two decimal places on such a total. It is apparent that Campbell had great difficulties in associating the LUP material from Kent's Cavern with any particular portion of the fauna, most of which shows clear evidence of hyaena activity (Chapter 5.2, p 106). Is there in fact good evidence for any change in large mammal fauna with time during the Devensian?

Re-examination of the Wookey Hole Hyaena Den deposits (Tratman et al 1971; Campbell 1977: 89, 100) suggests that occupation there, both by man and hyaena, occurred solely prior to the maximum Devensian ice advance, on the basis of pollen and granulometric evidence. As Campbell himself admits, in the absence of radiometric dates it is difficult to be precise with this kind of evidence, but taken together with the lack of LUP implements at the site the findings are extremely suggestive. Like Kent's Cavern, the site produced a large quantity of horse and woolly rhinoceros remains, with high proportions of the specimens showing gnawing consistent with hyaena activity.

Coygan Cave in Carmarthanshire has received the attention of a number of excavators, the most recent being Grimes and Cowley (1935) and Clegg (1970). Grimes' report is uninformative, quoting animal specimens in percentages only and giving a stratigraphy as follows:

Layer 5: top stalagmite

Layer 4: cave earth with stones and bones 3 to 3.5 feet thick

Layer 3: stalagmite 1.5 inches thick

Layer 2: stony layer with bones up to 2.5 feet thick

Layer 1: clean yellow sand

Clegg attempted to align his stratigraphy with that of Grimes and Cowley, having established the following sequence:

Top stalagmite "A"

Layer (5) buff sandy earth with stones and bones

Stalagmite "B"

Layer (4) brown sandy earth with stones and bones

Stalagmite "C"

Layer (1) maroon clay with specks of charcoal and rare bones

According to Clegg, the stalagmite layer 3 of Grimes and Cowley is most likely to correlate with his stalagmite C. It would thus seem to be stalagmite C which constitutes the "lower calcrete" upon which a radiocarbon date of 33,200± 310 b.p. (GrN-4400) was obtained, a layer said to underlie the main bone accumulation and Mousterian industry. Mousterian industry may be rather overstating the case since the artefacts make a grand total of eight. However, the date is somewhat embarrassing,since the hand axes which make up three of the total are held to be typologically somewhat earlier (Mellars 1974: 62).

On the basis of either the date or the artefacts alone, a period prior to the Devensian ice advance is indicated, the apparent problems of the two together make it difficult to decide just how early the deposit may be. The lack of later human artefacts of Upper Palaeolithic aspect may confirm the date, but then man may not have found the cave attractive for occupation even if he was in the area. It is possible that the period of occupation may be of similar duration to that at Wookey Hole. As with Wookey Hole, the two species best represented, after the hyaena, are horse and woolly rhinoceros.

A third site which seems to have produced material datable to before the maximum Devensian ice advance is Uphill Cave in Mendip (Wilson and Reynolds 1901; Harrison 1977). The implements described and illustrated by Harrison seem all to be of either Middle or Early Upper Palaeolithic type. Again, the fauna is dominated by hyaena, horse and woolly rhinoceros. The report by Wilson and Reynolds gives little detail of the deposits and their stratigraphy, but the parallels with Wookey Hole and Coygan are clear.

In the Vale of Clwyd, Flintshire, two caves excavated last century produced material which suggests a pre-Devensian maximum date of deposition, the caves having probably been sealed by tills (Hicks 1884, 1885a,b, 1886a,b, 1888; Hicks and Davies 1886; Hicks and Rance 1888; Rowlands 1971). The caves, Cae Gwyn and Ffynnon Beuno, once again produced remains chiefly of hyaena, horse and woolly rhinoceros, and a carpal bone of mammoth from Cae Gwyn has produced a radiocarbon date of 18,000 +1400-1200 b.p. (Birm-146, Rowlands 1971), a date rather similar to that obtained on the Paviland human specimen although having a larger standard deviation.

King Arthur's Cave in Herefordshire produced a considerable quantity of bones when first excavated by Symonds (1871). Various attempts have been made to correlate his findings with those of later workers, with Campbell (1977: 44) reworking an unpublished interpretation of ApSimon. This latest investigation suggests, on the basis of associated EUP tools, that the quantities of hyaena, horse and woolly rhinoceros remains found by Symonds once more predated the Devensian maximum.

As one of the few early excavations to have been recorded stratigraphically, the site of Pin Hole Cave at Creswell Crags, Derbyshire, has, like Kent's Cavern, considerable potential for unravelling problems of chronology. The major excavator, Armstrong (1929) recorded his finds two-dimensionally by distance into the cave and distance down, usually to the nearest foot, although at times to the nearest six inches. The scheme of measurement did not involve a horizontal datum, although for approximation purposes one may be used, and the precise manner of recording is still under examination (R. D. S. Jenkinson, pers. comm.). For the purpose of this study, plots were made of the two dimensional data for each species and gnawed bone fragments. These are shown in Figures 5-13. Since most specimens cannot be located to more than the nearest horizontal and vertical foot, it is impossible to make a detailed examination of the proximities of various species. Most importance therefore attaches to the overall distributions of the remains, within the total depth of the deposit and in relation to the positions of the flint artefacts. For the present discussion, the most significant feature of these plots would seem to lie in the relative positions of horse, woolly rhinoceros and hyaena, all of which find their major concentrations some way below the top of the deposits.

Another distinctive feature of the Pin Hole stratigraphy is the position of reindeer remains, which appear to group towards the top of the deposits while being moderately well represented throughout. A high stratigraphic position is particularly marked for female cast antler, and this contrasts with the deposition of horse and woolly rhinoceros. This feature may also be seen, although to a lesser extent, in the deposits from Tornewton Cave, Devon (Sutcliffe and Zeuner 1962). However, the number of remains recovered from the latter site poses difficulties for any clear comparison. At Tornewton, the first major deposit overlying the Ipswichian Hyaena Stratum was the Elk Stratum , named on the basis of a specimen now identified as giant red deer (A. Lister, pers. comm.), a deposit thought by the excavators to correlate with the Dark Earth Stratum of Widger (1892), the original excavator. This layer contained a high proportion of hyaenas. Above it lay the reindeer stratum as defined by Sutcliffe and Zeuner and by Widger, which contained an abundance of shed antler from young and juvenile reindeer, pointing to a summer presence in the area (see Table 22 and Chapter 5.11 for further discussion). The number of hyaena remains found in this deposit by both sets of excavators appears to have been small, and in both the elk and the reindeer stratum the horse and woolly rhinoceros are poorly represented, but general parallels with Pin Hole seem clear bearing in mind the degree of geographic separation.

Rackham (1978) has claimed that the mammal faunas recorded at the Lincolnshire sites of Tattershall Castle and Tattershall Thorpe show change with time. The former, with radiocarbon dates of 43,000 (Birm-341) and 42,000 (Birm-409) has a fauna dominated by bison and reindeer, while the latter, with a date of 34,800 (Birm-250), has one dominated by mammoth and woolly rhinoceros with, to a lesser extent, horse. Rackham suggests that the Tattershall Castle fauna, associated with temperate deposits, points to environmental differences and to significant variations in ungulate presence at the two dates. However, the Pin Hole stratigraphy (Figures 5-13) shows bison, horse, mammoth and woolly rhinoceros overlapping considerably, and it is possible that the difference between the two Lincolnshire deposits owes more to taphonomy than to real change. These sites are discussed further in Chapter 5.12.

Finally, it is of interest to consider the site of Sandford Hill, Mendip. Excavated some time during the last century, the material from the cave, now housed in Taunton Museum, has never been published to date. The excavations would seem, from the identifications on the bones, to have been carried out by William Beard, perhaps in association with the Reverend Williams, since they investigated a number of the caves in the area during the eighteen twenties and thirties (Rutter 1829; Dawkins 1874). The site produced a quantity of hyaena jaws, teeth and bones, in addition to a few remains of woolly rhinoceros and four specimens of horse: at least that is the material seen in the Taunton Museum. In addition, a large number of reindeer remains were found which contrast markedly with those of the other species, being more complete and representing most parts of the reindeer skeleton, whereas those of the hyaena and rhinoceros show signs of having been gnawed, with only the more robust portions of the bones tending to survive. It would thus seem that the reindeer remains were not contemporaneous with the other specimens. Since so little was known about the site, it seemed worthwhile to obtain a date by radiocarbon assay, and Mr Richard Burleigh of the British Museum Laboratory kindly agreed to obtain a date under the British Museum research project on Pleistocene faunal extinctions. The Archaeological Sub-Committee of the Somerset Archaeological and Natural History Society permitted me to select a sample of hyaena skull, which was submitted to the British Museum following a preliminary fixed nitrogen analysis at the Oxford Microanalytical Laboratory which produced a figure of 2.95% nitrogen. The date subsequently obtained was as follows:

BM-1526. 36,000 ± 1900 b.p.

While this of course only dates one specimen from an unstratified site, the figure falls very much in line with the evidence of mid-Devensian hyaena activity derived from the sites discussed above. Permission is now being sought to obtain a direct date on a specimen of reindeer from the site, but this will not be available for inclusion in this study.

In general, it seems that a faunal change may coincide with the Devensian maximum, but the details are unclear. Hyaena, horse and woolly rhinceros are less clearly associated with LUP industries and predator occupation of a number of sites may have ceased prior to the main ice advance. The general increase in reindeer numbers seen in the upper levels at Pin Hole and Tornewton is apparently at the expense of horse and woolly rhinoceros, although it is difficult to know whether this simply reflects changes in ungulate species composition or a change in predator species'and prey selection also. At Pin Hole, where hyaena numbers in the upper levels are still fairly high, the evidence suggests a change in ungulate species to be a major factor, but this tends to conflict with the general impression of a fall in non-human predator numbers with time.

Problems of interpreting variation in assemblage composition are discussed further in Chapter 5.2.

(ii) Vegetation and climate

West (1977a) provides the most up-to-date summary of the vegetational history during the early and middle portions of the Devensian. He points out that the known sites represent a partial coverage of the British Isles, being restricted in the main to the Midlands, and that their stratigraphical relationships are not always clear.

At Amersfoort, Brørup and Odderade, the interstadial deposits are defined by woodland pollen, whereas later parts of the north-western Continental sequence show no such wooded conditions. This observation has played a large part in the decision to assign British Devensian deposits with woodland to these same interstadials, and if correct points to the gradual disappearance of woodlands during the period in north-west Europe. Once the woodlands went, the British evidence suggests some local diversity, although the overall picture has been described by West (1977a: 232) as one of "... a regional vegetation of tundra physiognomy, probably predominantly grassland."

As West makes clear, some consideration must be given to the sedimentary regime of fossil floras, to their taphonomy. Most Devensian floras are from channel infills in fluviatile environments, and provide both pollen, which may originate both locally and from the surrounding region, and macroscopic remains which are of more local origin. Both kinds of material were found at Chelford and Beetley, and together with the pollen evidence from Wretton and Four Ashes point to two interstadials. The earlier, that at Wretton, is separated from that at Chelford by a period in which herb pollen is marked, but both interstadials show presence of pine, birch and spruce.

During the later Upton Warren interstadial, and in the periods before, during and after the Wretton and Chelford interstadials, the pollen spectra are dominated by non-arboreal pollen. These spectra seem to derive from vegetation with a high grass component with little evidence for widespread scrub. Macro fossil evidence at some sites such as Earith indicates local communities of dwarf shrubs, including dwarf birch (Betula nana) and several species of willow (Salix spp), but the overall lack of such elements in the pollen spectra suggests that they were not extensive. Perhaps the most interesting aspect of the macro fossil evidence lies in its indication of a variety of habitats and vegetation categories, which West lists as aquatic and marsh, tall herb, ruderal and weed and grassland. These latter categories in particular fit in well with the evidence for open and disturbed ground which comes from periglacial phenomena, discussed further below.

Bell (1969) discussed the appearance of three ecological elements in the macro floral evidence: southern, steppe and halophyte. These in turn point to a continental climate with warm summers, grassland and dry mineral soils, and to high soil salinity produced by a mixture of wind-induced evaporation, low summer precipitation and impeded drainage. Further support for the interpretation of this last category again comes from periglacial phenomena, which in northern Eurasia may result in saline soils.

The vegetation of the Late Devensian receives its most recent discussion in the summary by Pennington (1977). She considered the period between 15,000 and 10,000 B.P., and pointed to considerable diversity in the flora. A significant feature of the floral record lies in the suggestion of range contraction for many species since that time, indicating that the Late Devensian flora was considerably less geographically differentiated than that of the present day. However, this uniformity may also owe much to deposit conflation, since sediments may cover several thousands of years in which conditions fluctuated greatly. The development of the Late Devensian vegetation is nonetheless extremely complex, and does not represent a uniform response on the part of trees and plants to changes in climate.

Figure 14 shows Pennington's scheme for the Late Devensian chronostratigraphy, including correlations with Continental sequences, which she feels can be demonstrated at sites with adequate C14 dating of the pollen record. In general terms, there is evidence for a woodland biozone between 13,000 and 11,000 B.P. in western Britain, a true interstadial. Juniper seems to increase in most areas at around 13,000, and between then and 12,000 birch trees may have been present in most areas of western Britain, forming up to 50% cover in favoured areas. At around 11,000 B.P., a major impoverishment in vegetation occurred, with widespread appearance of Artemisia.

Interpretation of climate from these vegetational indicators is not a simple matter, as West (1977a: 238) is at some pains to point out. Attempts to model the climate at various times in the past, simulating a time-averaged three-dimensional atmosphere numerically, are now in progress (CLIMAP 1976; Gates 1976), but such approaches are necessarily coarse in their resolution. For the British Isles at around 18,000 b.p., taken to be the height of the Devensian, an estimated July mean surface air temperature of 10 degrees Celsius has been given by the model (Gates 1976: Figure 7). The generally accepted position of the ice front in Britain at this time is shown in Figure 15. For a fuller picture of conditions in Britain, particularly in relation to change over time, we must return to the terrestrial data, from which the following broad outline now emerges.

The Chelford interstadial seems to have been a time of warm summers, perhaps as high as 12-16° C, with enough precipitation for boreal forest growth. January temperatures may have fallen to -10 to -15° C with an annual mean at 2 to -3° C. During the Upton Warren complex, high summer temperatures are again indicated, although winter temperatures are more difficult to assess, since they tend to be based on absence among floral elements, and competition may be a large factor in such matters. West suggests that the lack of trees, despite the apparently high summer temperatures, may be largely the result of a short growth season during the Upton Warren interstadial.

For the Late Devensian, Pennington reiterates the difficulties of estimating climatic parameters, and eschews any attempt at suggesting temperatures. In general, there is a trend towards climatic amelioration from before 14,000 B.P. until around 12,000 B.P., at which latter point a short-lived regression took place. Recovery during the subsequent period until 11,000 was followed by a second marked drop in temperature.

Fortunately, vegetational indications of climate during the Devensian are enhanced by the evidence of periglacial phenomena preserved in soil profiles and visible as surface features. Watson (1977) discusses such phenomena in relation to the extent of permafrost, basing his examination on the appearance of two contemporary permafrost indicators, ice wedges and pingos.

Ice wedges may be observed in section, or on the surface where they form polygons. Their major distribution pattern in Britain is shown in Figure 15. It seems likely that they can develop only in areas of continuous permafrost. Pingos are ice-cored mounds which form in permafrost: when the ice melts, a lake with a rampart tends to form. Two types have been identified, open and closed, occurring in discontinuous and continuous permafrost respectively. The known British examples shown on Figure 15 are of open system type, pointing therefore to discontinuous permafrost , and pollen evidence from samples taken at Welsh and East Anglian sites suggests a Late Devensian episode of formation. A third class of phenomenon, thaw lakes, have not yet been investigated in Britain, although Watson (1977: 188) is of the opinion that they are also important permafrost indicators.

On the basis of these indicators, Watson suggests the sequence of Devensian temperatures shown in Table 27. In the Early Devensian ice wedges occur in the sands covering organic deposits at Chelford, so that although there is little evidence for permafrost prior to around 55,000 B.P., there are indications that something approaching a polar desert existed by the beginning of the Middle Devensian. Between 50,000 and 26,000 B.P., permafrost is indicated from a number of deposits such as Earith (c. 42,000 B.P.), Syston (c. 37,420 B.P.) and Four Ashes (c. 42-30,000 B.P.). Taken in conjunction with the floral evidence for both facultative and obligate halophytes, and the lack of trees, an environment fluctuating between tundra and sub-polar desert is implied. Only during the time of the Upton Warren interstadial complex is there any suggestion of amelioration during the middle period of the Devensian.

Between 26,000 and 10,000 B.P. ice wedges are recorded in later tills at Four Ashes and Chelford, although none are datable to the period of major ice advance. Again, the evidence taken in conjunction with that of flora and microfauna points to severe conditions south of the ice margin, including actual polar desert and continuous permafrost. Such conditions imply an annual mean air temperature at least 16-17°C below that of today, and in view of the active ice-wedge formation this is more likely to have been around 20°C. At the very height of the ice advance, when a true polar desert existed, the fall is likely to have been 25°C.

The climatic outline derived from these various lines of evidence is consistent. Perhaps the point to be stressed is the very great difference in January temperature and mean annual temperature compared with the present day, while the July temperatures, although lower, show a much smaller difference. The variation in floral communities during the period is marked and, together with the extent of diversity within these communities, suggests a considerable large mammal fauna could be supported on a seasonal basis for much of the period. In general, it is an environment most likely to have suited grazing herbivores, and during the full advance of the ice it is difficult to imagine Britain occupied by any but the most cold-adapted of these species.

(iii) Fauna

The fauna for this period is summarised in Table 28. As in the preceding Ipswichian, the major predators are hyaena, lion, wolf and bear, with leopard perhaps present in some numbers. As prey for these animals, horse may have been the most important, but reindeer and woolly rhinoceros are also well represented. Other species include bison, red deer, giant deer, mammoth, saiga antelope and musk ox, although the latter two are very poorly represented. Most of these herbivores are at least facultative grazers, but many of the plants, such as the sedges, are likely to have been extremely abrasive, and not an ideal diet for the less hypsodont species. It is therefore quite likely that some animals were more abundant at some times than at others, although it remains possible that the dwarf birch and willows were able to support a diverse fauna. However, limited distribution of such dwarf shrubs suggested above may have in turn limited the movements of the less hypsodont species. A knowledge of vegetational change with time would be most useful for interpretations of faunal change. It is therefore particularly unfortunate that we cannot at present separate non-arboreal pollen into categories of herb biozone, or place macrofossils into substantially different vegetational conditions. This difficulty stems from the multivariate nature of both pollen and macrofossil assemblage production, and is unlikely to be resolved in the near future (West 1977a: 235; Pennington 1977: 253).

The numbers of predators present in Devensian deposits is perhaps at first sight surprising, particularly since the most common species, hyaena, has a southerly distribution at the present day. This distribution is misleading: as discussed in Chapter 4.1 many of the predators have a wider range than might be imagined, and it is clear that the primary restriction is food availability. The relative richness of the glacial herbivore fauna would in itself suggest the likely presence of a number of predators. Also, as Table 28 shows, a number of small species were also present, and are likely to have provided food for the larger predators from time to time.

(iv) Sea level

During a glaciation, a drop in sea level is to be expected as a result of ice formation locking up a great proportion of the available water. During past glaciations the sea level has been estimated to have fallen by various amounts ranging from 80 to 150 m (West 1972:

137) on the basis of ice volume calculations. Summarising the available evidence, and pointing out that estimates of ice volume are just that, Butzer (1972: 217) suggested that a general lowering of sea level by 100 to 150 m could be argued for the height of the Devensian ice advance. CLIMAP (1976: 1131) took an estimate of -85 m at 18,000 b.p. as their figure, based on several lines of evidence, but as they point out the precise level was not particularly important for the purposes of their model.

Thom (1973) has discussed the suggestion that at some point during the last glaciation, perhaps clustering on 35,000 B.P., the sea actually rose to within 25 m of its present height. He cited a number of instances of dates in the 28-38,000 B.P. range for coastal deposit samples. As he goes on to show, however, problems of sample contamination are particularly acute in the most frequently used material for these dates, marine mollusc shell. Furthermore, oxygen-isotope studies on ice cores from Greenland do not indicate sufficient temperature rise between 65,000 and 10,000 B.P. to produce a major ice retreat, and the Upton Warren interstadial complex seems in any event too short to have produced such an effect.

More recently, Synge (1977) has suggested that the evidence of moraine deposits in Ireland, produced by the Irish Sea glacier, points to the glacier being afloat, as an ice-shelf, on a sea little different in level from that of today. He quotes dates of around 30,000 B.P. for Irish Sea till on the Welsh coast, and similar dates from Staffordshire, in support of his claim that a major ice advance occurred at around 30,000 B.P.. However, his suggestion is perhaps a little ill-conceived: as Shotton (1977: 116) argues, the question of dating the Irish Sea glacial movements and of relating them to the movements of ice over England is far from being resolved.

Furthermore, dates such as those quoted by Synge for the Welsh coast tills were obtained on marine shell. Synge makes much of the horizontal nature of the moraine deposits at 100 m O.D. on the Irish coast, claiming that these point to shelf ice in the southern part of the Irish Sea. Well they may, but that hardly clarifies the issue of sea level. As Figure 15 shows, the 100 m submarine contour vastly increases the land area around the present British Isles. A drop in sea level of less than 100 m could still have produced an ice-shelf phenomenon in the southern Irish Sea, but in the absence of knowledge about ice thickness a 100 m moraine contour says nothing about sea level.

If the maximum fall in sea level did occur during the generally accepted glacial maximum, between 26-15,000 B.P., the sea-bed contours suggest that contact with the Continent would still have been possible with lesser drops during the earlier and later parts of the Devensian. Clearly the sea level did not drop overnight, but neither do we know just how early Devensian communication with the Continent would have been possible. The appearance of horse, mammoth and woolly rhinoceros in deposits likely to be of Ipswichian date, as discussed above, may have resulted from these animals finding refuge in Scotland during the Ipswichian Zone II, the period of maximum forest cover. Alternatively, one would have to suppose early immigration from the Continent, but for reasons discussed further in Chapter 5.16 (p 192) I am inclined to believe that immigration did not take place until the Devensian, and that these species did indeed occupy British interglacial refugia. This would argue that sea level drop sufficient to enable European contact with Britain was a Devensian rather than an Ipswichian phenomenon.

3.4 Sites and Their Settings

In the past decade some stimulus has been given to the study of prehistoric sites of human activity by the technique of site catchment analysis, a product of the British Academy Major Research Project in the Early History of Agriculture (Vita-Finzi and Higgs 1970; Higgs and Vita-Finzi 1972). The essential and sensible basis for this approach lies in the observation that modern peoples, hunter-gatherers or agriculturalists, make greatest use of territory adjacent to their settlements. Consideration of the resource potentials inherent in a site setting may therefore permit the prehistorian to begin a reconstruction of the economy and thus begin to assess some of the major factors determining past human behaviour.

Like all techniques and approaches, the method can be applied too rigidly. Many studies resulting from the Higgs "school" present ten kilometre circles and the enclosed vegetation as though therein lies all wisdom, but as Dennell (1979: 130) has recently observed, such faults lie in the main with adherents rather than principles. In the present study, dealing as I am with predators other than man, ten kilometers may have enclosed much of the main area of prey selection and killing, but it may have failed to witness much of the activity. Caves are the main occupation context available for study from both Ipswichian and Devensian times, and while a large range of limestone uplands with numerous caves might present a predator with considerable choice of den or lair, it is unlikely that the relatively few which we have in Britain were so chosen.

Rather than deal in detail with the precise location of the sites therefore, I shall confine my comments here to some general observations, necessarily anticipating some of the evidence and discussion to be presented later.

The major Ipswichian sites are Kirkdale in Yorkshire, Joint Mitnor and Tornewton in Devon, Barrington in Cambridgeshire and Hoe Grange in Derbyshire. Mother Grundy's Parlour at Creswell on the Derbyshire-Nottinghamshire boundary is also of relevance. These and other sites are shown on Map 1. Most of the sites mentioned above, with the exception of Barrington and, to a lesser extent Creswell, are situated near high ground, and close to present-day water courses. It is clear that all of them would have been attractive locations for herbivores, either within the immediate vicinity or within a few kilometres. (Even the remains from the fluviatile deposits of Barrington, in their relatively fresh condition, suggest initial deposition close by.) The high land close to the remaining sites provides sheltered basin areas, seen especially well in the case of Kirkdale, in the Vale of Pickering, and at Joint Mitnor and Tornewton. Both Kirkdale and Joint Mitnor are particularly well sited on what may have been seasonal movement routes for ungulates spending the winter in the lower-lying lands to the south of the North Yorkshire Moors and Dartmoor respectively and the summers on the uplands. To the west of Creswell lie the southern Pennines and the Derbyshire Peak District, and it is conceivable that the faunas of Mother Grundy's Parlour and Hoe Grange represent different seasons of occupation.

The major Devensian sites under discussion are Kent's Cavern in Devon, Uphill, Sandford Hill and Wookey Hole in Mendip, Coygan in Carmarthenshire, Paviland in Glamorganshire, King Arthur's Cave in Herefordshire, and Pin Hole, Church Hole and Robin Hood's Caves again at Creswell. These and other locations are shown on Map 2.

Of course many of the Devensian sites have some evidence of human occupation. As Campbell (1977: 158) points out, there is some hint of a change in distribution between Early and Later Upper Palaeolithic occupation, as seen on Maps 3 and 4, and it is possible that conditions following the Devensian maximum permitted exploitation of more northerly areas to a greater extent. However, it is likely that much of the hyaena occupation occurred prior to the Devensian maximum, although the long stratigraphy at the northern site of Pin Hole suggests the presence of considerable numbers of predators and prey throughout much of the period. If these animals were present in significant numbers during the Middle Devensian, then we should perhaps look to reasons other than climate alone to explain relative human absence. (This problem is discussed further in Chapters 5 and 6.)

The sites on Map 2, like many of the Ipswichian period, lie in areas where game was probably at its most plentiful. As the sea level dropped during the Devensian, Britain would have assumed a position as a band of higher land to the north and west of a greatly enlarged North European Plain, attractive to ungulates in summer and thus to a range of predators. Sites in the Mendips, south Wales and along the south coast would have been ideally suited to permit exploitation of ungulate herds in the Bristol and English Channels, while those at Creswell would have continued to present similar advantages to the site occupants as they did during the Ipswichian.

In all, it seems clear, without unduly labouring the point with respect to any one site, that while the deposits known may be special only in so far as they are situated in the few areas to have limestone caves, and that many other predator dens, lying up areas and occasional shelters have no doubt been lost to us, the occupants of these sites were well placed for ungulate exploitation.

3.5 Site List

The following list gives the major sites mentioned in the text, maps, tables and figures of this study. Order is simply alphabetical. The list is intended purely as a summary, giving location, map reference, collections examined as appropriate, major references, and an indication of chronology and any clash of opinions concerning the sites. Fuller discussion of any points of contention will be found in the main text.

The most recent major syntheses of the British Pleistocene and its mammalian faunas are to be found in Mitchell et al (1973), Stuart (1974), Sutcliffe and Kowalski (1976) and West (1977b). Discussions specifically related to the faunas of the Ipswichian and the Devensian may be found in Stuart (1976) and (1977) respectively.

The collections of British Upper Pleistocene large mammal remains examined and recorded during the course of the study are given the following abbreviations after the name and location of appropriate sites.

BCM	Bristol City Museum
BUG	Bristol University Department of Geology
BMNH	British Museum (Natural History)
CCM	Cheddar Caves Museum
CUDZ	Cambridge University Department of Zoology
CUDA	Cambridge University Department of Archaeology
GML	Geological Museum, London
GCM	Gloucester City Museum
HCM	Hereford City Museum
HMG	Hunterian Museum, Glasgow University
LCM	Leeds City Museum

LM	Leicester Museum
MUM	Manchester Univesity Museum
NMW	National Museum of Wales, Cardiff
OUM	Oxford University Museum
RAME	Royal Albert Memorial Museum, Exeter
RSME	Royal Scottish Museum, Edinburgh
SM	Sedgwick Museum, Cambridge
SCM	Sheffield City Museum
TCM	Taunton Castle Museum
TNHSM	Torquay Natural History Society Museum
UBSSM	University of Bristol Spelaeological Society Museum
WM	Wells Museum
YM	Yorkshire Museum

Aveley, Essex (Map 1) TQ 552807.

Stuart (1976); West (1969), Sutcliffe (1976). Ipswichian open-air site, Zone II/III, excavated 1964.

Bacon Hole, Glamorganshire (Map 1) SN 560868.

BMNH

Morgan (1913); Stringer (1975). Ipswichian cave site, probably covering Zone II and later, currently under investigation. The material was unsuitable for examination at the time of this study.

Badger Hole, Somerset (Map 2) ST 532479

WM

Balch (1938-53); McBurney (1961). Devensian cave site with small quantity of EUP and LUP material. Fauna poorly known.

Banwell, Somerset (Map 2) ST 383588.

BMNH, TCM

Rutter (1829); Davies (1926); Sutcliffe (1955); Sutcliffe and Kowalski (1976). Probably Devensian cave site. Excavated early 19th century.

Barrington, Cambridgeshire (Map 1) TL 384493.

BMNH, CUDZ, SM

Fisher (1879); Hughes (1911); Sparks (1952); Norris (1962); Gibbard and Stuart (1975). Ipswichian open-air fluviatile site, Zone II, material recovered from various gravel workings between about 1878 and 1910.

Beetley, Norfolk (Map 1) TF 987181.

Phillips (1972); Stuart (1976), Ipswichian open-air fluviatile site, material recovered from various gravel workings during the 1960s.

Bench Cavern, Devonshire (Map 1) ZX 924567 (approximate).

BMNH, RAME

Pengelly (1871); Jackson (1937), Devensian cave or fissure, destroyed during quarrying in 1861, material recovered during work.

Bielsbeck, Yorkshire (Map 1) SE 864383.

YM

Vernon Harcourt (1829); Boylan (1977), an open-air site probably Ipswichian Zone III or IV date, having abundant horse but no hippopotamus or hyaena. Most of the material was unavailable for examination at the time of this study.

Bleadon Cave, Somerset (Map 1 and 2) ST 360580 (approximately).

BMNH, TCM

Barrington and Stanton (1976); Sutcliffe and Kowalski (1976). A cave of possibly Ipswichian and Devensian deposits which may have been a fissure trap, excavated in the early 19th century.

Bobbitshole, Suffolk (Map 1) TM 148414.

West (1957); Mitchell et al (1973); Stuart (1976), Lacustrine deposits constituting the type site for the Ipswichian.

Brixham Cave, Devonshire (Map 2) ZX 925561.

BMNH

Busk (1872, 1873); Dawkins (1874); Jackson (1937). Devensian cave, notable for being a test case when excavated in 1859 to determine the co-existence of man and extinct fauna.

Brundon, Suffolk (Map 1) TL 863417.

Moir and Hopwood (1939); Sparks and West (1963); Stuart (1976). Ipswichian fluviatile deposit of probable Zone III-IV age, material recovered during 1930s.

Cae Gwyn Cave, Flintshire (Map 2) SJ 085725.

GML

Hicks (1884); Rowlands (1971), a cave site on the east side of the Vale of Clwyd, adjacent to Ffynnon Beuno Cave. Apparently a hyaena occupation site, the material from which is extremely dispersed and not always distinguished from that of Ffynnon Beuno. Devensian deposits.

Clevedon Cave, Somerset (Map 2) ST 419727.

GML, BCM

Davies (1907); Reynolds (1907); Palmer and Hinton (1929); Gilbertson and Hawkins (1974). A slope and cave deposit exposed during quarrying. Sutcliffe and Kowalski (1976) suggest that rodent evidence points to a pre-Ipswichian cold stage date, but Gilbertson and Hawkins suggest a Devensian date for the slope deposits at least. Vertebrate remains were found, although their exact provenance is not clear. Included were small horse specimens which also argue for a Devensian date.

Church Hole Cave, Derbyshire (Map 2) SK 536743.

BMNH, MUM, OUM, SCM

Mello (1877); Dawkins (1877); Heath (1879). A Devensian cave deposit at the site of Creswell Crags, excavated in 1876.

Coygan Cave, Carmarthenshire (Map 2) SN 284091.

CUDA, NMW, SM

Hicks (1884); Grimes and Cowley (1935); Clegg (1964-70). A Devensian cave deposit excavated several times from the 1880s onwards; now under threat of complete destruction by quarrying.

Crayford and Erith, Kent (Map 1) TQ 519764.

BMNH, GML, YM

Kennard (1944); Chandler and Leach (1912); Sutcliffe (1975, 1976); Stuart (1976); Sutcliffe and Kowalski (1976). A series of brickearth quarry sites argued by some (e.g. Stuart) to be later Ipswichian and Devensian and by others (e.g. Sutcliffe) to be a pre-Ipswichian warm-cold stage. Material recovered in second half of 19th century.

Durdham Down Fissure, Somerset (Map 1) ST 567752.

BCM

Donovan (1954). Material recovered in the middle of last century. Probably dates to Ipswichian Zone II. May have been a natural trap deposit.

Eastern Torrs Quarry, Devon (Map 1) SX 5875519.

BMNH

Sutcliffe (1960, 1975). A cave discovered in 1954 through quarrying. A small amount of material of Ipswichian Zone II character.

Ffynnon Beuno Cave, Flintshire (Map 2) SJ 085725.

SM, GML

Hicks (1885a, 1885b, 1886b); Hicks and Davies (1886). A Devensian cave deposit recovered from a site adjacent to Cae Gwyn Cave.

Four Ashes, Staffordshire (Map 2) SJ 914082.

Morgan A. (1973); Morgan, A. V. (1973); Mitchell et al (1973); Shotton (1977). A Devensian gravel pit deposit, defined as the type site of the glacial.

Gough's Cave, Somerset (Map 2) ST 465538.

CCM

Davies (1926); Parry 1928, 1930; Donovan 1955; Tratman (1963). A Devensian cave deposit containing the largest known assemblage of LUP tools, located in Cheddar Gorge. Sutcliffe and Kowalski (1976) suggest that part of the deposit may be substantially earlier.

Harkstead, Suffolk (Map 1) TM 188338.

Sparks and West (1963); Stuart (1976), sandy brickearths suggested by Stuart to correlate with those of Stutton and thus to be of Ipswichian Zone III-IV. Material obtained in 1960s and 1970s.

Histon Road, Cambridge (Map 1) TL 444610.

Hollingworth et al (1950); Sparks and West (1960); Stuart (1976). Gravel deposits placed at Ipswichian Zone III/IV boundary. Material obtained in 1940s.

Hoe Grange, Derbyshire (Map 1) SK 232556.

BMNH, GML

Bemrose and Newton (1905). Quarry deposits of probable Ipswichian Zone II date. The material shows many similarities with that from Joint Mitnor, and probably accumulated in the same way, as a natural trap. Material recovered during quarrying and by excavation during 1902. Relatively few specimens were located for study.

Hutton, Somerset (Map 2) ST 360580 (approximately).

TCM

Buckland (1823); Rutter (1829); Dawkins (1874); Davies (1926); Sutcliffe and Kowalski (1976); Barrington and Stanton (1976). A cave of probable Devensian age, although Sutcliffe and Kowalski place it earlier on the basis of rodent fauna. May well have been a trap deposit. Material obtained from 1756 to around 1830.

Ilford, Essex (Map 1) TQ 453871.

BMNH, GML, YM

Woodward and Davies (1874); West et al (1964); Stuart (1976); Sutcliffe (1975, 1976); Sutcliffe and Kowalski (1976). Brickearth deposits of disputed age: Stuart suggests Ipswichian Zones III and IV, Sutcliffe puts them to a pre-Ipswichian warm stage. Material recovered in 19th century.

Joint Mitnor, Devonshire (Map 1) SX 43665.

BMNH, TNHSM

Sutcliffe (1960), an important deposit dated to Ipswichian Zone II on the basis of the fauna. A fissure trap deposit.

Kent's Cavern, Devonshire (Map 2) SX 934642.

BCM, BUG, CUDZ, GML, HMG, LCM, MUM, OUM, RAME, RSME, SM, TNHSM, YM

Pengelly (1865-80); Lowe (1922-3); Beynon et al (1929); Jackson (1937); Campbell and Sampson (1971); Campbell (1971, 1977). A cave deposit containing material of (probably) Cromerian age to Devensian, one of the most important Devensian deposits known as a result of Pengelly's stratigraphic recording. Provides probably the largest sample of British Devensian large mammal fauna. Material collected from 1820s onwards.

King Arthur's Cave, Herefordshire (Map 2) SO 545156.

BMNH, BCM, HCM

Symonds (1871); Thacker 1914-15; Hewer (1926); Taylor (1928); Campbell (1977). A Devensian cave deposit, like those of Creswell first excavated by a man of the cloth.

Kirkdale Cave, Yorkshire (Map 1) SE 678856.

BMNH, GML, OUM, RSME, SM, YM

Buckland (1822, 1823); Boylan (1972), an Ipswichian cave deposit probably of Zone II date. Excavated by William Buckland and published by him as a hyaena den in a serious, though erroneous, attempt to explain such deposits as generally co-eval with the biblical flood.

Levaton Cave, Devonshire (Map 2) SX 810680 (approximately).

BMNH, RAME, TNHSM

Sutcliffe and Zeuner (1962); Sutcliffe and Kowalski (1976), an unpublished site excavated some time during the 1950s. The fauna suggests a Devensian date of accumulation.

Lexden, Essex (Map 1) TL 978253 (approximately).

Shotton et al (1962); Stuart (1976). Terrace deposits of probable Ipswichian Zone IV date, on the basis of material collected last century.

Milton Hill, Somerset (Map 1) ST 539468.

WM

Balch (1948). A trap deposit containing material of Ipswichian Zone II character. Little detail available on the find or its circumstances.

Minchin Hole, Glamorganshire (Map 1) SN 555869.

BMNH

Sutcliffe and Bowen (1973); Sutcliffe (1976); Sutcliffe and Kowalski (1976). A sea cave on the Gower coast held by Sutcliffe to be an important site for determination of the precise Ipswichian sequence. Material first recovered in the 1850s when Falconer examined it, and work continues. Material unsuitable for examination at the time of study.

Mother Grundy's Parlour, Derbyshire (Map 1 and 2) SK 536743.

BMNH, MUM, SCM,

Dawkins and Mello (1879); Campbell (1977). Another of the Creswell Crags caves, important for having produced both Ipswichian and Devensian material. First excavated in the 1870s. Material from the two Upper Pleistocene phases is now inextricably mixed, however, and therefore unsuitable for examination.

Mundesley, Norfolk (Map 1) TG 315366.

Newton (1879); Phillips (1972, 1974); Stuart (1976). Cliff section in deposits filling a channel cut in Anglian till. Dated to Ipswichian Zones I and II. Vertebrate remains recovered in 19th century.

Oreston, Devon (Maps 1 and 2) SX 505532 (approximately).

BCM, BMNH, GML, OUM

Buckland (1823); Cottle (1829); Pengelly (1872); Whidbey (1821, 1823). Material recovered from a number of caves and fissures during quarrying of breakwater stone. An extremely rich site, but poorly recorded and clearly containing a fauna of mixed date (probably Ipswichian and Devensian) which cannot now be separated with certainty.

Paviland (Goat Cave), Glamorganshire (Map 2) SN 437859.

NMW

Buckland (1823); Sollas (1913); Bowen (1970); John (1971); Oakley (1968); Molleson and Burleigh (1978). A Devensian cave site particularly famous for the "Red Lady" skeleton excavated there by Buckland (later found to be male), and the site of the largest known collection of EUP material. Reworked by Sollas early this century, but poorly stratified and difficult to interpret. One of the major lost opportunities as a result of early discovery.

Picken's Hole, Somerset (Map 2) ST 396550.

UBSSM

Tratman (1964); Savage (1969); Stuart (1974, 1977). A Devensian cave site, inadequately published with a radiocarbon date which the excavator (Tratman) refused to accept. The material was only partially recorded at the time of study because of practical difficulties of access.

Pin Hole, Derbyshire (Map 2) SK 536743.

BMNH, GML, MUM, SCM

Mello (1875); Busk (1875); Armstrong (1929); Kitching (1963); Jenkinson (1978). A Creswell cave, ranking with Kent's Cavern in importance for Devensian material as a result of stratigraphic recovery by Armstrong. First excavated in the 1870s by Mello and given up as complete. Work on reinterpretation continues (Jenkinson pers. comm.).

Ravenscliff Cave, Glamorganshire (Map 1) SS 550872.

Allen and Rutter (1948); Sutcliffe (1960). A Gower Coast sea cave with a mixed fauna suggesting Ipswichian and Devensian material, although this may be only Ipswichian Zones II - IV. Material not located for study.

Raygill Fissure, Yorkshire (Map 1) SE 017530.

LCM

Davis (1882); Sutcliffe (1960). A cave found during quarrying in 1873, seemingly containing Ipswichian material of Zone II character, notably hippopotamus and no horse. Material difficult to trace, and little seen.

Robin Hood's Cave, Derbyshire (Map 1 and 2) SK 536743.

BMNH, MUM, SCM

Mello (1876, 1877); Dawkins (1876, 1877); Laing (1889); Campbell (1969, 1971, 1977). The largest cave at Creswell Crags, with a great amount of material recovered by Mello and Dawkins, much of which has now been lost. Laing also recovered a considerable amount of evidence by his own account, including some apparently Ipswichian deposits, all of which has completely disappeared. All presently known material from the cave is Devensian in date.

Sandford Hill, Somerset (Map 2) ST 423592 (approximately).

TCM

Barrington and Stanton (1976). A Devensian deposit recovered early in the 19th century; no details of provenance recorded. A radiocarbon date of 36,000 B. P. was obtained on a specimen of hyaena in the course of this study, and remains one of the few details known about the site.

Selsey, Sussex (Map 1) SZ 863923.

West and Sparks (1960); Stuart (1976). Two horizons of vertebrate remains lay in freshwater silts. Dated to Wolstonian through to early Ipswichian Zone II.

Soldier's Hole, Somerset (Map 2) ST 469540.

Parry (1930). Cave deposit of Devensian age with small quantity of EUP and LUP material and a fauna which appears to have consisted largely of reindeer.

Stone, Hampshire (Map 1) SZ 458984.

West and Sparks (1960); Stuart (1976), chiefly marine deposits, with an elephant tusk from Ipswichian Zone II.

Stutton, Suffolk (Map 1) TM 149330.

Sparks and West (1963); Stuart (1976). Brickearth deposits dated to Ipswichian Zones III and IV.

Swanton Morley, Norfolk (Map 1) TG 018191.

Phillips (1972); Stuart (1976); Coxon *et al* (1980). Brickearth deposits dated to Ipswichian Zones III and IV.

Tattershall Castle, Tattershall Thorpe, Lincolnshire (Map 2) TF 207570 and TF 228605 respectively.

Girling (1974, 1977); Rackham (1978). Devensian gravel deposits with organic horizons containing large-mammal faunas.

Tornewton Cave, Devonshire (Maps 1 and 2) SX 815675.

BMNH

Sutcliffe and Zeuner (1962); Kurtén (1973a); Sutcliffe and Kowalski (1976), a most important site, containing an evidently Ipswichian deposit sandwiched between two cold stage deposits. The Ipswichian Hyaena Stratum contains material of a classic hyaena den, and may have contained the largest assemblage of Pleistocene hyaenas known in this country. The Devensian deposits included two major fossiliferous horizons, the so-called Elk and Reindeer Strata. Excavated in the 1950s.

Trafalgar Square, London (Map 1) TQ 302806.

Franks (1960); Sutcliffe (1975, 1976); Sutcliffe and Kowalski (1976); Stuart (1976). A key site in the dispute over the number of interglacials represented by "Ipswichian" deposits. Excavated in the 1950s.

Uphill Cave, Somerset (Map 2) ST 315589.

BCM, BUG, BMNH

Rutter (1829); Wilson and Reynolds (1901); Davies (1926); Harrison (1977). A series of caves have been exposed in the quarry at Uphill, but the one dealt with here seems to have been clearly a hyaena den at some point during the Devensian. Poor recording combined with wartime loss of material make it slightly less useful than it might have been. Material mainly recovered towards the end of the 19th century.

Victoria Cave, Yorkshire (Maps 1 and 2) SD 837651.

Tiddeman (1876); Jackson (1938); Sutcliffe (1960). A cave which holds one of the most northerly of British Pleistocene deposits, and at probably the highest elevation. Contains material of both Ipswichian and Devensian age. Inadequate quantities of material located for study.

Willments Gravel Pit, Middlesex (Map 2) TQ 158746.

BMNH

Coope and Angus (1975); Sutcliffe and Kowalski (1976). An important fluviatile site with organic material dated to the Upton Warren complex. Insect and rodent fauna in addition to an interesting collection of bison remains.

Windy Knoll, Derbyshire (Map 2) SK 127831.

BMNH, MUM

Dawkins (1875). A rather enigmatic deposit of probably Devensian age. Numerous specimens of bison, reindeer, bear and wolf found in what the excavators considered to be a swallow hole which had functioned as a trap for animals which came there to drink. Particularly interesting as a ´cold´ deposit in view of the lack of hyaena.

Wookey Hole Hyaena Den, Somerset (Map 2) ST 532479.

BCM, BMNH, LCM, MUM, OUM, TCM, WM

Dawkins (1862, 1863a, 1863b); Balch (1914, 1947); Tratman et al (1971); Campbell (1977). One of the most important Devensian sites of hyaena activity. Excavated in the late 1850s and early 1860s by Dawkins, and probably supplied proof (accepted by the excavator that is) of human and extinct animal contemporaneity before the Brixham Cave results were made known, although it seems to have received little acknowledgement. Re-excavated by Balch and finally by Tratman et al, without adding significantly to the earlier findings.

Wortwell, Norfolk (Map 1) TM 275844.

Sparks and West (1968); Stuart (1976). Ipswichian site of Zone II in organic river deposits.

Wretton, Norfolk (Maps 1 and 2) TL 686 992

Sparks and West (1970); West *et al* (1974); Stuart (1976; 1977). River terrace deposits containing late Ipswichian and early Devensian material.

CHAPTER 4. Predicting British Upper Pleistocene Palaeoecology on the basis of Modern Etholgy

The purpose of this chapter is to present information on modern animal and human behaviour most relevant to a palaeoecological reconstruction, and to integrate this with the environmental data discussed in Chapter 3 to produce a series of predictions about evidence likely to be found in British Upper Pleistocene deposits. The animals actually present in Britain at that time are shown in Tables 24 and 28, and relationships to the modern species are outlined here as appropriate. Species now extinct are discussed in the light of information on their closest modern analogues.

This is necessarily a brief summary of the available information on modern behaviour. At the end of the section on each species references are given to the sources of the information quoted.

4.1 The Predators

4.1.1 The Hyaena

The Pleistocene cave hyaena of Europe, *Crocuta crocuta spelaea*, is a sub-specific variant of the modern spotted hyaena, *Crocuta crocuta*, of eastern and southern Africa. Useful data on modern behaviour derive from the Serengeti Plain and Ngorongoro Crater, Tanzania, and the Timbavati Game Reserve, South Africa (Figure 16).

Hyaenas are strong animals, weighing up to 70kg, and show little sexual dimorphism. Both sexes engage in hunting and territorial defence. The teeth are highly specialised for bone crushing (Figure 2), and the digestive system can extract and assimilate the entire organic portion of bone. Prey may thus be almost entirely consumed. Although previously regarded as solely a scavenger, recent work by

Kruuk (1972) reveals that they may obtain virtually all their food by hunting in areas of Tanzania. The details of predation and consumption vary with circumstances in a manner which suggests broad predictability.

The Plain and the Crater presented hyaenas with markedly different circumstances. In the former, seasonally migrant prey prevented hyaenas from increasing their numbers to a point where they could begin to control prey population fluctuations. The low density of hyaenas, the number of prey surviving to old age and dying naturally and the relative lack of competition from lions and other predators combined to ensure adequate food for each adult hyaena without the need for complex social organisation and strenuous competition. In the Crater, by contrast, sedentary prey produced a high density of hyaenas which, coupled with intense competition from lions, meant that virtually every hyaena meal was hard-won by cooperative hunting of prime stock. As a result of these differences in circumstances, adult Plains hyaenas tended to die at an older age than those of the Crater (Figure 17).

Although less detailed than Kruuk's work, that of Bearder (1975) on Timbavati hyaenas suggests that forest terrain may also make food acquisition difficult for hyaenas. Unfortunately, for present purposes, the observational difficulties in the woodland, together with the policy of minimal disturbance to animals under study, meant that little could be done to quantify either hunting strategies or population structure. However, it is clear that woodland hyaenas are forced to adopt a more solitary approach to food acquisition than their open-country counterparts, and that this is likely to place some pressures on the animal.

Hunting strategy depends not only on terrain and prey availability but also upon the prey species sought. Zebras exhibit complex defence patterns, with stallions defending their mares and offspring strenuously, and are attacked by groups of hyaenas which may number up to 25. Since mares offer less direct resistance they tend to be caught in preference to stallions, to the extent that they may comprise 70% of adult kills to hyaenas. The overall success rate observed for zebra hunting was 34% in 47 cases, 31% of the victims being foals under one year. Length of chase has some apparent effect on the outcome (Figure 18). Wildebeest exhibit little organised defence, and although roughly the same size as zebras the adults can be taken by solitary hyaenas. Young of all species are of course taken, but hyaena consumption abilities may destroy all traces of such activity. Crater hyaenas consumed far more of a carcase, including the bones, than did their Plains counterparts.

Hyaenas use dens and lying-up areas and tend to accumulate bone in them. Sutcliffe (1970) undertook the excavation of modern East African hyaena dens, and found numerous remains of prey species. He pointed out that cubs are responsible for many of the larger bones being incorporated, since they appear to regard them as "toys". He listed four main types of hyaena damage to bone.

1. Adult splintering. Robust bone survives, cancellous bone is destroyed. Distal ends of humeri and complete metapodia may survive, and jaws show damage to ventral margins and ascending rami.

2. Juvenile gnawing. Lack of adult dentition prevents splintering but results in striations. Many bones show this characteristic in addition to adult splintering

3. Scooping out of cancellous bone. More robust bone may form a surrounding wall.

4. Digestion damage. Bones which have been regurgitated during the elimination of hair balls, or which come from the gut of dead hyaenas, are eroded, and have scalloped surfaces and holes.

Dens in the strict sense are used mainly by females for bringing up their young, and males are excluded. Lying up areas are used by both sexes. Dens tend to be narrow and difficult of access.

Hyaenas may consume prodigious quantities of food, but Kruuk (1972) estimated an overall 2kg per day of killed prey weight for Crater hyaenas. Thus an estimated 430 hyaenas killed at least 313,900 kg of prey per year, or 3,139 animals weighing 100kg each. This included 289 adult zebra and 1,140 adult wildebeest.

Female hyaenas are polyestrous, and young are born year-round with a gestation period of 110 days. There is some evidence of a trend towards seasonality in areas of periodic resource fluctuation. Cubs are dependent on the female's milk for approximately a year, and although they are given some protection at the kill by their mothers, adults do not regurgitate food for them. The shortest birth interval is approximately sixteen months. (Bearder 1975, 1977; Boylan 1972; Dart 1956; Ewer 1973; Fletcher 1974; Goodall and Van Lawick 1970; Kruuk 1971, 1972, 1975; Kurtén 1956, 1957b, 1968a; Mathews 1939; Parker and Parker 1877; Percival 1924; Pienaar 1969; Racey and Skinner 1979; Schaller 1972; Sutcliffe 1970, 1978; Verheyen 1951)

4.1.2 The Lion

The European Pleistocene lion is the same species as the modern lion, *Panthera leo*. Data on modern lion behaviour derive from the Serengeti, the Kalahari Desert, and from Kruger National Park, South Africa.

Males average 170kg, females 120kg. Dentition is highly adapted to meat eating (Figure 19.), and the large canines are used in conjunction with the highly manipulative paws to bring down and kill prey before eating it. Precise techniques of killing depend upon the reactions of the prey.

Large prey may be taken, up to 900kg commonly, and the lion at times adopts cooperative hunting tactics. Such cooperation increases killing efficiency considerably, and old male buffalo may be taken by groups of male lions. Zebras are killed with litle evident selection for sex. The lion is a stalker, and simply takes what it gets closest to. Old stallions may be taken preferentially, but this may result from there being more of them in the population. Females are possibly more prone to disease, and hyaenas attack them preferentially. Wildebeest and zebra are hunted communally with a day-time success rate of 27% and a night-time rate of 42%. Females do most of the hunting, since the large size and prominent mane of the males makes it difficult for them to approach prey unseen.

Lion consumption may be prodigious. 35kg at a sitting has been observed for a male, but requirements of 7kg per day for a male and 5kg for a female are given by Schaller (1972), or 3833kg and 2738kg of carcase weight respectively, allowing for 33% wastage. Wright (1960) estimated that a male, two females and three offspring which he observed made 219 kills in a year, which consisted of 107 wildebeest, 33 zebras, 22 Thompson's gazelles and 57 miscellaneous prey.

Lionesses are polyestrous. Estrous may correlate with prey abundances, and there is some suggestion that reproduction could become seasonal if circumstances demanded. Birth interval tends to be around two years, but the females will mate if the cubs die within that period, and there is evidence that recruitment rate depends upon circumstances. (Bertram 1975; Boule 1906; Dawkins and Sanford 1866-72; Eaton 1970; Elliot and Cowan 1978; Eloff 1973; Guggisberg 1975; Kruuk 1972; Kurtén 1968a; Pienaar 1969; Sankhala 1978; Schaller 1972; Wojtusiak 1953; Wright 1960)

4.1.3 The Wolf

The modern wolf, Canis lupus, is co-specific with the Pleistocene European form. North American wolves have been studied in some detail.

Wolves are sexually dimorphic, with males and females weighing around 55kg and 45kg respectively. They are good runners, with great stamina. Their teeth are relatively unspecialised (Figure 20), although bone may be consumed, and like hyaenas they kill prey by eating it which tends to limit the size of animal which they can successfully tackle and consume. Predation tactics again vary with prey, and success is often hard-won as Figure 21 demonstrates. Reindeer are a common prey, but there is little evidence of selection by sex. Bison may be attacked over several days, until the weakened animal is finally overcome.

The wolf is an intensely social animal. Packs are made up of related animals, and tend to break up when numbers are sufficient to create tensions. Group size therefore generally remains at below 20 animals, and packs of ten are more usual. Adults regurgitate food for the young who thus receive attention from the entire pack. Dens are used for rearing the young, but tend to be abandoned after they reach two months of age. Although adults regurgitate food and may bring some back to the den, there is little evidence in the literature that wolves accumulate bones to the extent that hyaenas do, since most of the material is actually eaten. Consumption is similar to that of the hyaena.

Mating takes place annually between January and April, and the young are born between March and June. (Fox 1975; Geist 1971; Hall and Sharp 1978; Klinghammer 1978; Kurtén 1968a; Mech 1970; Murie

1944; Pulliainen 1965, 1975; Rausch 1967; Stephenson and Ahgook 1975; Young and Goldman 1944; Zimen 1976)

4.1.4 The Leopard

Co-specific with the European Pleistocene species, the modern leopard, Panthera pardus, has the widest modern-day distribution of all the large predators except man. It is highly adaptable and exceptionally stealthy, and impressions of its numbers in an area may be misleadingly low. It is a strong, sexually dimorphic animal in which males may weigh up to 70kg and females some 9-13kg less. It is fast over short distances, climbs well , and can drag carcases heavier than itself into the branches of trees. It is an accomplished stalker, and tends to take smaller gazelle, antelope and ovicaprines. Its expertise makes observation of hunting technique extremely difficult. Consumption is of similar proportions to that of the hyaena.

Little social activity is evident, and hunting is a solitary occupation. Cubs are given good attention by their mother, but the males show little or no attachment to their offspring. Reproduction is seasonal in areas of climatic variation, and birth intervals of two years are similar to those of the lion. (Brander 1927; Dawkins and Sanford 1866-72; Guggisberg 1975; Kruuk 1972; Kurten 1968a; Pienaar 1969; Sankhala 1978; Sanford 1867; Schaller 1967, 1972; Turnbull-Kemp 1967)

4.1.5 The Bear

The modern brown bear, Ursus arctos, is cospecific with the European brown bear of the Pleistocene. The other Pleistocene bear relevant to the present study, the cave bear, Ursus spelaeus, is now extinct.

Brown bears are sexually dimorphic, powerful animals. Male Alaskan specimens may weigh up to 780kg. Limb mobility is related to climbing, but the heavier bears have this advantage offset by bulk and are mainly ground feeders. Their dentition is adapted to an omnivorous diet, and they will take meat readily although most of their food comes from plants. They scavenge from wolf kills, but no details of their killing efficiencies or patterns are available.

Bears exhibit little social behaviour, but the young stay with the mother for some time and reproduction tends to be every other year. Partial hibernation is undertaken in winter, often in caves, and the young are born during this period. Insufficient pre-hibernation nourishment for the mother will result in the death of her and the offspring, with the bones remaining in the den. Large samples of the European cave bear have been found in evidently just such circumstances. (Ewer 1973; Johnston 1903; Kurtén 1955a, 1955b, 1957a, 1957b, 1958, 1959, 1964, 1968a, 1968b, 1969a, 1969b, 1972, 1973b, 1976; Mech 1970; Walker 1964)

4.1.6 The Wolverine

Identical with the Upper Pleistocene species, the wolverine, Gulo gulo, is a small powerful predator which may attain an adult weight of 28kg. Although much of their food comes from carrion, eggs and berries, they will attack trapped animals. They have a reputation for fierceness and have been observed to drive mountain lions and bears from kills. The long,dense fur is much prized by Eskimos since it retains litle moisture and makes excellent hood trimming. (Kurtén 1968a, 1973a; Walker 1964)

4.1.7 The Lynx

Again identical with the Upper Pleistocene species, the modern lynx, Lynx lynx, is also at the smaller end of the range of large carnivores, with male adults weighing up to 38 kg. Like the wolverine, it may take some portion of the smaller or younger ungulate population. Unlike the wolverine it is easily driven from a kill, and would offer little competition to the larger predators. They seem particularly unable to coexist with wolves. (Guggisberg 1975)

4.1.8 Man

Modern man, Homo sapiens sapiens, is considered co-specific with Upper Pleistocene hominids. The Neanderthals are at most different at the sub-specific level, being assigned to Homo sapiens neanderthalensis, although there is no skeletal evidence that such hominids were present in Britain. It is therefore reasonable to treat Upper Pleistocene man as identical, from the point of view of general behavioural repertoire and reaction to environment, to modern man.

This study of Upper Pleistocene predators specifically includes man without automatically assigning him the central role. Man is clearly a predator, but his technology enables him to hunt at a level far beyond that of his basic physical adaptations, and makes summary assessment of predatory activities difficult. He can run, swim, climb and throw all with reasonable proficiency. The last characteristic makes him particularly dangerous. High intelligence and planning ability combine with these physical attributes to make a very competent hunter.

A wide range of game may be taken with primitive implements. Hadza tribesmen kill impala, zebra, eland, giraffe, buffalo and rhinoceos with poisoned arrows, and Masai youths kill rhinoceos with spears. Scavenging may also be employed. Eskimo kill reindeer with harpoons and spears, and American Indians at one time killed buffalo with arrows. Elephant hunting by African tribes made use of hamstringing techniques, or spearing in the belly and subsequent tracking until the animal died.

In temperate and arctic areas the production of clothing and shelter from animal by-products is of considerable importance. Tents and clothing may be made from skin, and reindeer are particularly valuable for the range of items which they can provide: antler and bone for weapons and tools, hides for clothing and bedding, fat for heating and lighting, sinews for binding.

Available information suggests that hunting tactics relate to prey behaviour. Mass kills are only possible with large herds, and tend only to be undertaken by large groups of people. Although data on non-human predation already discussed makes it clear man would also operate some selective bias in his killing, it nevertheless remains difficult to point to clear evidence of such behaviour. It is also clear that closer control of animals may produce patterns of selection from the herd which show great similarities with those resulting from hunting.

Human society is clearly social, and language permits close instruction and cooperation. Hunting societies in areas of extreme climate seek to minimise risk and to adopt strategies which give a good chance of adequate return, characteristics made possible by communication. Ritual activities no doubt play a large part in enhancing social cohesiveness which in turn has important influences on hunting strategy.

In areas of considerable climatic fluctuation, group size and mobility varies to make best use of resources. Summer hunting bands of around 25 have been proposed by Wobst (1974), with winter aggregations into larger groups of 300-500 persons on the basis of numerous ethnographic examples. Summer bands are unlikely to leave extensive traces since their equipment is carefully selected before setting out, and replenishment and discard is more likely to take place at sites of winter aggregation.

Harrison et al (1977) quote claims for Eskimos and Yakuts eating 10 kg of meat at one sitting, but food requirements would seem from their figures to average out at just over 1 kg per day, assuming necessary levels of fat, protein, carbohydrate, vitamins and minerals to be met. In times of scarce vegetation, such supplements may be obtained by consumption of reindeer stomach contents and milk.

Human sexual receptivity is non-seasonal, and with cultural care of the offspring a fairly high birth rate may be maintained. However, ethnographic data suggests that population limiting mechanisms, such as infanticide, are likely to be adopted by hunters. (Ardrey 1961, 1966, 1970, 1976; Bahn 1978; Balicki 1968; Bilsborough 1972, 1976; Binford 1974, 1978, 1979; Boule 1911-13; Brace 1978; Brain 1967a, 1967b, 1970, 1974, 1975a, 1975b, 1976a, 1976b; Brose and Wolpoff 1971; Campbell, B.G. 1962, 1967; Campbell J.B. 1977; Dawkins and Oakley 1877; Haldane 1956; Harrison et al 1977; Higgs 1972, 1975; Higgs and Jarman 1969, 1975; Howells 1974, 1975, 1976; Isaac 1970; Jarman and Wilkinson 1972; Kowalski 1967; Kruuk 1975; Laughlin 1968; Lee and de Vore 1968; Lewin 1979; Mellars 1973; Morris 1967; Pfeiffer 1970; Pfizenmayer 1939; Pilbeam 1975; Rightmire 1975, 1979; Roe 1972; Sahlins 1968; Schaller and Lowther 1969; Selous 1907; Sinclair 1953; Speiss 1979; Stefansson 1923; Straus and Cave 1957; Stringer 1974; Sturdy 1972, 1975; Wobst 1974; Woodburn 1968)

In summary, the large predators are adapted to securing large game. Variations in behaviour relate to prey capture, and are thus broadly predictable, but this is less true of man in view of his greater behavioural repertoire and culturally-based flexibility. Predation efficiency varies considerably between species, and within species depends to a considerable extent on the tactics adopted and the response of the prey (Table 32a). In many cases, success rates may be low. This underlines the fact that predation by man is not a routine matter of casual attack on the nearest ungulate but an activity requiring care and attention, and that in a harsh environment every effort must be made to achieve the necessary return.

Food consumption by large predators is prodigious, and killing rates may be extremely high. The assessment of human culling rates on ungulate herds would have to make sufficient allowance for this pressure on resources. The total diversity of prey taken by various predators may be high, although the greatest weight of predation in an area may tend to fall on relatively few species (Tables 31 and 32). Such specialisation is made possible by the selection of different components within each prey species. Stalkers take those to which they get closest, whereas the cursorial predators take the old, young, infirm and least aggressive in defence.

Predator recruitment rates are seen to vary considerably with circumstances. High rates, leading to increased predator density, will in turn affect social interaction and predation strategy.

Table 34 summarises characteristics of a range of modern predators observed in the Serengeti Reserve.

4.2 The Herbivores

4.2.1 The Horse

All Pleistocene and modern horses, asses and zebras belong to the genus Equus, but the specific designation of Pleistocene horses is a subject of debate. For present purposes the term horse should simply be taken to refer to all specimens under discussion. The central feature of equid social organisation is the stallion and his hareem of five to six mares plus offspring. Stallions offer aggressive defence of the group. Upper Pleistocene horses varied in size (see Chapter 5.9(i) and Figures 22-24), but Devensian specimens resembled modern zebras and Przewalski horses in height while being somewhat more robust.

Russian horses exhibit considerable cold tolerance, and fend for themselves in temperatures of $-50^{\circ}C$ with 50-70 cm of snow. Protection is afforded by thick hair and subcutaneous fat deposits. However, these animals are controlled, and might well seek to migrate from such winter conditions if given the opportunity. Serengeti zebra make considerable annual movements in search of pasture.

The high crowns of horse teeth are part of their adaptation to feeding on coarse, relatively poor quality fodder. Serengeti zebras take the most fibrous part of the vegetation, the portion lowest in protein, and extract the necessary value by eating a larger quantity in a given time than a ruminant of similar body size. Horses may thus survive in areas of poorer vegetation while a ruminant would not.

Horses breed annually and give birth in spring. The ratio of males to females may be below unity in wild populations, reflecting the greater stresses on males which result from defence and inter-male rivalry. The skeleton exhibits little sexual dimorphism, but males may be generally distinguished by the presence of canine teeth in the upper and lower jaws. (Barmintsev 1974; Bell 1971; Groves 1974; Gwynne and Bell 1968; Janis 1976; Jelinek 1975; Kruuk 1972; Kurtén 1968a; Nobis 1971, 1974; Powers and Stringer 1975; Schaller 1972; Simpson 1950; Ucko and Rosenfeld 1967)

4.2.2 The Rhinoceros

Both the steppe rhinoceros, *Dicerorhinus hemitoechus*, and the woolly rhinoceros, *Coelodonta antiquitatis*, are now extinct. Both are thought to be most closely related to the modern Sumatran rhinoceros, *Dicerorhinus sumatrensis*, but the most detailed assessment of rhinoceros behaviour available is that for the African black rhinoceros, *Diceros bicornis*.

Calves of this species are vulnerable to hyaena and lion predation up to the age of four months. Adults are generally invulnerable, but may be taken at times by groups of male lions acting in concert. Speed is clearly a factor in defence, and lions may be gored during attacks. Borsuk-Bialynicka (1973) suggests that woolly rhinoceros was a rather ponderous animal, and it is possible that it may have been rather more prone to cooperative predation by lions than its interglacial counterpart. (Borsuk-Bialynicka 1973; Goddard 1967; Guggisberg 1966; Kruuk 1975; Kurtén 1968a; Sankhala 1978; Walker 1964; Zeuner 1945)

4.2.3 Cervidae

(a) The Reindeer

Pleistocene and modern reindeer belong to one species, Rangifer tarandus. Males may weigh up to 300 kg, and females around 200 kg. Both sexes carry antler. Male antler is shed in November, following the rut, and fawns retain theirs until April or May. Growth begins in March for adult males, with compacting around June and velvet shed in late August. In females growth begins in May-June, compaction around mid October and loss in April-May. Male and female cast antler may be readily separated by size and the form of the pedicle (Figure 67).

Reindeer are herd animals and migrate seasonally in groups of varying size. They avoid deep winter snow, and changes in migration timing and pattern may covary with changes in snow fall. This makes movements somewhat unpredictable, and may lead to occasional overwintering in an area against the longer term trend of seasonal movement.

Bulls are in their best condition just prior to the autumn rut, during which they rapidly deplete their fat reserves. For man, bulls would be at their best for meat, fat and antler just prior to the rut and for skins during the winter when the coat thickens and provides excellent insulation. Reindeer meat is high in calories, and in conjunction with the range of non-meat products serves to make this a most useful animal for man to exploit.

The calves, born in spring, receive little active defence from predation, but show rapid development which tends to compensate for this. Within a few days they are able to keep up with the running herd, and must take part in the following autumn migration. (Baker 1978; Banfield 1954; Bouchud 1966; Delpech 1975; Kelsall 1968; Kurtén 1968a; Mech 1970; Pruitt 1959; Pyke 1970; Stefansson 1923; Sturdy 1975; Walker 1964)

(b) Other Cervids

Of the various deer species inhabiting Britain during the Upper Pleistocene, the giant deer, *Megacerous giganteous*, and the giant red deer, *Cervus strongyloceros*, are now completely extinct. However, a reasonable impression of their general behaviour patterns may probably be obtained from a consideration of red deer, *Cervus elaphus*, and fallow deer, *Dama dama*, animals cospecific with two of the Upper Pleistocene species. Red deer are a tree-line marginal species, population body size depending largely on the quality of fodder. Sexual dimorphism is marked. Modern British deer are at the small end of the size range, whereas Ipswichian specimens from Joint Mitnor were of similar size to large Continental specimens of Neolithic date (Table 30).

Only male cervids carry antler, reindeer excepted, and size plays a clear part in success in the competition to breed. Antlers are therefore unlikely to be primarily for defence against predators. However, all cervids seem to exhibit strong defensive behaviour, success being dependant to some extent on body size.

Large antlers may have been disadvantageous in thick forest, and those of the giant deer could have presented particular difficulties. Modern elk are a forest species whose antler span falls below the regression line of antler against body size (Figure 25), and giant deer may have tended to frequent areas near watercourses where the vegetation was more open. The large antlers may also have made defence difficult, limiting fast head movement (Gould 1974), and may have made males an easier prey at times of full antler growth. (Baker 1978; Chapman and Chapman 1978; Clutton-Brock *et al* 1979; Delap 1977; Gould 1974; Guiness *et al* 1978; Huxley 1931, 1932; Kurtén 1968a; Lowe 1961; Milne *et al* 1976; Owen 1846; Walker 1964; Walvius 1961)

4.2.4 The Bison

The bison of the British Upper Pleistocene is generally referred to *Bison priscus*. The two modern species are the American one, *Bison bison*, and the European form *Bison bonasus*.

In the modern species, adults range in weight from 450 to 1350 kg, and exhibit considerable sexual dimorphism. Modern American bison suffer some predation by wolf, and are approximately the same size as African buffalo which are at times attacked by hyenas and groups of lions. Young are born in spring and receive considerable protection from the herd, which may number in the thousands. Lengthy migrations may be made, and the young must be capable of keeping up with the herd.

A range of food is taken, from grasses to leaves, twigs and bark. (Kurtén 1968a; Mech 1970; Roe 1972; Walker 1964)

4.2.5 The Hippopotamus

The hippopotamus commonly found in Ipswichian deposits is considered to have been a large variety of the modern species Hippopotamus amphibius. Modern specimens may weigh up to 4500 kg, and size combined with a largely aquatic lifestyle renders them unlikely to suffer extensive predation. Most live in groups, and their habit of defecating in the water might easily have some effect upon the proportions of plant fossils preserved in the sediments.

In Africa, numbers are shot because of the damage which they may inflict upon riverside crops, but they tend to move on when local vegetation becomes depleted. (Kurtén 1968a; Walker 1964)

4.2.6 The Elephants

Two species of elephant are of relevance to this study: the straight-tusked elephant Palaeoloxodon antiquus of the interglacial and the mammoth, Mammuthus primigenius of the Devensian. Since both are now extinct, the African elephant will be discussed as a behavioural model.

The basis of elephant society is small groups, and herds are composed of multiples of these. The society is markedly matriarchal, with the leader usually the largest female. At times of danger the group will bunch around her, and her death is followed by confusion. Modern large herds are thought to be gross manifestations of bunching following indiscriminate shooting of females.

Elephants may take a great toll of the vegetation, but bunching may exaggerate this effect. Daily food intake is certainly prodigious at around 4% of body weight when an adult male may weigh 4500 kg. (Kurtén 1968a; Laws et al 1975)

4.2.7 Musk Ox

The behaviour of Pleistocene and modern musk ox, Ovibos moschatus, has been conveniently summarised by Wilkinson (1972). A low density species, its defensive behaviour makes it difficult for predators to break through the ring of adults who form an outward facing circle. Man can only kill individuals, except with modern technology, by taking the entire herd. Reproduction rate is low, and it is an unreliable species on which to base a long term strategy. (Kurtén 1968a; Walker 1964; Wilkinson 1975)

4.2.8 Ibex

Capra ibex is a small, fleet-footed animal which tends to inhabit high ground and is difficult for a predator to capture. However, they are taken by leopards in the Caucasus, and wolf predation on Dall and bighorn sheep in America indicates that prey capture in rocky terrain is by no means impossible. (Kurtén 1968a; Walker 1964)

4.2.9 Saiga Antelope

Saiga tartarica is a herd animal which may exist in large groups in grasslands. They do well on the saline barrens of Siberia, and would have been an attractive prey for Devensian predators. (Bannikov 1967; Kurtén 1968a; Walker 1964)

4.2.10 The Pig

Modern pigs, Sus scrofa, are generally thought of as woodland dwellers. They can be extremely agressive animals, and hyaenas take care to avoid the tusks of the African warthog, a similar species. Pigs tend to have a high reproduction rate, and provide an attractive target for predation if their defences can be overcome. (Kruuk 1972; Kurtén 1968a; Walker 1964)

4.2.11 The Aurochs

Now extinct, the aurochs, _Bos primigenius_ was a species which became rather more common in the post-glacial period. It was a very large animal, skeletally similar to the bison, and probably as difficult for a predator to kill. Reproduction rates and general behaviour may have been similar to that of the bison, although Kurtén (1968a) suggests that it may have been rather more sedentary. (Kurtén 1968a)

In summary, food supply and habitat are major determinants of ungulate numbers (Kruuk 1972; Schaller 1972), with predation tending to act as a damper on number fluctuations in areas where the density of predators is high in relation to prey. Herbivore adaptations appear more related to the avoidance of predation than to the prevention of habitat overexploitation, and have resulted in complex mechanisms to take account of the range of potential predators. However, one general phenomenon of ungulate behaviour is the tendency to make seasonal migrations to take account of variations in vegetation. Like features of predator behaviour, these movements permit general predictability, although some account must be taken of year-to-year vagaries in behaviour such as that discussed for reindeer overwintering.

In areas where a number of ungulate species coexist, grazing successions and associations produce considerable benefit for the herbivore communities (Vesey-FitzGerald 1960; Gwynne and Bell 1968; Bell 1971; Leuthold and Leuthold 1975). Earlier members of the grazing succession prepare the vegetation for the later arrivals, and thus permit a greater diversity of animal species to exist in an area than would otherwise be the case. Existence in mixed herds provides a more thorough anti-predator warning system, and open country ungulates tend to congregate in larger and more diverse herds than those inhabiting bush country.

4.3 The British Upper Pleistocene

While most of the species discussed above have adequate Upper Pleistocene records, a number do not. Wolverine is little known, but seems to have been absent in the Ipswichian. Lynx may have been present during both phases of the Upper Pleistocene, but is also scarce. (Kurtén 1973a; Stuart 1974). Musk ox, ibex, saiga antelope, aurochs and pig are also poorly known and may never have been important components of the Pleistocene ungulate fauna, although pig might be expected to have found interglacial conditions congenial. Few specimens of these species were seen in the course of this study, none at all in the case of wolverine, musk ox and saiga antelope, and their relationship to other species' remains and to predator bone-accumulation is unclear. They will therefore play little part in the following discussions, although they should be kept in mind as possible resources and exploiters of resources.

The information presented above on animal behaviour, when considered in conjunction with the climatic and environmental background discussed in Chapter 3, leads to the following series of predictions about British Upper Pleistocene predator-prey interactions and the nature of the physical evidence. These predictions are summarised in Tables 34a and 34b.

1. During the Devensian, ungulates and hence predators are likely to have made seasonal migrations from Britain during the winters. Evidence to support this suggestion should take the form of:

(a) Presence of reindeer antler pointing to summer occupation

(b) Periodicity in tooth wear in high tooth crowned species such as the horse

(c) The appearance of bear remains, including juveniles, in deposits containing other predator bones and evidence of hyaena activity.

2. Man is likely to have been a summer visitor if other species on which he depended for food were so constrained. Evidence for this should take the form of sparse occupation debris contrasting with those of sites in Europe where winter aggregations of larger groups are more likely to have occurred. Such sparse occupation traces would also rule out overwintering in Britain while subsisting on stored foods, since one would expect evidence of maintenance activities performed on tools during this time to add considerably to the lithic assemblage. Small summer groups are likely to have taken animals in small numbers at a time, rather than by mass slaughter, and reindeer would most probably be a prominent part of any human kill.

3. Ipswichian hyaenas are likely to have had a faster rate of reproduction than those of the Devensian, whereas lion and wolf recruitment is likely to have remained more constant. As a result of more sedentary Ipswichian prey and faster hyaena reproduction, the density of hyaenas is likely to have been highest during the interglacial. The wooded conditions of the Ipswichian Zone II would have favoured stalking predators, but the small pack size of the wolf is likely to have given the animal an advantage over the hyaena. The evidence for these effects is likely to be shown in:

(a) Mortalities in the hyaena population: Devensian hyaenas would be expected to live to a greater age

(b) Possible differences among the lion and wolf population: Ipswichian lions and wolves may have lived longer and shown size differences between the two periods, but there is no modern evidence to clarify this.

4. Wooded interglacial conditions would have prevented hyaenas hunting in packs and would have meant more concentration on small prey and a tendency to scavenge. Any carcases eaten would have been subject to full consumption. Evidence reflecting this should take the form of extensive damage in hyaena-accumulated Ipswichian bone assemblages. Only the most robust portions of bones would be likely to survive, and teeth might well tend to be the only well-represented body part.

5. By contrast, bones in Devensian hyaena accumulated assemblages should exhibit considerably less extensive damage, and a greater variety of body parts should be represented.

6. If woolly rhinoceros were more prone to lion predation than Ipswichian steppe rhinoceros, their remains would be rather more available to hyaena scavenging. Rhinoceros remains might therefore be more common in Devensian deposits.

7. Devensian horse remains might be capable of revealing the original predator responsible for horse killing. Samples of horses killed by lions should have roughly equal quantities of adult males and females, whereas those killed by hyaenas should show a higher proportion of females. Hyaena scavenging from lion kills should tend to retain the distribution of sexes represented in the lion kill. Wolves are unlikely to have killed many adult horses, in view of of

their relatively small pack sizes in comparison with those of hyaenas, and are likely to have concentrated on reindeer.

8. Increased vegetation during the Ipswichian, making stalking easier for species like the lion, may have meant a higher proportion of bison kills by groups of lions than in the Devensian when sparser vegetation would have tended to make approach more difficult. Hyaena scavenging might, therefore, have resulted in the incorporation of more bison bones in Ipswichian deposits, making this species a higher proportion of the faunal remains. However, it should be born in mind that increased consumption of bone by Ipswichian hyaenas could easily obliterate such evidence.

In addition to these specific predictions, it is necessary to have some regard to interactions between the various species. It is clear that modern predators take differing portions of the available range of prey. Upper Pleistocene predators would have maintained similar separations, taking different prey, different portions of various species, operating in different parts of the vegetation and acting as both scavengers and primary killers.

It is difficult to take adequate account of the likely problems faced by Upper Pleistocene predators and prey in dealing with adversaries for which there is no complete modern analogue. Whether reindeer had similar fleeing distances from lions, wolves and hyaenas, for instance, is unknowable but likely to have been an important factor in the outcome of many hunting attempts.

CHAPTER 5. The Data

5.1 Introduction

This part of the study presents details of the material examined: the numbers, measurements and distributions.

In order to address the predictions made in Chapter 4, and to provide a clear presentation and discussion of the data, it will be convenient to deal with the information in two ways. Firstly, there will be consideration of the bone damage patterns observed in support of the view that most of the material was accumulated through hyaena activity, together with an analysis of the differences between hyaena bone-accumulations of Ipswichian and Devensian age. Secondly, with the agency of accumulation identified, the relevant biometrical details for each species will be given. This will involve tabulations and summary statistics in view of the sheer quantity of remains of many of the animals, as well as graphical display for a number of characteristics of the data best discussed in that manner. In this second part the emphasis will be upon the individual species being considered, although reference will be made to wider aspects of ecology.

5.2 Bone Accumulation and Damage

Chapter 4.1.1 summarised criteria established by Sutcliffe (1970) for recognising bone accumulated and damaged by modern hyaenas. In this section, discussion is given to the evidence for bone accumulation and damage by British Upper Pleistocene hyaenas in material recovered from cave deposits. Tables 2-23 present the basic data in the form of skeletal part distributions recorded for each species in the major cave assemblages examined. Figures 26 and 27 and Plates 1-7 present a pictorial summary of the kind of damage inflicted on bones. In the first part of this section, attention is directed towards the identification of the accumulating agent, while the second part deals with the differing extent of the damage seen in Ipswichian and Devensian deposits. In this discussion, sites of natural trapping such as Joint Mitnor (Sutcliffe 1960) and Hoe Grange (Bemrose and Newton 1905) are excluded. Picken's Hole is also omitted because of practical difficulties of recording at the time of study, although the material seen together with the published description (Tratman 1964) suggests that the general conclusions reached on the basis of other sites would apply in that case also. The sites to which the following discussion does apply are shown in Tables 23a and 23b.

(1) Agency of accumulation

Figure 26 uses long bones of woolly rhinoceros to illustrate typical patterns of damage seen in material. Precisely the same patterns were observed on the bones of every other species, although size variation had produced differences in the extent of the damage.

It is clear from the discussion given by Sutcliffe (1970) that the remaining portions of the bones, those shaded in Figure 26, are the more robust. A predator will destroy the most easily damaged part of a bone, and will produce an impressively consistent pattern. A number of workers have been misled by this fact, failing to appreciate that non-randomness alone is not sufficient evidence of intentional fabrication by man, and one may cite the writings of Dart (1956, 1957, 1958, 1959, 1962) and Kitching (1963) as prime examples of this oversight.

The first two of Sutcliffe's criteria of hyaena bone-damage, adult splintering and juvenile gnawing of bones, are well illustrated in Plates 1-5 and 7 which show material from Pin Hole Cave, Creswell.

These two categories produced most of the damage which resulted in the levels of destruction of bone shown in Table 23b columns 1-4. Clearly, the level of damage inflicted on the rhinoceros bones shown in Figure 26 and Plates 4 and 5 is largely the work of adults, with only the more compact bones of the shafts tending to survive. A marked feature, emphasised by Sutcliffe (1970: 1112) and shown diagramatically in Figure 26, is for the proximal ends of humeri to be attacked more than the distal ends, and it should be emphasised that all rhinoceros humeri from every site exhibiting hyaena damage to bone showed this pattern, a point amply demonstrated in Plates 4 and 5. Many of the bones exhibit both adult and juvenile damage, as shown in Plates 1-3, being splinters broken off complete or larger specimens prior to attack by the young. One end of such a fragment may retain the sharp edges from initial splintering while the other end may appear gnawed and "sucked". The gnawed ends of such bones may be fairly smooth, a feature which has led to interpretations of human use and deliberate manufacture as skin-processing tools. However, bones of similar appearance are equally well known from sites unsuited to human occupation such as Kirkdale Cave, a low, narrow cave where no trace of human occupation has ever been found, as they are from sites such as Kent's Cavern, Pin Hole or Coygan from which varying amounts of human artefacts have been recorded.

The third criterion, scooping out of cancellous bone is also clearly demonstrated at all sites listed in Table 23b. Rhinoceros bones, being filled with spongy matter rather than marrow in a cavity, exhibit this kind of damage well, as seen in the specimens from Pin Hole in Plate 4. These particular bones were interpreted by Kitching (1963) as scoops made and used by man for obtaining water, an interpretation which ignored the clear evidence of hyaena damage on the specimens.

Digestion damage, the fourth criterion, occurs in most site assemblages although it is somewhat less common than the other categories of bone destruction. Plate 6 shows Pin Hole specimens eroded by gastric juices, with a number of the pieces having holes right through them and a characteristically serrated outline. Scalloping of the bone surface, again suggesting attack by stomach acids, is particularly evident in a series of reindeer antler points from the site, presumably regurgitated rather than excreted by the hyaenas. Even teeth up to the size of horse molars have been found to exhibit digestion damage, which gives them a curiously smooth appearance. Many of the specimens falling within this category of damage may of course have been derived from the gut of hyaenas which either died in the cave or were dragged in by others.

Hyaena bones themselves show precisely the same general patterns of damage as those of other species, to the extent that size estimations based on long bone dimensions are rendered almost impossible. Mandibles exhibit consistent damage to the ventral margin and ascending ramus (Plate 7), and whole skulls are extremely uncommon. The teeth, the instruments of this destruction, are usually the most common hyaena body part by far (Table 23a), and even some of these show digestion damage.

In Chapter 4.1.1, I pointed out that modern hyaenas may accumulate bones in a number of contexts. Thus in addition to dens, which are strictly speaking sites where young are brought up and protected, we must consider lying up areas used for weather protection, escape from enemies and for simply eating in peace. These aspects of deposit formation are discussed further in the section on hyaena data in 5.4 of this chapter, but it should be noted that they do not alter the basic argument for mode of accumulation.

There is thus clear evidence that bones from British Upper Pleistocene caves listed in Tables 23a and 23b exhibit damage characteristics fully compatible with specimens recovered from modern sites of hyaena bone accumulation. The Pleistocene specimens have clearly been gnawed and digested, and the quantities of hyaena remains in these same caves, as summarised in Table 23a, leave no doubt about the involvement of this species in the patterning. Clearly, it is not possible to say that every bone was brought to the cave by a hyaena and that no other agency was involved, but it would be difficult to argue that the hyaenas simply exploited bones which they found conveniently left in the caves. The high numbers of hyaena remains argue that the animal was living and dying in and near the sites, and was accumulating and devouring carcases and carcase portions as a result of its own labours. That such carcases may have been appropriated from another predator is not in dispute.

(2) Extent of bone damage in Ipswichian and Devensian deposits

In this section the differences between the assemblages of bones found in Ipswichian and Devensian sites of hyaena bone-accumulation are discussed. The basic data on which this discussion is based are again presented in Tables 2-23. Abstractions from this data are given in Tables 23a-g, and in Figures 68 and 69.

The aim of this discussion is to examine the evidence in support of the prediction that Ipswichian hyaenas were forced to consume more bone as part of their diet, as a result of unfavourable conditions during the interglacial, than were their Devensian counterparts. However, problems of specimen recovery, recording and curation of the kind mentioned in Chapter 1.1 (p 6) intrude most markedly at this point in analysis, and make direct interpretation of the bone assemblages very difficult. In consequence, it is necessary to avoid simple acceptance of the data at face value and to look instead for patterns which take account of both accumulation processes and events following discovery.

The quantities given in the relevant tables refer to specimens seen and recorded during the course of this study. In a number of cases it is clear that these quantities are substantially less than those initially recovered: material from Uphill was largely housed in Bristol Museum and suffered greatly in World War II bombing, and much of the Kirkdale material housed in the Royal College of Surgeons Museum suffered a similar fate, for instance. Because of losses of this kind, acting in conjunction with uncertainties about the method of recovery, it is thus impossible to use numbers of unidentified fragments as an index of hyaena bone-destruction. This attractive approach would appear, from the numbers given in Table 23b column 13, to point to Kent's Cavern and Pin Hole as sites of major hyaena activity, but is misleading. These sites are by far the best recorded, as discussed in Chapter 3.3 (p49), and the material was clearly recovered with care. Unidentified bone fragments are simply an index of this fact. A further misapprehension would result from comparing the unidentified fragments from Pin Hole and Kent's Cavern with the evidence from Tornewton Hyaena Stratum. The lack of unidentified bone at this latter site could suggest that Ipswichian hyaenas actually consumed less bone than their Devensian counterparts, since most of the Tornewton deposit was also excavated and conserved with care. However, as discussed below this would be entirely wrong.

Absolute numbers of specimens from a site will obviously tend to depend upon the size of the deposit, so that any comparison must be based upon assemblage proportions. Attention is therefore given to identifiable specimens. Identifiability presupposes a reasonable amount of each bone being present: such specimens are more likely to have been recovered and curated. Comparison of destruction levels on such items should tend to overcome problems of differential treatment by past investigators, and thus permit some analysis of the processes leading to assemblage formation.

As an initial comparison, Table 23b columns 1-4 and Figure 69 show proportions of the post-cranial assemblage of all species which exhibit various levels of hyaena-caused damage. (The material from Tornewton Elk Stratum is omitted from this analysis because of its small sample size, but all of the specimens exhibited some gnawing damage.) The amount of damage was judged by a visual estimation of the percentage of each specimen remaining. This portion of the total skeletal assemblage includes long bones and girdle bones of all species and the metapodia of ungulates. This association is used because such bones provide the most attractive portions of the skeleton from the point of view of a predator, being meat carrying, relatively fragile and generally rich in marrow. From Figure 69 it may be seen that material from the two Ipswichian sites exhibits greater hyaena-caused damage than that from Devensian sites, and that the interglacial bones have been more extensively consumed. All of the specimens so consumed have been damaged in precisely the manner described by Sutcliffe (1970), as indicated in Plates 1-7 and Figures 26 and 27 and discussed in the preceding part of this section, with the most easily destroyed portions of the bone attacked first. The difference between Ipswichian and Devensian material in this respect is entirely one of degree.

A second approach is to examine the proportions of different body parts surviving among the identifiable component of the assemblage. For this purpose, comparison is made between (1) the numbers of long bones, girdle bones and ungulate metapodia, (2) the numbers of vertebrae and (3) the numbers of foot bones and patella of all species with the exception of ungulate metapodia. These three categories represent bones of differing attraction and ease of destruction to a predator, with vertebrae being particularly prone to destruction and foot bones probably the least. Proportions of these bones are given in Table 23f and displayed in Figure 68. It may be seen from Figure 68 that the general trend between the two periods is for the Ipswichian sites to have high proportions of foot bones while the most common signature for the Devensian sites is in the form of a "V" of roughly equal-lengthed arms. Proportions of vertebrae are generally very low. Exceptions observable on Figure 68 will be discussed further below, but it may be emphasised once more that a general pattern of difference between Ipswichian and Devensian assemblages has been isolated by these two analyses of the identifiable post-cranial material.

Two categories of body part, antlers and skull and dental material, have not been considered in this comparison so far. Their distributions are shown in Table 23a and in Table 23b columns 10 and 11. Changes in antler frequencies cannot really be assessed because of the variations in species composition between the two periods. At a first approximation, it could be argued that the only difference is the replacement of Ipswichian fallow deer by reindeer in the Devensian, but the problem is more complex. Both sexes in reindeer carry antler, and the population density of reindeer is likely to have been considerably greater than that of Ipswichian fallow deer, rendering comparisons between antler proportions difficult. Skull and dental material is not included in the body part analysis made so far because the numbers reflect both isolated teeth and jaws, and are likely to be inflated by events which produce isolated teeth. On the one hand that could be argued to result from increased hyaena bone-damage, but could also reflect mishandling and careless recovery, since many teeth fall from the jaws quite readily.

With the general pattern of comparison between Ipswichian and Devensian bone assemblages outlined, it is worth examining individual samples in rather more detail. To begin with,it is clear from Figure 68 that the Uphill material bears a close resemblance to the Ipswichian samples when assessed in terms of the three post-cranial categories. However, as Figure 69 shows, this is not true of comparisons on the basis of gnawing damage. As pointed out at the beginning of this section, the Uphill material may have suffered from war damage, and may have to be considered as an anomaly from the point of view of post-cranial proportions. The material from Tornewton Elk Stratum also exhibits some similarity with Ipswichian body-part proportions, but consideration of this sample poses a number of problems. It is a small quantity for adequate comparison, and was in any event recovered from outside the main cave (Sutcliffe and Zeuner 1962: 137). It therefore differs from the other samples in deposition context, and makes analysis extremely difficult.

Why King Arthur's Cave, Robin Hood's Cave, Levaton and, perhaps, Brixham should have such low proportions of foot bones is also not totally clear. In so doing they differ markedly from the Ipswichian samples, and from Figure 69 may be seen to agree with other Devensian samples on the basis of destruction levels, but the proportions of foot bones are peculiar, and for the present no worthwhile explanation can be offered. It is possible that variations in body-part proportions between Devensian sites are monitoring local differences in hyaena bone-transport to the caves which may in turn relate to differing circumstances, but in the absence of adequate modern comparative data such answers must remain obscured. There therefore seems little point in indulging in vague speculations about the particular reasons for this pattern at each site.

The material from Sandford Hill shown in Figure 68 is distinctive because of the high proportions of vertebrae. As discussed in Chapter 3.3(i) (p51), this site would seem to have more than one context of deposition since the reindeer remains show no signs of hyaena damage (Table 23b). Natural trapping is one possible explanation for this latter feature of the assemblage, and it is therefore possible that some of the non-reindeer bone also reflects this mode of accumulation.

Material from Tornewton Hyaena Stratum exhibits a number of noteworthy features. From Table 23a it may be seen that hyaena is by far the best represented species at the site, and Tables 2 and 23b show that this predominence is produced by dental material and foot bones, for the most part. I mentioned above (p 111) the possibility of interpreting Tornewton as a site of little bone-consumption, since few prey bones are actually recorded. Most of the specimens listed under hyaena-damage categories in Table 23b columns 1-4 are clearly of hyaena, as shown in Table 23c. However, some process must be invoked to explain the preponderance of hyaena teeth and foot bones in the deposit, together with the extent of gnawing on the relatively few other skeletal parts present, and only hyaena activity can be considered. The assemblage is most probably the direct result of hyaena consumption of most parts of the hyaena bodies in addition to the complete destruction of most other material brought to the den, a conclusion reached by the excavators (Sutcliffe and Zeuner 1962).

Table 23b column 9 shows proportions of foot-bones and patellae of all species in the deposits which show evidence of hyaena gnawing. As may be seen, Kirkdale material shows a higher incidence of such damage than does that from Devensian sites, again suggesting that Ipswichian hyaenas were indeed consuming more bone. Specimens from Tornewton Hyaena Stratum do not exhibit comparable levels of damage, however, and actually fall below levels recorded for Devensian material in this characteristic. The reason for this is clarified by reference to Table 23e, where the number of foot bones at each site is shown by species. It is clear that the vast majority of such bones at Tornewton are of hyaena, whereas at most of the Devensian sites this species forms a smaller part of this portion of the total assemblage. (Uphill again presents an anomaly here, but as already discussed the history of the material since recovery may explain this.) At Devensian sites relatively few of the gnawed foot bones are those of hyaena or any other of the predators, and the proportions of specimens damaged in this way can be taken to apply almost entirely to the ungulate portion of the total assemblage. It would seem that even the hyaena finds such portions of its own species unattractive as a food source. The feet of predators are not particularly valuable as a food item, so that there is no reason to suppose that any aesthetic judgements operate in this matter. It is thus clear that the low incidence of foot-bone gnawing at Tornewton is related to the high proportion of hyaena remains found there, rather than to an absence of hyaena bone-consumption.

There is every reason to consider the predicted differences between Ipswichian and Devensian assemblages upheld, whatever the difficulties of explaining features of individual site patterns. Problems of sample recovery and curation render more detailed evaluation of pattern distinctions hazardous, however. Relative species abundances are therefore difficult to assess. The extent of fragmentation in Ipswichian deposits makes inter-period comparisons almost impossible to begin with, although the relatively high numbers of bison specimens from Kirkdale shown in Table 23a may offer some support for the prediction that lion killing from cover during the interglacial might make these animals more available to a scavenger. Within the Devensian, the problem is scarcely any easier. Table 23a summarises the numbers of specimens of each species given in Tables 13-23 for this period , and it is clear that woolly rhinoceros, reindeer and horse form the bulk of the prey species sample. (It should be emphasised at this point that shed antler specimens listed in Tables 19,21 and 22 cannot, of course, convey information on killed animals.) With the exception of a handful of metapodia, and two of the Kent's Cavern radii, all the woolly rhinoceros long bones from Devensian sites exhibit hyaena damage of the kind illustrated in Figure 26 and Plates 1-7, and this suggests that reindeer bone, and that of other species smaller than rhinoceros, may have been either completely consumed or rendered unidentifiable. Clearly the unidentifiable fragments listed in Table 23b for each site derive from some species, and partial destruction of reindeer bone may have simply resulted in lessened recovery and non-identification. Similar problems apply to assessments of prey age structure, in view of the increased fragility of immature bone.

5.3 Man

(i) Introduction

In a recent summary of the evidence for human occupation of Britain during the Pleistocene, Mellars (1974: 54) pointed out that human presence in Europe in general is scarce during the last interglacial. In Britain, no more than two or three deposits seem to date from this period, with the richest being Crayford in Kent, where a "flake-blade" industry was found in association with mammoth and woolly rhinoceros remains. Both Mellars and Stuart (1976: 235) suggest that the sparse finds at Selsey may be asssociated with mid-interglacial deposits, possibly Zone II. Stuart suggests that the lack of human implements with hippopotamus finds may point to a general absence of man during Zone II, a point made previously by Sutcliffe (1960), although man's overall scarcity makes it difficult to assess the significance of this relationship. It is possible that human implements in association with hippopotamus remains were found in the rear portion of Robin Hood's Cave at Creswell (Laing 1889), although the brevity of the report and the lack of knowledge regarding the present whereabouts of the finds makes this difficult to substantiate. It is perhaps significant, however, that horse was conspicuously absent from the faunal list given by Laing.

Mellars (1974) suggests two major phases of occupation during the earlier part of the Devensian, separated on the basis of Middle Palaeolithic tool type. The first, with so- called "bout coupe" hand axes, has been found at Little Paxton in Huntingdonshire (Paterson and Tebbutt 1947), Christchurch in Hampshire (Calkin and Green 1949), Coygan Cave in Carmarthenshire (McBurney unpublished; Hicks 1884; Grimes and Cowley 1935; Clegg 1964-70) and Kent's Cavern in Devon (Campbell and Sampson 1971). At Little Paxton, the finds were associated with reindeer. Mellars argues that typological comparisons with Continental material point to a period prior to the Chelford interstadial.

Slightly different, so-called cordiform hand-axes have been found at Oldbury in Kent (Collins and Collins 1970), Wookey Hole in Somerset (Tratman et al 1971), Pont Newydd Cave in Denbighshire (Hughes 1887) and Creswell Crags in Derbyshire (Mello 1876; Dawkins 1876; Armstrong 1929). In view of their apparent similarity with French "Mousterian of Acheulian Tradition", held to be a late Middle

Palaeolithic industry (Mellars 1969), Mellars suggests that these may date from around the time of the Upton Warren interstadial.

Whatever the time of occupation, all indications point to a fairly sporadic appearance. Only Oldbury had any real quantity of material, and that consisted of no more than 40 hand-axes and 600-700 flakes. Single layers of Middle Palaeolithic sites have produced forty times that amount (Bordes 1972), and existing sections at, for instance, Le Moustier consist of more flint than matrix. Certainly I would agree with Mellars suggestion of brief occupations of Britain, seasonal and most probably during the interstadials.

For the Upper Palaeolithic, there is somewhat more material. This has recently received detailed treatment by Campbell (1971, 1977), the first published reinvestigation since Garrod's work in 1926, and it will be convenient to discuss man against the background of Campbell's study. Campbell has put forward the idea of two phases of Upper Palaeolithic occupation, separated by the major advance of the Devensian ice-sheet, and which he has termed Early and Later Upper Palaeolithic (EUP and LUP respectively). The distribution of the major sites is shown in Maps 3 and 4. EUP industries, dating from between approximately 38,000 and 28,000 b.p., are characterised by leaf-shaped implements, but little else is known about the total toolkit as a result of highly selective recovery by early workers.

The LUP material, dating between approximately 15,000 and 10,000 b.p., is somewhat more abundant than that of the EUP. It is characterised by backed blades, collectively termed 'Creswellian', which exhibit considerable parallels with other stone industries of northern Europe. A number of bone implements have also been found, and they too exhibit features in common with Continental material.

(ii) Lithic evidence

The total number of stone artefacts presently known for the British EUP is 6,420, a figure which includes 4,464 waste products from the site of Paviland (Campbell 1977: 141). For the LUP the total is 20,692 (Campbell 1977: 161). These figures, however, include doubtful specimens and those known to be missing. The actual figures are 5,850 and 11,962 respectively for the two periods. At the time of writing, Campbell (1977: Map2) listed 37 EUP sites and 92 LUP ones, but many of these have produced very small numbers of finds.

The sites with the greatest concentration of artefacts in the two periods are Paviland and Gough's Cave respectively. Campbell has suggested that these sites may have served as home bases, pointing to the convenient appearance of a number of other sites within the edge of a 10 kilometre circle drawn around the sites. Other sites with material from the two periods are seen by Campbell as mainly temporary in nature, although sites from various regions are also ascribed base camp status. The criterion for status seems in the main to be number of artefacts, which makes for some odd decisions: thus a mere 54 artefacts are enough to make Badger Hole in Mendip a local base camp during the Early Upper Palaeolithic (Campbell 1977: 143).

Binford (1972, 1973, 1974, 1978, 1979) has put forward a number of stimulating analyses of stone tool accumulations, based most recently on observations of tool discarding by modern hunting groups. It is now clear that factors of function, curation and discard play a complex part in determining the formation of a lithic assemblage. The effect of Binford's work should be, at the very least, to induce caution in stone tool studies, and to prevent overinterpretation and the introduction of spurious accuracy. The assignment of status within a site hierarchy on the basis of changes in tool proportion in small samples is therefore clearly a hazardous procedure. Unfortunately, Campbell's study of the British Upper Palaeolithic is marred by a number of such overinterpretations, a point discussed by Stringer (1979).

It is also clear that interpretations of tool function require detailed analysis of wear patterning under a high-powered microscope, and cannot be based upon visual impression of tool form in any simple manner (Keeley and Newcomer 1977). Until such studies have been undertaken on adequate samples of British Upper Pleistocene artefacts, it would appear that little can be said about assemblage function and the relationship of particular samples to exploitation strategies.

(iii) Economy

In his general ecological reconstruction, Campbell (1977: 134-39) makes some interesting points regarding human presence and activity during both phases of the Upper Palaeolithic. I would agree that man and fauna were seasonal occupants of Britain during the Early phase, and it is conceivable that during the subsequent phase, following the major advance of the ice, climatic amelioration permitted man and animals to remain in Britain year-round, at least at times. In view of this amelioration, it would make sense to interpret the increase in tool numbers and sites of occupation from the LUP phase as evidence of increased human presence. However, this amelioration was followed by a sharp deterioration in climate in Zone III (Figure 14), so that the contrast with conditions during EUP occupation is less than complete.

In his discussion of human economic activity during the Upper Palaeolithic, Campbell makes a considerable attempt to integrate the results of his own excavations at a number of important sites. His section on the faunal evidence for economy (Campbell 1977: 107-34) makes interesting reading, and if taken at face value presents a useful synthesis. However, when one turns to the actual evidence of numbers of specimens recovered, given in his tables 32-43, it is apparent that the evidence is woefully inadequate for this purpose. The largest component of all samples is unidentified fragments, and at most sites the number of specimens for each of the large mammals scarcely if at all reaches double figures. For example, the Robin Hood's sample recovered by Campbell (1977: Table 41) consists of 135 identified specimens of large mammal bone, 39 of which were of predators. Upon that evidence rests the interpretation of change in human economic emphasis over five identified layers.

But while the evidence on which Campbell based his interpretations may be considered inadequate, criticism of his approach may be levelled at an even more fundamental point in the argument. One may question his assumption that even the small samples actually recovered during his excavations accumulated exclusively through human activity.

Human importance

At this point, two further criticisms of Campbell's approach can be raised. Firstly, he made no significant effort to incorporate the results of earlier excavations at the sites which he dug, citing only the work of Pengelly (1865-80) at Kent's Cavern and Parry (1930) at Soldier's Hole to any extent. The omission is of course understandable in many respects , since the earlier investigations were made without regard to stratigraphy. It is extremely difficult to correlate the results of earlier explorations with those from the kind of modern controlled excavation which Campbell undertook.

Secondly, and perhaps more importantly, however, he also failed to realise that the majority of the earlier excavations had produced overwhelming evidence that hyaena, and not man, was the main agent of bone accumulation. Campbell's reference (1977: 115) to hyaenas being interested in similar resources to man is virtually his only acknowledgment of that species presence, and suggests a failure to examine the existing faunal material adequately. Had he made a closer study of the bone debris, it would have been apparent that both the number of hyaena specimens and the condition of the fragments argues clearly against man having been the main occupant of sites such as Robin Hood's Cave, Church Hole, Pin Hole, Mother Grundy's Parlour, Wookey Hole Hyaena Den, Uphill, Coygan, Brixham Cave, King Arthur's Cave, Cae Gwyn, Fynnon Bueno and Kent s Cavern, as argued above in Section 5.2.(2). Among these sites, Robin Hood's Cave, Pin Hole, Wookey Hole and Kent's Cavern provide a major portion of Campbell's evidence, largely on the basis of his own recovered samples. But the bulk of the bone recovered from these sites, largely disregarded by Campbell, forms samples many times larger than his own and affords a better basis for interpretation. There is, in short, every reason to suppose that the small samples recovered by Campbell were also the result of hyaena activity, and that they represent gleanings from the almost complete excavations of previous workers. In fact, only Paviland and Gough's Cave stand out as having been solely occupied by man during the EUP and LUP phases respectively (see below p 123)

There is clearly an inverse relationship between evidence of human presence and that of his competitors. There can be no suggestion that these predators were simply occupying favourable sites at times of the year when man was absent, because seasonal movements would have been dictated by food availability. Ungulate migrations, discussed further in Sections 5.8, 5.9 and 5.11 of this chapter, would have been the determinants for all carnivore movements, those of man included.

The Upper Pleistocene evidence from South-West France suggests a reversal of the man-carnivore number relationship observed in Britain. The density of sites of human occupation there is matched by a relative scarcity of remains of large predators (de Lumley 1976; Prat pers. comm.). Bouchud (1966, 1970, 1975) has argued that this area of France was occupied year-round, on the evidence of reindeer remains, but this claim has been refuted by Binford (1973), Sturdy (1975), Bahn (1977) and, most recently, by Speiss (1979). It now appears most likely that the area was the scene of winter aggregations, perhaps of the kind envisaged by Wobst (1974) and Gamble (1978). At that time, the relatively dispersed hunting groups which had spent the summers following ungulate herds, perhaps up onto the Massive Central or even south towards the Pyrenees, are likely to have regrouped, with clear social and biological advantages for the communities. Such temporarily large groups are highly likely to have occupied favourable sites, those offering the best shelter and prime access to resources, and it is really not surprising that predator remains should be scarce in the deposits in such circumstances. However, this neither proves that man was the most important predator in the area nor that his competitors were actually scarce on the ground. Seasonal groupings over long periods of time, performing likely winter tasks of toolkit replenishment and skin preparation, for instance, are likely to have built up considerable occupation debris. Even sites such as Combe Grenal (Bordes and Prat 1965), with enormous deposits, do not necessarily imply a huge human population when the likely annual territory of the inhabitants is considered. In the case of the predators, clear evidence of their continued presence in the area is afforded by occasional finds in the deposits of sites such as

Abri Pataud (Bouchud 1975), and it is likely that these species occupied sites some way from those of man. Since the main thrust of Pleistocene research in South-West France has been directed towards the finding of archaeological sites, with attention concentrated in the areas of prime siting, the paucity of predator remains is a natural consequence. Thus the French evidence need not be interpreted as a full reversal of the British situation, with man as the dominant carnivore, but merely as a seasonal influx of human groups seeking winter quarters.

Although it is probably extremely unlikely that human and animal migrations took place between Britain and South-West France, the discussion of the French evidence raises an issue of some importance. If human groups migrated into an area in winter, increasing numbers and population density, then a similar effect must have occurred with populations of large predators. For this reason alone the numbers of lions, hyaenas and wolves in South-West France are likely to have been considerable, and the winter sites of the British summer inhabitants would in all probability have been located in areas of heightened predator density also. The interactions which occurred between the human and predator migrants from Britain falls outside the scope of this study, and if they took place in what is now the English Channel or the North Sea then they are in any event unobservable, but they underline the importance of being aware of the entire annual range of movement and activities. The British data reveal only a portion of the evidence for human and animal behaviour.

It is conceivable that human hunting groups made use of tents during their Devensian summer visits to Britain. Apparent increases in activity during the LUP may simply reflect a shift to cave occupation at that time. Evidence for this during the EUP should take the form of both dwelling sites and killing sites, with bones, tools and resharpening flakes in addition to hearths and perhaps stone tent outlines of the kind found in East Europe (Jelinek 1975). Although organic remains may have been destroyed in these deposits, any such evidence should be clear in Britain, where fieldwork has been a notable feature of archaeological research.

Open air sites are indeed known, but most of them, and certainly those with the largest quantities of material, have produced LUP material. Although artefact quantity is not necessarily the most important criterion of population density, EUP occurrences are nonetheless rare (Campbell 1977: Maps 24 and 34; Maps 3 and 4 this study). It would seem that the case for any substantial human occupation of Britain during the EUP is at best unproven, and of course the same would apply to earlier Devensian occupations associated with Middle Palaeolithic implements.

Campbell's interpretations of human exploitational emphasis and its importance within the ecosystem therefore require to be treated with some caution. This is particularly so for the EUP, but applies in general to many of his conclusions. In Chapter 3.3 (i) I pointed to the dubious validity of his interpretations of human predation patterns at Kent's Cavern on the basis of inadequate sample size, and have made the same point in this present chapter (p 122) concerning his work at Robin Hood's Cave, Creswell. In this latter case, his suggestion of changes in proportions of horse and reindeer exploited by the human inhabitants (Campbell 1969, 1977: 115) is based on quite inadequate evidence, and while it may be correct, is unsubstantiated. Some consideration of human exploitation of horse is given the section on that species which occurs later in this chapter.

In all, Campbell seems to have given insufficient attention to the results of earlier workers in terms of faunal remains recovered. It is clear that he expended considerable efforts in his project, and he certainly provides a most useful summary of the archaeological evidence. There must, however, be some doubt that he gave more than a cursory glance to the existing non-lithic material. He made no real attempt to analyse and integrate it with his own findings, and thus completely failed to appreciate the extent and importance of predator presence from at least the earlier part of his period. It is also unfortunate that the two other most recent syntheses of the British Palaeolithic, those by Mellars (1974) and Megaw and Simpson (1979), lean heavily, and in the latter case particularly uncritically, on Campbell's work for their discussion of Upper Palaeolithic economies. As a result, these discussions suffer from the same problems of misinterpreted evidence as Campbell's own study. In all fairness it must be accepted that any attempt at an overview will meet with this kind of difficulty, but equally one could argue that a brief examination of Campbell's data would reveal how inadequately based such interpretations are. It is possible that the conclusions reached by Campbell on the basis of his own recovered samples have simply been assumed to apply pro rata to the rest of the vertebrate fauna recovered by earlier workers. That is certainly the clear implication of Campbell's own discussion.

It is less easy to understand the conclusions reached by Kitching (1963) in his analysis of the bone from Pin Hole Cave,Creswell. Clearly influenced by the work of Dart (1956), who dismissed any notions of hyaena bone-accumulation out of hand, Kitching interpreted virtually every item of bone from the cave as the deliberate handiwork of man. Most of the specimens from the site exhibited in Manchester University Museum and labelled as fashioned by man show instead clear evidence of hyaena damage in full agreement with the criteria of hyaena-damaged bone listed by Sutcliffe (1970), as outlined in Chapter 4.1.1 (p 34). A number of such specimens are shown in Plates 1-7, and their mode of origin can be in little doubt. That such items, once fashioned, may have been used by man cannot be disputed, but there is no evidence for such use. Interpretation of function given on labels which accompany specimens rests entirely on the general shape and appearance of the specimens, and seeks to draw its support from the consistency of patterning on various bones. This overlooks the point made by the work of Sutcliffe (1970) and Brain (1976a), who have shown that non-human predators are capable of damaging bone in a consistent manner too. This regularity reflects the method of attack and the mechanical properties of bone itself, which will break in a consistent manner for consistently applied forces. In short, examination of the Pin Hole material in conjunction with Kitching's analysis, and in the light of recent work on hyaena bone-damage, points to clear misinterpretation of the material's patterning.

The sparseness of British Middle and Upper Palaeolithic material, when considered in the light of hyaena activity and the evidence of human occupation in South-West France, seems to offer strong support for the prediction that man occupied Devensian Britain seasonally during the summer. In particular, the paucity of evidence implies that he did not overwinter here, subsisting on stored food products and performing maintenance activities on his gear. The only sites where the remains remotely suggest such activities are Paviland and Gough's Cave, the only likely sites of exclusively human activity during the EUP and LUP phases respectively. It is particularly unfortunate, therefore, that the material from these caves has been so depleted, a point acknowledged by Campbell (1977: 7). Although adequate numbers of artefacts are still available for some typological assessments of the lithic technology to be made (Campbell 1977: Gazeteer), it is difficult to discuss human economy on the basis of the remaining portions of the faunas from the sites. In particular, the absence of other sites where man was clearly responsible for the bone assemblage (as opposed to being simply present as indicated by artefacts) makes the discernment of patterns impossible.

Table 23g lists the specimens seen and recorded from Paviland. No hyaena was present in the sample, and a humerus labelled as belonging to that species was actually of wolf. Hyaena is recorded from the site by Sollas (1913), where it is given as rare, but on the basis of the mistaken identification of the humerus it is possible that all the small sample of the species was misidentified. Much of the material has been lost over the years, and it is now impossible to check the matter further. However, none of the bones showed evidence of gnawing, although a number were broken and showed evidence of cutting, a point emphasised by Sollas (1913: 372)

The presence of bear may suggest winter absence of man (see below Section 5.8 of this Chapter), but it is difficult to offer any significant interpretation of the ungulate component of the assemblage. Teeth and jaw fragments predominate, particularly in the case of horse, although bison and reindeer remains include meat and marrow-bearing portions of the skeleton (Tables 22 and 23). To what extent the frequency of species represents economic emphasis is extremely problematic. Leaving aside the partial nature of the existing assemblage, it is clear that one cannot simply take proportions of, say, reindeer to bison specimens as indicative of past strategy. For one thing, larger animals are likely to have been butchered and boned at the kill site, while cuts of smaller species, such as reindeer, may have been brought back on the bone. Binford

(1978) has recently discussed such problems, and there is clearly no simple answer.

The age range of the horse teeth, the only portion of the sample from the site to approach adequate size for analysis, is discussed in Section 5.9(iii) of this Chapter, when comparison can be made with the exploitation patterns for horse at sites of non-human predation activity.

In the case of Gough's Cave, Campbell (1977: Gazeteer) estimated over 3,000 artefacts to have been lost from the recovered assemblage, and how much of the fauna has been lost is unknown. Certainly much of both categories was probably lost during World War II bombing of Bristol City Museum. Donovan (1955) and Parry (1928) list wolf, bear, _Bos_ sp., red and giant deer, horse and reindeer as the most clearly Pleistocene elements of the fauna, together with pig, roe deer and sheep, and there is every indication of mixing for some of the Pleistocene and later material (traces of Iron Age occupation were found in the cave). Just how reliable any present-day assessment of the remaining fauna would be is unclear: a small quantity is held at the Cheddar Caves Museum, but again there is every indication of contamination. Parry (1930: 49) pointed out that claimed finds of hyaena, rhinoceros, cave bear and lion from the cave were based on specimens from another site with which the material appears to have been mixed at some point. For this reason, no attempt is made to analyse the extant remains claimed to be from Gough's Cave. All that can be said on the present evidence is that horse does seem to have been a common element of the assemblage (Parry 1930: 49).

Whether these two sites actually provide evidence of human overwintering with associated activities is extremely difficult to say. Making every allowance for known losses, the quantities of artefacts recovered scarcely support suggestions of numerous overwinterings which would have to be made in aid of claims for major human presence. They may instead point to no more than occasional occupations over a long timespan which need not actually have taken place in winter at all, and do not substantially alter the general picture of low human numbers.

Activities

The activities of the human groups who occupied Britain are at present unclear. As pointed out already, the behavioural repertoire of man is such that the details of any particular behavioural pattern must remain unknown without certain evidence to indicate its features. Loose herding of ungulates such as reindeer and horse, as suggested by Sturdy (1972, 1975) for other northern groups in Europe is highly possible, but the presence and bone-accumulating habits of hyaenas in Britain prevents attempts to clarify this. In addition, the relative fragility of the tundra and the susceptability of the soil to erosion under the effects of heavy localised trampling may have hampered any attempts to control herds more closely, at least in significant numbers. Wright (1960) has pointed to similar problems facing East African pastoralists, within an admittedly different environment, where closely packed herds of cattle consume plants down to root level, cut the root mat with their hooves and churn the loose soil. Wind and water erosion lead to subsequent gullying and loss of feeding areas.

Necessary exploitation of herds for skins, sinews, fat, meat and so forth in the conditions of the time would imply that, like modern Eskimos, the human group were well organised, familiar with and able to meet the demands of their environment and in no sense simple creatures reacting on an ad hoc basis to their circumstances. The difficulty of applying ethnographic examples based on Bushmen, Hadza and other modern groups of semi-tropical primitive hunters who may show comparative hunting inefficiency (Woodburn 1968) rests not so much perhaps in the comparability of technologies and competence, which in all probability show many parallels, but in the pressures and requirements upon hunters in very different circumstances. British hunters of the Devensian had no mongongo nuts to fall back on.

Change over time

On page 64 above the apparent shift northward in human occupation of Britain seen in the LUP phases was referred to, and Campbell's suggestion that this might be due to climatic amelioration was briefly mentioned. The apparent intensity of predator occupation prior to the Devensian maximum, as pointed out then, makes it difficult to argue that climatic factors alone prevented man from occupying the area and exploiting its resources during the EUP in the same numbers as he apparently did during the LUP phase. Furthermore, the climate was by no means uniformly more benign during the post glacial-maximum phase (Pennington 1977). If we accept that the shift in human activity is genuine, it is perhaps more tempting to see this as related to the apparent drop in predator numbers which also occurs after the Devensian maximum, although it should be stressed once again that both phenomena are far from clear.

It is difficult to apportion cause and effect in this relative density shift, however. *It seems unlikely that predators prevented man from* occupying Britain in any numbers during the EUP phase, and it is possible that he was simply unable to operate efficiently at these latitudes. Klein (1975) has suggested that man was only able to colonise Siberia at around 35-40,000 B.P., and if general human movements into the fully arctic areas were only made at or after that time then his view may have much to commend it. Changes in fauna, which include not only predators but also herbivores such as woolly rhinoceros, mammoth and bison, may simply have resulted from climatic shifts and be unrelated in any causal way to human movement and numbers. On the other hand, to assume that man was unable to colonise Britain extensively during EUP times may be to do less than justice to his abilities, and it is highly probable that a wider view of late Upper Pleistocene movements and extinctions should be taken in any attempt to understand the evidence from this country. I shall return to this point in Chapter 6.2 and attempt to make a broader analysis of the problem.

(iv) A European parallel

It may be useful to draw a number of parallels between events in Britain during the Upper Pleistocene and those suggested by Gamble (1978) for the Swabian Alb area of southern Germany during a similar period. He also stressed the diversity and productivity of the area under glacial conditions, permitting the human occupants to exploit a predictable environment with a generalised strategy. Summer occupation by small groups operating in only a part of their annual terrritory was predicted by Gamble (1978: 166), who was able to show a close correlation between sites of human activity and terrain, to the extent of deducing home bases and satellites. In this case, relatively small and clearly demarcated areas of useful land allow much closer argument of likely behavioural constraints and appropriate evidence, aided, one suspects, by better stratified and recorded data, but the overall similarities of patterning to those of Britain remain apparent.

Gamble also emphasises the need to consider the complete yearly cycle of the inhabitants, and points to the folly of interpretations which consider partial evidence derived from seasonal strategies as the sum total of human activity and repertoire. While much of what he argues makes good sense, however, exposing numerous contradictions in previous approaches to this kind of problem, his model works best at his regional and inter-regional levels. Application to a specific site, the Stadel cave in Hohlenstein (Gamble 1979: 37), produces a less satisfactory explanation of human hunting strategies, overlooking as it appears to the role of large predators in deposit formation.

An examination of Gamble's Table 4 (1979: 40) reveals high numbers of teeth for predators and ungulates, considerable hyaena presence in all but the topmost layers, and considerable occupation by cave bear, all features noted by Gamble. Taken together with the paucity of juvenile material for all species except bear, mammoth and woolly rhinoceros, the paucity of animal limb bones and the relative scarcity of human implements (although the latter are admittedly greater in number that at most British sites), the site would appear better characterised as a summer carnivore den or lying up area in which bear wintered and man sought occasional shelter. The parallels with both Ipswichian and Devensian hyaena sites in Britain are indeed rather striking.

Gamble (1979: 43) summarises his view of deposition as follows: "This brief summary of the formation processes and internal variation of the Stadel sample leads to the following reconstruction of long term trends. Winter mortality of the bear, and possibly some carnivore bone collecting activity have combined with human agency to form the deposit. The altered skeletal population of the predators and herbivores and their contrasted age patterns all combine when compared with the element and age representation of the cave bear, to indicate selective human use of available animal communities. The sample provides a long-term perspective on evolving animal communities and their exploitation by man during the last ice age. Man is the major agency for the incorporation of species, other than cave bear, into the deposits and the available evidence suggests a consistency through time in the processing of the prey population."

Unfortunately, Gamble does not mention the presence or absence of bone damage, and it is possible that no such damage was observed. In that case I am wrongly reinterpreting his evidence, but if damage is a marked feature of the material then I must disagree with the conclusion quoted above. The evident selection and consistency through time seen in the bone debris, together with the older age grouping among the predators, point to successful predation by large carnivores, and the faunal patterning produced is simply an inevitable result.

The evidence from south Germany may offer further support for the view that man was present in small numbers during the Pleistocene, seasonally migrant and no more than one predator among many. This aspect of Pleistocene human importance is discussed further in Chapter 6.

5.4 The Hyaena

Kurtén (1956, 1963, 1969a) published some comparisons between Ipswichian and Devensian hyaenas of Britain, and was able to show consistent size and proportion differences between the two groups. In this study I have extended Kurtén's data considerably, remeasuring most of the material recorded by him and adding further details of age at death on the basis of dental wear categories. Remeasurement was necessary since most museums do not assign individual catalogue numbers to their specimens, and it was therefore impossible to locate and age many teeth recorded by Kurtén. The sole exceptions to this concern hyaena remains from Kent's Cavern and Joint Mitnor in the collections of the British Museum and Torquay Museum. In both establishments, in view of identifiability of some specimens, Kurtén's measurements could be used and age categories could be assigned to a number of items. However, even in these cases, the vast bulk of measurements are my own.

It will be convenient to discuss the hyaena data under a number of headings, beginning with size:

(i) Size variation

Tables 35-45 and Figures 28-30 list and display relevant statistics on size in modern and fossil hyaenas. The figures show general limb and tooth proportions. The method of display is that of logarithmic ratio plot, first used by Simpson (1941) and utilised frequently by Kurtén. The plot permits comparisons of specimens or samples with a reference, represented in Figure 28 by the vertical straight line CC BM(NH) 1932.6.6.10, and in Figure 29 and 30 by the vertical line at the side of each plot which in turn represents the modern Balbal population. For each specimen or sample to be compared, the base 10 logarithm difference from reference measurements are then plotted, utilising the actual specimen measurement or the mean of a sample. Specimens or samples which fall to the right of the reference are larger, with a positive logarithmic difference. Specimens or sample means which tend to fall in a straight line have similar proportions to the reference specimen, those which deviate markedly from a straight line less so, as discussed further below. The reference used may be a series of means, as in Figure 29, and the choice of reference among the items to be compared is arbitrary.

Figure 28 shows skull and limb proportions in two modern samples, with one modern specimen used as a reference, and with the means and observed ranges of Devensian hyaenas. (Ipswichian samples proved inadequate for this purpose.) The data from which these plots derive are shown in Table 44. Having regard to the small sample sizes available, it is clear that skull basal length in the Pleistocene hyaenas tends to be higher than among modern specimens, suggesting increased body size, although as discussed further below, bodily proportions appear somewhat different. Figure 29 supports this view, with all means of teeth measurements falling to the right of the reference population which in this case is of a group of hyaenas measured by Kurtén and *not* the same as the reference used in Figure 28. Figure 30, which repeats Figure 29 but for upper teeth, presents the same picture, although unfortunately Kurtén did not obtain measurements on upper canines of the Balbal population and thus they cannot be used for comparison.

Size variation between the Ipswichian and Devensian hyaenas is somewhat less easy to judge. Kurtén (1963) pointed to a number of features of the dentition which seem to suggest a size increase in the last glaciation, although changes in dental proportions have a masking effect. As Figures 29 and 30 show, Ipswichian hyaenas tended to have an absolutely larger lower premolar 2, compensated by a smaller lower premolar 3. The tables and figures suggest a general increase in tooth size in Devensian hyaenas, although by no means all the differences are statistically significant, but it is only really in the upper and lower canines that a consistent difference appears, as well as in the width of the lower premolar 4 and lower carnassial, M1.

Kurtén (1963: 228) suggested that the thickness of the lower jaw bone might serve as a good guide, being consistently thicker in the Devensian hyaenas, but I am inclined now to doubt this. As discussed below, evidence of age at death suggests that Devensian hyaenas tended to live longer than Ipswichian ones, and the jaw bones thus show age-dependent thickening. (Kurtén was of course careful to leave juveniles out of the consideration in such a comparison, but was unaware at that time of the considerable difference in adult age distributions for the two periods which may now be demonstrated.)

The limb bones depicted in Figure 28 and listed in Table 44 shed little light on the problem, being too few in number although informative on the question of bodily proportions. Since limb bone fragments are available for both periods in some quantity, however, some assessment may be made on the basis of limb widths, although caution is needed here, since these bones will also show thickening with age to some degree, particularly in the width of shafts. Table 45 shows results of pooling samples from Ipswichian and Devensian contexts, using distal maximum width for the bones in question and thus tending to avoid the question of age by using only skeletally mature material. The data suggest that there was no significant difference in body size between the two populations, and may indicate that the differences in dental proportions were not carried over into the post-cranial skeleton. Thus on the evidence now available for the British Upper Pleistocene hyaenas it would seem that they were in general larger than modern forms but showed little consistent size difference between Ipswichian and Devensian times. Rather than simply being a mask for actual size changes, the changes in dental proportions between the two periods may be an effect in their own right, and thus worth further examination.

(ii) Dental proportions

On the basis of an apparent overall size increase during the Devensian, Kurtén (1963: 230) suggested that a reaction to climatic cooling in accordance with Bergman's rule might be the explanation. As he showed (Kurtén 1957b), this certainly explains the size variation in modern spotted hyaenas and even relates the Upper Pleistocene population to the modern day one. But in the absence of body size increase from Devensian to Ipswichian, the explanation of dental proportion changes must relate to dental function. Kurten (1963: 230) indeed pointed out that prey size variation might explain certain features of the dentition, as might actual considerations of jaw mechanics.

Canine size increase in Devensian hyaenas could well be related to prey seizure. As pointed out in Chapter 4.1.3 (p 87), the cursorial species kill their prey by eating it, being unable to bring down and dispatch an animal often considerably larger than themselves in the manner adopted by the cats. Gaining a hold on the prey is nonetheless an important consideration, and if the Devensian hyaenas were dealing with large prey in open terrain then selection pressure on this ability may well have increased. The capture of horse may have been an important consideration in this. Other changes may well relate to differences in prey species exploited between the two periods, and the increased thickness of the lower carnassial is probably an important case in point. In the harsher climate of the Devensian the thick skins of the ungulates coupled with the layers of subcutaneous fat may have required larger cutting teeth for making access to the carcase, and larger canines would also help in ripping off portions of skin and hair.

Kurtén (1967) demonstrated the existence of correlation fields in mammalian dentitions, and discussed a number of phyletic instances of compensation where teeth increase in size at the cost of teeth next to them, particularly evident in the case of the cats. The reduction in size of lower premolar 2 seen in the Devensian hyaenas may well be a case of this correlation, related to the increase in size of the lower canines. The upper canines also increase, to be expected since they operated together in seizure. However, the Devensian hyaenas show an increase in size of upper premolar 2, as shown in Figure 30 and Table 36. This tooth, although close to the upper canine, is separated from it by the small upper premolar 1, and therefore less correlated with the upper canine, but it also occludes with the lower premolar 2, and has to maintain an acceptable fit. It would therefore make good sense for the upper premolar 2 to increase in size to match the decrease in size of the lower premolar 2.

(iii) Bodily proportions

Figure 28 and Table 44 display the body proportions of Ipswichian and Devensian hyaenas to the extent that such features can be determined from the rather sparse remains. Perhaps the most significant feature is the marked reduction in size of distal limb elements, the radius and metacarpal 3, the tibia and metatarsal 3, in relation to the body size as indicated by skull length. Figure 32 shows length and distal breadth of Upper Pleistocene third metatarsals compared with a small number of modern specimens, and it will be seen that the trend to shorter metapodials in the fossil sample is heightened by an increased robusticity.

Kurtén (1956: 30) suggested that these features might be an adaptation to size increase, by analogy with those seen in the more graviportal ungulates and paralleled in the cave bear Ursus spelaeus. The adaptation is even more remarkable since, as Figure 32 shows, this shortening is both relative and, on average, absolute. In other words, although larger than modern hyaenas, the Upper Pleistocene ones had absolutely shorter metapodials.

By comparison with the modern spotted hyaena, the Upper Pleistocene ones would have been rather slower moving as a result of these proportional differences. At the same time, these differences coupled with increased size would have made the hyaena a rather powerful animal, so that what it may have lacked in running speed would have been compensated for by an increased ability to subdue prey once within range. These features may well reflect adaptations to prey responses somewhat different from those of modern African ungulates, and it is possible that these differences are some indication of more active defence by Pleistocene herbivores than that met with by hyaenas today. It is also possible that the size and bulk of the prey is being monitored, the more passive and perhaps "unintentional" defence side-effects of size adaptations towards other features of the environment.

(iv) Age structure

Figure 31 summarises the age structure of adult hyaenas at a number of Ipswichian and Devensian sites in comparison with those of the Serengeti and Ngorongoro. All, it should be noted, are from animals found dead, and point to the death rate not to the living population.

In the case of the two modern populations, the essential difference lies in the proportion of animals which died during the first two adult stages. Clearly, at the time of Kruuk's initial study, the crater hyaenas were dying at a younger age, and the differences between the death-age structures were found by Kruuk to be significant.

Visual inspection alone suggests that the Devensian sites align more closely with the Serengeti distribution than that of the Ngorongoro, whereas the reverse is true of the Ipswichian sites. The most striking feature lies in the high proportion of animals which died in the two oldest age groups, IV and V, during the Devensian, and which clearly supports the prediction made in Chapter 4.3 (p103) about the lessened pressure on glacial hyaenas.

Among the Ipswichian site samples, those from Joint Mitnor exhibit a somewhat abberrant pattern, although the proportion of deaths in the youngest adult group remains high. This site, however, is itself unusual, having functioned as a fissure trap (Sutcliffe 1960), and the age structure of the hyaenas from it might therefore be expected to deviate from the normal.

One possible objection to the interpretation of different adult age structure in the two periods should be considered. Since the environment of the Ipswichian and the Devensian was so different, one could argue that the Ipswichian population used caves only as dens, while the Devensian hyaenas used them also as refuges for adults seeking shelter, and that the younger ages of the interglacial hyaenas therefore reflects no more than this. But while this may explain some features of the relative juvenile representation in the two periods, it does not explain the differences in adult age frequencies. If the Ipswichian samples were composed solely of den occupants, then by analogy with modern hyaenas they would be made up of both juveniles and females. Even if those females were the only adult deaths represented in the Ipswichian caves, as seen in Chapter 4 the peculiarities of the hyaena social organisation and sexual dimorphism do not put one sex more at risk than the other, and either females or males alone could therefore adequately represent population parameters. In any event, one suspects that dead hyaena remains would have been introduced from outside by the activity of the cubs and by acts of cannibalism. One should also bear in mind that longer periods are being considered than those which result in the East African denning evidence, and that context of use of any one site is likely to have changed over that period. Palaeontologically we are observing trends and similarities, not identical situations with a one to one correspondence.

If the age distributions of the two periods are genuinely different, the implications are rather interesting. As shown, hyaenas appear to have been absent from the British Isles during Zones III and IV of the Ipswichian, periods according to the floristic record when the vegetation was becoming open and more suitable for a pack hunting animal. By contrast, it is clear that the time of hyaena presence during the Ipswichian, Zone II, was less attractive for the animal, and it is possible to point to features in modern hyaena reproduction and hunting repertoire which suggest that some pressure on the population would have resulted (Kruuk 1972: 38). These points taken together with the evidence of death rate derived from tooth wear categories suggest that the hyaena may actually have died out towards the end of Zone II. Sea level at the time would have prevented the population from moving into Europe, the alternative to death or adaptation in situ.

(v) Context of deposition

As pointed out at the beginning of this chapter and in Chapter 4.1.1 (p84), bone accumulation by hyaenas may occur in two contexts. Firstly, the true den, which may include only females and young, and secondly, the lying-up site of the adult, seeking peace or shelter.

Sutcliffe (pers. comm.) has observed a cave in Ethiopia which served both purposes, with adult bone accumulation towards the front and narrow passages towards the rear occupied by cubs. In Britain, sites such as Kirkdale and Wookey Hole may have been similarly occupied, in view of the descriptions given at the time of excavation (Buckland 1823; Dawkins 1862).

It is possible that the contents of the various sites may give some clue to their context, although changes over the time-span of deposition may confuse matters. A consideration of Tables 2 and 13 shows that some sites have higher proportions of juvenile hyaena remains recorded than others, and that in absolute terms a number of sites have produced almost no juvenile material. Excluding the natural traps of Hoe Grange and Joint Mitnor and the fluviatile site of Barrington, the two Ipswichian sites of Kirkdale and Tornewton (Hyaena Stratum) both suggest a den context from the number of juvenile remains, which would tie in with their physical appearance as rather narrow and cramped caves. This is particularly so in the case of Kirkdale (Buckland 1823). Among the Devensian sites, the highest proportions of young are seen in Uphill, Wookey Hole, Coygan, Picken's Hole and Pin Hole. From their descriptions, Bench Cavern (Pengelly 1871) and Hutton (Buckland 1823) were probably natural traps, and can therefore be excluded. It therefore remains possible that Kent's Cavern, Sandford Hill and Church Hole were not dens but lying-up areas, although the sample size for the latter is rather small.

Of course destruction of juvenile remains, differential recovery and so forth make estimation of complete age structures difficult, and I have quite deliberately refrained from attempts at quantification in this study. In support of the theory that Devensian sites were dens, however, are the physical appearances of Wookey Hole, Picken's Hole and, to a lesser extent, Pin Hole, together with some evidence of bone destruction from these sites. Thus at Wookey and Pin Hole in particular, the number of specimens exhibiting juvenile gnawing and "sucking" is especially high. But this kind of damage is also seen at other sites, and the exclusiveness of this feature should not be stressed, nor can it be claimed that denning only took place at these sites.

For the Creswell sites, it would make good sense to see a division in use since they are close together (Jenkinson 1978). Unfortunately, the samples from Church Hole, Robin Hood's Cave and Mother Grundy's Parlour have been so depleted by inadequate curation (although this in no sense reflects upon the present staff of the Manchester Museum, where most of the remaining material is kept) that it is difficult to use them for comparison with Pin Hole, the fauna from which is relatively extensive. In terms of physical appearance, one would expect that Pin Hole and Church Hole would have served as dens, since they are long and narrow, while Robin Hood and Mother Grundy's Parlour would have served better as lying-up sites.

5.5 The Lion

Unlike the hyaena the lion is sparsely represented in British Upper Pleistocene deposits (Tables 4, 15, 23a, 23c, 23d and 23e). For this reason the samples are too small for any realistic evaluation of the size changes and age range variation on a site-by-site basis. Even when the material is split into Ipswichian and Devensian provenances the samples remain frustratingly meagre.

The marked sexual dimorphism in lion, as in any species which exhibits this phenomenon, makes for even greater difficulties when searching for evidence of size change between groups represented by few individuals. Figures 33 and 34 present scattergrams of length and breadth in teeth for Ipswichian and Devensian lions. The spread of tooth length within any one site is considerable, and suggests the presence of both sexes. In a recent study of American puma Kurtén (1973c) found that the mean length of lower molar 1 in males and females might vary by up to two millimetres, and the pooled samples for Ipswichian and Devensian lions shown in Figures 33 and 34 suggest a similar although slightly larger separation. In the same paper Kurtén pointed out that the pumas showed even greater variation between the sexes in size of canine teeth, and as the rather sparse data show this also appears true in the British Pleistocene lions.

Taken together, the scatters of tooth measurements in Figures 33 and 34 point to the presence of both sexes in the deposits and to a decrease in the size of both sexes in the Devensian compared with the Ipswichian. This is best indicated in the lower canines, the upper canines and, less clearly, the upper premolar 3 and 4. The other teeth are less well separated, although the scatters do not in any way contradict this division and rather tend to support it. Unfortunately, the amount of post-cranial material available for lion is even less than the teeth, and so cannot offer further clarification of these size differences. The lion dental material measured is shown in Tables 46-54.

Decrease in lion size from the Ipswichian to the Devensian would fall in line with expectations, particularly in view of the difficulties of stalking in open terrain. Even if lion scavenged from hyaena and wolf kills extensively, smaller size might be desirable, since less food would then be required. The animals were in no sense dwarfed, however, and would have remained capable of dealing with any prey or of driving off rivals. Further consideration is given to lion predation patterns in section 5.9 (p 162) on horse.

As pointed out when discussing modern lion behaviour, the actual number of lion remains is likely to be an unreliable guide to its relative presence. Since the remains found resulted in the main from hyaena accumulation, it is therefore difficult to assess any changes in numbers from Ipswichian to Devensian. In the case of Joint Mitnor Cave, Devon (Sutcliffe 1960), which produced a deposit clearly resulting from animals falling into a fissure, lion is represented by quite high numbers in proportion to hyaena, by comparison with the more normal hyaena accumulated deposits. It would be unwise to draw too many conclusions on the basis of one sample, but since Kruuk estimated a ratio of 40-60 lions to 430 hyaenas, say one to five, in the Ngorongoro during his study, it is of some interest to compare the Joint Mitnor figures. I estimate 22 hyaenas in the deposit, against some four to nine lions, a ratio which may therefore approach one to two. This is closer to the parity ratio which Bearder (1975, 1977) suggested for hyaenas and lions in the woodland environment of the Timbavati Game Reserve. Whether the Joint Mitnor ratio resulted from a reduction in hyaenas or an increase in lions is perhaps not clear, but since the wooded environment would tend to favour the lion, this suggests that it may be the hyaena numbers which suffered. Any increase in relative hyaena numbers during the Devensian would then have resulted as much from the group activity of this species as from any decrease in lion numbers.

With no modern lion population age structure to serve as a guide, coupled with the overall paucity of remains, it is difficult to make a full assessment of lion age structure changes between the two periods. As suggested in Chapter 4.3 (p 104), the Ipswichian lions are likely to have lived longer, but the remains found in hyaena dens may well fail to reflect this. I see no point in being spuriously precise about age proportions, and am therefore reluctant to attempt any quantification of difference, but Tables 46 and 50, lion lower cheek teeth and isolated lower molar 1, suggest a higher proportion of more worn teeth in the Ipswichian sample. Interestingly, nearly all of the teeth from Joint Mitnor show very little wear, indicating perhaps that only the young and inexperienced lions would tend to fall down a hole lured by the attraction of rotting bodies below. Older, more experienced animals may have found no need to seek food in this manner, which would tend to confirm that times were good from that animal's viewpoint, although one might have expected some evidence of old lions past their hunting prime. The age distribution of hyaenas from the site makes an interesting comparison, with very few juveniles and a more even distribution of age classes than in other Ipswichian sites. Clearly the hyaenas were attracted by the false promise of an easy meal.

5.6 The Wolf

Like the lion, the wolf is also represented by small samples which make evaluation of size and age range variation difficult (Tables 3, 14, 23a, 23c, 23d and 23e). Most of the available material is in the form of teeth, and again like the lion presents one with the problem of assessing size differences on an animal known to be sexually dimorphic with the teeth showing marked evidence of this. As with the lion, it is necessary to examine the range of size variation, and any grouping which may be evident within it, to avoid these difficulties.

A most convenient aid in this matter are the data collected by Young and Goldman (1944) on the wolves of North America. These authors list tooth measurements of males and females from a number of populations of North American wolves in a manner which permits the construction of histograms of tooth dimensions. Although their actual measurements may not be directly comparable with my own (although there seems no reason to suppose great divergence) the internal consistency which one may assume for their data allows one to consider the degree of sexual dimorphism in contrast to the samples measured in this study.

Figure 35 shows the dispersal of wolf lower molar 1 lengths from two of the largest samples given by these authors, together with specimens from Ipswichian and Devensian sites of Britain. The question of the sub-specific identity of the North American wolves is not at issue here, but since the groups have some geographic homogeneity and are considered by the authors to show clustering they may be considered a useful yardstick. Again like the lion, sample size has meant the lumping together of Ipswichian and Devensian material for the purpose of this present exercise, although separate consideration is also given to sites with large enough samples.

Figures 36 and 37 give details of a similar exercise carried out with upper premolar 4 and upper molar 1 respectively. The data for the Pleistocene wolves are given in Tables 55-59. All three figures show a spread in tooth dimensions in both periods compatible with male and female representation, judged on the basis of the modern sample. Furthermore, all three suggest that the Ipswichian wolves may have been somewhat larger than their Devensian counterparts. Post-cranial material is as useless here as it is in the case of the lion, being almost as scarce.

Kurtén (1968a: 110) reported little if any size differences between last interglacial and last glacial wolf sizes in Europe in general, but the somewhat larger samples available to me now suggest an adjustment to this view. However, Kurtén did also suggest that the Upper Pleistocene wolves of Europe were the largest, and cited evidence from Tornewton Cave in pointing to the smaller size of earlier populations. Figure 38 shows my measurements of breadths of wolf upper molar 1 from the Glutton Stratum of Tornewton. This stratum is clearly a pre-Ipswichian cold stage (Sutcliffe and Zeuner 1962) and it will be seen from Figure 38 that the wolves show some indication of having been smaller than those of the Ipswichian, in fact of rather similar size to those of the Devensian.

This would suggest that the Ipswichian was indeed the time during which wolves were most successful, when vegetational conditions combined with prey availability allowed then to use their social set up most efficiently. Never very common in most site deposits, the wolf is possibly better represented in sites where hyaena is absent (such as Banwell (Sutcliffe 1955) and Windy Knoll (Dawkins 1875)) or in Ipswichian sites, such as Tornewton, where the hyaena was dying young. The problems of accumulation agency and relationship of death to life proportions, however, are raised at once by any such attempt at assessment. The wolf is tolerably well represented at Joint Mitnor, and may, like the lion, have its proportions relative to hyaena best indicated there, although it is much less prominent at Hoe Grange, the other major Ipswichian trap deposit.

One of the most regrettable losses in British Pleistocene studies concerns the material from the Oreston Caves near Plymouth, first discovered during the construction of breakwaters (Whidbey 1821, 1823; Buckland 1823; Cottle 1829). A number of museums have specimens from the caves, the largest of which had a considerable fauna said by Cottle to include some 40 wolf jaws. Where the vast bulk of the material was deposited is unknown, although a certain amount was clearly destroyed during World War II in the Royal College of Surgeons and Bristol City Museum bomb disasters.

5.7 The Leopard

The evidence of leopard from British Upper Pleistocene sites is pitifully small. That seen by me consists of an upper and lower canine, a lower first molar, an upper milk canine and a left femur, all in Taunton museum. Sanford (1867: 44, Table V) suggests either Bleadon or Hutton for the first three, and gives the latter two as definitely Bleadon. He also listed an ulna and two metapodials held in Taunton as coming from Bleadon, but I was unable to find them during my visits.

I shall discuss the problem of dating Bleadon and Hutton deposits further when presenting data on horses, but with the lack of resolution available in conjunction with the doubtful provenance of the leopard remains it is clearly impossible to know whether the animal is represented in both Ipswichian and Devensian periods or only one. The general lack of ibex and saiga antelope in Devensian sites could be considered as support for the view that leopards were not members of the last glaciation fauna. If ibex and saiga were present in large numbers, although grazing some distance from the sites, it could be argued that hyaena activity would lead to some inclusion of these ungulates in the deposits, and their implied absence may therefore mark the lack of a major portion of leopard prey. But if the absence of these prey is a genuine feature, it remains unlikely that the Devensian ungulate population could fail to support a predator of the leopard's skill. Young reindeer, horse, giant deer and perhaps even bison would have been present in sufficient quantities in the Devensian summers to offer a considerable target for predation, so that leopard presence cannot be decided on the basis of optimum prey availability alone. Of course it remains possible that, like lion, leopard may have found some difficulty in stalking with the reduced Devensian vegetation.

5.8 The Bear

The bear remains from the various sites are summarised in Tables 5, 16, 23a, 23c, 23d and 23e). Because of the potential problems of separating cave bear and brown bear, I have made no attempt to analyse the bear remains metrically, although as pointed out in Chapter 4.1.5 (p 89) there is every reason to expect considerable sexual dimorphism in each of these species. In many cases the numbers of specimens are not high, and any analysis which could not take account of sexual and species variation would probably be misleading. Most of the older literature refers all specimens to cave bear, but this identification is unlikely to be correct. Kurtén (1957b, 1959, 1969b, 1972, 1976) found evidence of cave bear in only two British Devensian deposits, Kent's Cavern and Wookey Hole, and suggested that brown bear was the better competitor. On the other hand, it is possible that some of the material unseen by Kurtén should be ascribed to cave bear, in the same way that the greater time available to me has brought to light more extensive hyaena samples than were seen by him. As the aim of the study was to concentrate on the major predators, the bear material was simply recorded as Ursus sp.

I argued in Chapter 4.3 (p103) that one expectation of seasonal movement in predators and prey would be the inclusion of bear remains in sites normally occupied by hyaenas. It is inconceivable that the two species would have cohabited, and bear remains should therefore point to periodic absence of the hyaenas. It would also follow that in the Ipswichian, when both predators and prey were unable to migrate from Britain, that the number of bear remains should decrease, unless substantial seasonal movements took place within the British Isles. However, one obvious difficulty with any attempts to recover the Ipswichian events lies in the greater degree of bone destruction which took place, making such comparisons almost impossible. It remains true that the number of bear remains recovered from Ipswichian sites is less than that from Devensian deposits, as Table 23a shows, but little can be claimed beyond that.

Since the bears present during the Devensian would have hibernated in the caves, one would expect considerable evidence of juvenile deaths, because the young are born during this period, as well as some indication of annual mortality. Kurtén (1958) was able to demonstrate this clearly for the European cave bear. Unfortunately, none of the Devensian sites have produced remains in sufficient quantity for this purpose, although at Pin Hole a number of milk teeth were found. In deposits from Tornewton Cave, underlying the Ipswichian Hyaena Stratum and possibly dating to the previous glaciation, the numerous brown bear remains have, however, revealed just this evidence of annual mortality (Kurtén, pers. comm.). A few hyaena remains were recovered from this stratum (Sutcliffe and Zeuner 1962), but few by comparison with the remains of Ipswichian or Devensian date. It is possible that fewer hyaenas were present at that earlier time. The lack of bear in Devensian levels, by comparison with this earlier deposit, may be explained by hyaena destruction of rotting corpses found by them on their return each spring, with only a few surviving to become incorporated in the deposits.

It is clear that a more detailed evaluation of the bear remains needs to be done and that the present analysis is unsatisfactory, with few facts emerging from it. However, I would expect the general outline given here to be correct.

5.9 The Horse

As dicussed in Chapter 3.2 (p 33), horse was absent from Britain during the Ipswichian Zone II. It seems to have been present, however, during Zones III and IV, and sufficient specimens are known to afford some comparison with the horse of the following Devensian period. The vast bulk of the horse remains from the two periods consists of teeth, and this is particularly so in the case of the Devensian. For the Ipswichian post-cranial remains form a higher proportion of the assemblages. The details of these proportions may be found in Tables 6, 17, 23a, 23c, 23d and 23e. For convenience the horse data will be discussed under a number of headings.

(i) Size variation

Figures 22 and 23 show length and distal width measurements of horse metacarpals and metatarsals respectively. For comparative purposes a number of modern horse specimens are also shown on each graph, giving some idea of the stature of these Pleistocene representatives.

It is apparent that all the specimens clearly derived from Devensian deposits are of similar size, and compare well with Continental material of last glacial age from the French site of

Solutré shown in Figure 24 . Material from Ilford, the Crayford-Erith area and Bleadon is considerably larger, while that from Clevedon Cave is rather small and that from Hutton falls within the Devensian size range. It is worth considering the value of horse as a guide to the chronology of these sites.

As discussed in Chapter 3.2, there is dispute over the position of Ilford and Crayford-Erith within the British Pleistocene sequence. Whatever their precise position, it is clear that remains from these sites predate those from Devensian sites, and the size trend in horse remains observable in Figures 22 and 23, confirms the general reduction in horse stature referred to by Kurtén (1968a: 150). Unfortunately, horse specimens do not seem to offer any resolution to the problem of whether or not the sites should be considered to be Ipswichian. They do suggest, however, that Bleadon, Hutton and Clevedon may be better placed within the sequence.

Sutcliffe and Kowalski (1976: 66, Table 12) have suggested that Bleadon is of Devensian age, while Clevedon and Hutton of pre-Ipswichian age and correlate with the Tornewton Glutton Stratum.

The fauna from Bleadon held in Taunton Museum includes red deer, pig, bison, horse, bear, lion, probably Bos and probably roe deer. Leopard is represented by a milk canine and an immature femur. Coupled with the large size of the horse, this assemblage would suggest a pre-Devensian date. However, the Taunton collection also contains a number of reindeer specimens from the site as well as at least one mammoth tooth.

One specimen of hyaena in the British Museum (Natural History), a left maxillary fragment catalogue number 44748, is recorded as coming from Bleadon, but no hyaena remains were observed at Taunton Museum.

Reynolds (1902: 5) includes Bleadon among his list of sites known to have produced hyaena remains, but gives no details of numbers or source of information, although he also clearly examined material from Taunton during his study. I observed no clear evidence of gnawing on the Bleadon bones, although this in itself does not rule out hyaena presence as shown at Joint Mitnor, and from its description Bleadon could also have functioned as a trap (Barrington and Stanton 1976: 42). The almost complete absence of hyaena, together with the relative abundance of horse, would suggest a date other than Ipswichian Zone II for the interglacial remains, but it seems clear that two periods of deposition are indicated by the assemblage.

Hutton Cave, on the other hand, has both horse and hyaena, suggesting a Devensian date in agreement with the horse size. This site may also have functioned as a natural trap, as suggested by Buckland (1823: 57) and indicated by modern description (Barrington and Stanton 1976: 100). Interestingly, one of the early excavators, the Rev. David Williams of Bleadon, in a letter quoted by Rutter (1829: 104) referred to the remains of the horse being "....of different ages and sizes, from the little Shetland, up to the great London dray-horse", which may at first sight suggest earlier, and therefore pre-Devensian material. My own examination, however, suggested no such size variation. Williams may have been misled by the age grouping of the material, which includes a number of immature specimens and may therefore give the impression of variation in horse size.

Clevedon Cave, Somerset, is correlated with the Tornewton Glutton Stratum on the basis of two voles, Microtus nivalis and M. oeconomus. The former is said to be entirely absent from Devensian localities (Sutcliffe and Kowalski 1976: 115), although the latter is a common feature of Devensian deposits. The horse remains from this site suggest animals slightly shorter than modern Przewalskis but of rather similar robusticity. Context of deposition (Davies 1907; Reynolds 1907; Palmer and Hinton 1929; Gilbertson and Hawkins 1974) suggests that these remains are of Late Devensian date. One possible explanation for this conflict of evidence may lie in a confusion of _Microtus nivalis_ and _M. agrestis_: the two species are difficult to distiguish (Sutcliffe and Kowalski 1976: 66), and if the latter species was actually the one present then the Devensian date would really be in no doubt. The second possibility is that advanced by Stuart (1976: 228) in rejecting a pre-Ipswichian date for Crayford. He has argued that the _M. nivalis_ remains from Crayford are actually of _M. oeconomus_: if a similar misidentification has taken place in the case of the Clevedon material, then again a Devensian date would seem more likely for this latter site.

Of course if Ilford and Crayford-Erith are not Ipswichian deposits, then the reduction in horse size may well have taken place during the Ipswichian. In that case it would be unsafe to relate small horses solely to the Devensian, and the material from Bleadon could not be confidently assigned to the Ipswichian, for instance. At present, I feel that the balance of the argument may be in favour of Stuart's view: accordingly I would consider Ilford and Crayford-Erith to be Ipswichian, and would place Bleadon in the same category, with some portion of the deposits dating to the Devensian. Hutton and Clevedon I would consider to be Devensian. The rest of the analysis will proceed on this assumption therefore.

Referring again to Figures 22 and 23, it may be seen that most separation between the Devensian and non-Devensian specimens occurs in the metatarsal, in both length and robusticity. Since the hind limb of quadrupeds generally exhibits greater adaptation to running than does the forelimb (Coombs 1978) this is to be expected. Horses considered here to be Ipswichian approached the height of modern specially bred varieties without attaining similar robusticity. There can be no suggestion that the size of the Ipswichian horses was a factor in the disappearance of the hyaena in Zones III and IV, since the hyaena data showed that the Ipswichian hyaenas were dying at a young age during the horseless Zone II. It could be argued, however, that the forest conditions which led to the lack of horse during Zone II were also responsible for the demise of the hyaena, faced as it was with the difficulties of hunting in such conditions in competition with lion, leopard and wolf.

(ii) Sex ratio

It will be apparent that one of the problems confounding size estimations and comparisons in fossil populations is that of sexual dimorphism. In horses the problem of sex separation is complicated further, since little evidence for it exists and yet an estimate of sex ratios is required in an assessment of predator strategies. Nobis (pers. comm.) has pointed out that the horse skeleton is generally unsuited to sexual distinction. In his opinion, only the pelvis can be used reliably for this purpose, and of course this body part is rarely found in a suitable state of preservation. The one other possible indicator of sex is the presence of canine teeth, which are usually present in males and absent in females.

Most remains of horses from Devensian sites consist of isolated teeth, and finds of mandibular symphyses and premaxillae with incisors present are rare. The canine, if present, occurs in the diastema between incisors and cheek teeth, the thinnest and perhaps most fragile portion of the jaw, and the probability of finding canines in situ in a jaw is therefore remote.

Levine (pers. comm.) has also suggested that the chances of finding canines in deposits at all, particularly in view of old excavation techniques, would be small. This rarity would, in her view, preclude any assessment of sex ratios in terms simply of numbers of canines. However, consideration of the size of fragments found by many excavators of the previous century inclines me to believe that such a bias against canines need not be expected. Smaller teeth were regularly recovered, often in quantity. In particular, there is no reason to expect that they would be recovered either more or less frequently than horse incisors, which are of similar size. The expectation would include the natural ratios of canines to incisors, and may therefore be quantified.

If a null hypothesis of no significant difference in numbers between the sexes is proposed, then each female would be expected to contribute 12 incisors to the deposits and each male 12 incisors plus 4 canines, a total ratio of 4 canines to every 24 incisors or 1:6, and any differential representation to vary significantly from this. This is based on an initial assumption of sexual parity in the population. Table 60 shows the expected distributions expressed both absolutely and as percentages, together with the ratios of canines to incisors derived from a number of Devensian sites believed to have been the scene of predator bone accumulation.

The last entry of Table 60 shows the results of pooling the fossil samples, to see if the overall distribution of canines differs from expectation. To assess the extent to which this differs from 14.29%, the Standard Error of a sample of the same total size as the pooled fossil sample, 403 teeth, but with 14.29% canines, is calculated. This Standard Error is divided into the difference between 14.29, the expected percentage of canines, and 8.19, the observed percentage, to obtain the number of Standard Errors of Difference between the two percentages. Thus:

$$\text{Standard Errors of Difference} = \frac{14.29 - 8.19}{\sqrt{\frac{14.29 \times 35.71}{403}}}$$

$$= \frac{6.1}{1.74}$$

$$= 3.49$$

With over three Standard Errors of Difference between them, the two percentages suggest that at the total sample size of the pooled fossil population the canines are under-represented, and that both sexes are therefore not equally present. Examination of the individual samples making up the fossil population suggests, however, that many of them do not actually differ from the canine proportion expected for sexual equality. The danger of comparing each sample with the expected proportion is of course that by accepting a difference at say the 95% level one would actually be wrong in all probability five times in one hundred samples. Even with the seven fossil samples being considered here caution should be exercised. Coygan, the site with the lowest canine percentage, is 2.48 Standard Errors from the expected proportion, a figure which just fails at the 1% level of significance (Swinscow 1977: Table A) but which indicates real difference at 5%. Multiplying by seven to take account of the seven fossil samples would give a failure at the 7% level, which I am inclined to accept as a true indication that the Coygan horses were not represented by equal numbers of the sexes.

Taken individually, Uphill and Pin Hole caves have Standard Error differences from expectation of 1.99 and 1.56 respectively, indicating that Uphill only would differ from expectation at the 5% level, although when the other samples are considered along with this it cannot be said to differ from expectation. Thus although the overall proportion of canines in the fossil samples is lower than that expected for equal numbers of males and females, only Coygan can really be seen to differ from expectation on a site-by-site basis.

The measure used here may be a little coarse. Strictly speaking, the expected tooth representation for sexual parity would be a set of four canines, an upper left and right and a lower left and right, for every two complete sets of incisors. In a large sample drawn at random from a population of equal sex numbers a ratio of four canines to every 24 incisors irrespective of tooth identity would be expected, but the samples used here may be rather small and the results misleading. The assumption of horse population sexual parity may also be called into question, since modern Przewalski herds may have a ratio of only 85 males to 115 females (Groves 1974). However, if that ratio applied to Devensian horses, then the proportion of canines to be expected would be even lower than that predicted for sexual parity, in which case the samples listed in Table 60 would differ even less from expectation, and all samples would suggest that the sexes were taken in equal numbers. However, since it is not possible to determine the population sex ratio, I shall take sexual parity to be the case and accept the results obtained here at face value.

Thus equal representation of male and female horses could suggest, as argued in Chapter 4.3 (p104), that the hyaenas were not doing most of the killing but were obtaining meat from animals killed by a predator making less selection for sex. The lion would tend to kill in such a manner, and it could therefore be that in the vicinity of a number of sites the hyaenas were able to make a comfortable living exploiting lion kills. It is also possible that human kills were scavenged from: it is less easy to predict the specifics of human horse hunting, which would undoubtedly have depended on the intended use of the resource. If man was in fact controlling horse herds in some way then his major concern may have been with the females, but then the males may have been used for meat, hides, sinews and so on.

At Coygan the fairly clear under-representation of male horses suggests that the local hyaenas were doing more of their own hunting, and it is perhaps worth stressing at this point that there is no reason whatsoever to assume that precisely the same pattern should be seen in sites from different parts of the country. While it may not, in terms of the actual fossil evidence found, have been quite the lion metropolis suggested by Dawkins and Sanford (1866-72), the Mendip region has produced numerous lion remains, and the Wookey Hole hyaenas may have been in a very fortunate and advantageous position with respect to those at Coygan, being able to scavenge from lion kills. The differences in hyaena age classes at the two sites may be a reflection of this, with the Wookey animals having a slightly older population at death than Coygan (Figure 31). Location in Mendip may then explain the tendency to old age at death in hyaenas from Uphill, Picken's Hole and Sandford Hill, also shown in Figure 31, although Uphill does have the next lowest ratio of canines after Coygan. Unfortunately the sample of horse from Picken's Hole could not be adequately recorded at the time of this study, and is in any event probably too small, while Sandford Hill deposits seen by me have contained only one broken horse metapodial and four upper teeth (Table 17). However, even if horse was not being exploited by hyaenas at a site, nor being scavenged, the presence of lions could well ensure a supply of meat of other species for a group of hyaenas able to expropriate it .

Equal numbers of male and female horses, or close approximation thereto, would certainly support the view that hyaenas were not tending to scavenge this resource from wolves, who as I argued in Chapter 4.3.7 (p 104) were probably less equipped to tackle this prey. Wolves may also have found scavenging from lion kills a profitable occupation. The possibility that the horse specimens were scavenged from natural mortalities among the horse population should also be considered, however.

(iii) Age at death

Horse tooth crown height data may be used as an indicator of horse age at death. Clearly, such considerations lack knowledge of absolute age, and are only of use when considered over a fairly large sample of horses, but it is quite possible to estimate whether animals are being killed or dying early or later in life on the basis of their tooth wear.

In this study only adult teeth are considered, and the resultant age distributions refer to mature horses. Juvenile kills and deaths undoubtedly made up a considerable portion of the total, but as emphasised the problems of destruction by hyaenas prevent any reasonable assessment of their contribution to the diet.

The method adopted is quite simple. Taking one tooth, the upper first molar, and considering a pooled sample of both left and right teeth in order to obtain adequate sample sizes, the material for each site is grouped into ten millimetre classes. The result is displayed in Figure 39, where older horses with shorter teeth fall to the left.

The results are not easy to interpret. Data collected by Schaller and Kruuk on lion and hyaena predation on zebra respectively suggest that adult age classes are all taken with approximately equal regularity, although Schaller (1972: 223) felt that rather more old stallions may be taken by lions, perhaps as a result of hyaena predation on females making more old males available. Kruuk (1972: 98) suggests that hyaenas may prefer older zebra, but the data are sparse and inconclusive.

Sites with a greater proportion of older horses are Wookey Hole, Uphill and Pin Hole. Coygan and Kent's Cavern occupy an intermediate position, although the tendency is perhaps towards older animals. Finally, Paviland shows a tendency towards the younger horses although the sample is small. It may be significant that this last site is the only one in which the accumulation was clearly by man, and this may therefore reflect some features of human exploitation strategy, although scavenging from another predator cannot be ruled out.

It is possible that the high proportions of old horses at Wookey Hole, Uphill and Pin Hole reflect naturally dying animals scavenged by hyaenas. Such material would tend to have an equal sex ratio, as was indeed suggested by canine proportions, provided that no selection operated. However, if both lions and hyaenas also tend to take older horses, then it would seem difficult to carry the interpretation further and decide whether or not the remains were scavenged from lions. All that seems clear is that hyaenas are unlikely to have been the predators in view of the sexual parity indicated by horse canines.

In the case of Coygan, the concentration on middle-aged animals together with a higher proportion of younger ones than is seen at the three previous sites agrees quite well with the evidence of direct hyaena predation based on sex ratios. The lower proportion of old horses may be a reflection of hyaena predation preventing so many from achieving old age. This would tend to reinforce the difference in predation and lifestyle of Coygan hyaenas, which may have been faced with rather more difficult conditions than their Mendip and Creswell counterparts and therefore required to hunt rather more.

Kent's Cavern horses fall rather close to those of Coygan in their age range, while failing to agree with the latter in terms of sex ratio. In fact, the sex ratio in terms of canines, as shown in Table 60, is very close to those of Wookey Hole, Uphill and Pin Hole (together with those of Robin Hood and King Arthur's caves, which are not covered here through lack of adequate sample sizes). One possible, but highly unsatisfactory explanation for this observation may be sample bias. The numbers of canines and incisors given in Table 60 will be seen to be similar for a number of sites, particularly Uphill, Wookey Hole, Kent's Cavern and Pin Hole. Yet, as Table 17 shows, the number of adult cheek teeth available from Kent's Cavern is vastly greater than from any other site. Since each horse will have 12 incisors and 24 cheek teeth, the expected ratio in an unbiased sample would be one third incisors, so that the body part is clearly under-represented at Kent's Cavern. It is conceivable that Kent's Cavern should have a much higher number of incisors and thus a lower ratio of canines, similar to that of Coygan, which could explain the similarity in age ranges. But one could also argue that the proportion of canines should remain unchanged even if more incisors were known, and clearly the matter cannot be resolved.

(iv) Seasonal presence

In Chapter 4.3.1(p103) I argued that one indicator of seasonal presence by British Upper Pleistocene fauna could take the form of periodicity in tooth wear patterns among high crowned species, and that the horse would be among the species most suited to such an investigation. Accordingly, isolated cheek teeth of horse were measured as described in Chapter 2, and the crown height used as an indicator.

The basic expectation is as follows. If horses were regularly absent from the country over a period of time for a substantial part of the year, then one would expect the distribution of wear on individual teeth from a sample of individuals to peak at intervals rather than assume an even curve. Such an expectation depends upon five assumptions:

1. that each birth takes place at the same time of year

2. that each tooth can be identified in isolation

3. that each individual tooth is of similar height in the horse population at commencement of wear

4. that each horse wears its teeth at a similar rate to other members of the population

5. that tooth wear is similar throughout the year.

For assumptions 1 and 2 there is no difficulty. Horses, as discussed in Chapter 4, breed annually, and while some teeth cannot be consistently identified in isolation these may be left out of the assessment in favour of others which can. For assumption 3 one can argue that since horses exhibit little sexual dimorphism there is every reason to expect a central tendency in original tooth size and therefore length. Figure 40 shows a histogram of tooth diameters for upper molar 1 from Kent's Cavern, the largest sample examined, and there is clearly no suggestion of other than strong unimodality. For assumption 4 a similar answer of central tendency may be given, at least as a working hypothesis: there seems no pressing reason to assume otherwise. For assumption 5 the factors to be invoked in any explanation which involves different wear at various times of the year have to be considered. Clearly tooth wear bears some relationship to food consumed, as discussed in Chapter 2, and any changes in food type over the year could result in some wear changes. But as has been pointed out to me (A. Hall pers. comm.), any significant changes in vegetation would probably necessitate movement from one area to another. If the difference in abrasion which resulted was enough to cause a marked decline in tooth wear, then this could result in peaks in a distribution of tooth heights among animals killed in the area of lessened wear. In the area of increased wear, no such peaks would be observed, because the animals would be present and dying during the major part of the total annual wear period. Thus if peaks are observed it means that one has either a death assemblage from the area of little wear or a death assemblage from a seasonal portion of the range of a species with a more even spread of annual wear rate. In either event, the evidence is of seasonal movement, and that is the issue here.

Two further points should also be made. Firstly, if the distribution of wear rates among the horse population does produce a blurring of the wear peaks, then any peaking noted during analysis may be taken to be of considerable significance, provided of course that it first satisfies conditions of statistical validity. Secondly, if the tooth wear is evenly distributed over the year, or closely approximates to evenness, then any significant peaking which results would suggest that the season of presence in the area of accumulation was short. This latter point could result in a rather circular argument if pushed too far, but is well worth bearing in mind.

If peaks are to be expected, therefore, at what intervals should they appear? The crown height of a horse upper molar may reach 80 mm. Full wear occurs at around 20 mm, since the measurement is taken from the root. Domestic horses attain full adult dentition at around 4 years (Silver 1969) and life expectancy tends to be around 25 years (Walker 1964: 1340), say 20 years from the appearance of adult teeth. Sixty mm of wear in 20 years suggests that an annual wear of around 3 mm might be expected, and that the peaks in any distribution which represented a seasonal cull should be separated by that amount. Spinage (1973) suggests that tooth wear is actually linear only during the mid-life of a tooth, being more rapid at first and rather slower in old age, so that the expectation should be modified somewhat. It would be reasonable to expect periodic peaking towards the middle of the distribution only, and with an interval of other than 3 mm. For the present purpose the interest is in the demonstration of periodicity in wear, however, rather than in the distance between the peaks.

Naturally the assumption of such periodicity requires adequate samples for its demonstration. Samples with few teeth are of little value. Ideally, one would also wish for large assemblages from a short time range. The largest samples, those from Kent's Cavern and Wookey Hole, satisfy the first requirements but in all probability no samples could be claimed to come from a short time range, and it is difficult to know exactly how much of the Devensian they span. Small samples could perhaps be amalgamated but any attempts would require caution, since widely separate sites could have been reached by horses at different points in the year, with consequent blurring of the peaking.

Dr. N. Fieller of the Department of Probability and Statistics at Sheffield suggested that it might be possible to search for periodicity in horse tooth wear and to assess the significance of any derived periods statistically. He kindly agreed to carry out the analysis for me and to make the results available for inclusion in this study.

The method employed was adapted from that proposed by Kendall (1974) to aid the search for the so-called megalithic yard. Based upon a Fourier analysis, it attempts to find previously unknown quanta present within a set of measurements and, by assessing the probability of each, to determine which of these best fits the observed data. A full description of the technique together with its theoretical justification may be found in Kendall's paper, and no attempt is made here to give more than a brief outline.

Consider a set of measurements which are believed to be rational multiples of a single measurement q, the quantum. To test that belief, consider a circle of perimeter q with the set of measurements marked off round it from a common starting point. If the measurements were rational multiples of q then the marked points should all coincide with the origin: they would go round the circle once, twice and so on. Suppose that each measurement, although quantal, had a small error component added to it. Then although the points would still tend to align on the circle perimeter they would have a scatter, and the fit of the measurements with the assumed quantum could be assessed on the basis of that scatter. That assessment could be based on the comparison with a standard distribution of marks on a wheel perimeter derivable from a circular Gaussian distribution, in the same way that one could assess any distribution for fit with a statistical norm.

Instead of measuring the degree of point dispersal around the circle perimeter in linear terms, it is possible to express dispersal in angular measurement, using angular displacement Theta in radians. It may equally be expressed in terms of Cos Theta which ranges from +1 to -1. This takes the value of +1 at the zero point as the markers appear there, and falls towards -1 steadily for each more distant marker in either direction. The extent of clustering may then be shown by summing Cos Theta and taking account of sample size or number of measurements. It may be shown that high clustering of the summed points is given by the formula

$$\emptyset(r) = ((2/N)\sum_{j=1}^{N}\mathrm{Cos}(2\pi X\ r))^{\frac{1}{2}} \qquad (1)$$

Where $r = 1/q$

N = number of measurements

X = the jth measurement, comprising a rational multiple, M, of the quantum plus an error component, e which takes the high value $(2N)^{\frac{1}{2}}$ if q has been correctly chosen and the errors zero.

In the case of the horse teeth, however, although the rule of thumb expectation is of 3 mm wear per year the precise value of the quantum is unknown. It is therefore necessary to search for possible quanta, prescribing a range for the search to prevent an infinitely long process of hunting impossible values. The limits to the value of q were therefore set at 1.95 mm and 5.05 mm, using the 3 mm figure as a guide.

The method computed and plotted Phi(r) against r over the range of assumed possible values of the quantum, using the Sheffield ICL computer and a special programme written by Dr. Fieller. However, since the method plots cosine sums, a number of peaks are produced, not simply one relating to the high value derived from formula (1) in the simple situation of testing one assumed quantum. One has then to assess the significance of the peak, or peaks, produced by the Cosine Quantogram, as Kendall has termed the technique.

Two points must be considered here. Firstly, peaks which are artefacts of the unit of measurement, quanta which appear as multiples of that unit must be elmiminated. To overcome this rounding effect, a result of measurement only to the nearest whole millimetre in view of the impracticalities of achieving greater consistent accuracy, a small random addition was made to each measurement, having the effect of 'unrounding' the data. Comparison of the results of such adjustment with those derived from unadjusted data suggested that the additions were unnecessary, however, and this procedure was abandoned. This move was justified because the values of the quanta subsequently produced were well away from the accuracy of measurement.

The second point concerns an observation made early in the analysis by Dr. Fieller, namely that one is interested in increments in wear within the portion of tooth removed, rather than in the portion remaining, although this latter part is of course the only piece of the tooth which can be measured. This problem may be approached in the following manner (Figure 66)

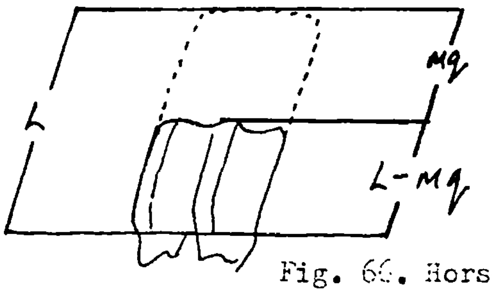


Fig. 66. Horse tooth wear quantum search

Let q = the quantum sought

L = the original tooth length

mq = the portion of the tooth worn away over m years prior to the death of the horse

Then $L - mq$ is the measurement made, and on the assumption that this is some rational multiple of q we search this measurement for the quantum. In effect, we assume that $L = kq$, a simple multiple of q.

But suppose $L = nq + r$, where r is a non-integer: testing $L - mq$ for the quantum will fail, since

$$L - mq = (nq + r) - mq$$

$$= (n - m)q + r, \text{ which cannot be quantal.}$$

If we add small amounts to $L - mq$ and test the result of each for quantatality, we hope eventually to add $q - r$.

Then

$$(L - mq) + q - r = (nq + r - mq) + q - r$$

$$= (n - m + 1)q, \text{ which must be quantal.}$$

Thus a grid search approach was used, adding small fixed amounts to the measurement of each tooth in a data set and testing the result for quantality. This could be compared with the result of using no such addition but searching the data themselves. However, Dr. Fieller found no significant alteration in the results to be achieved by this approach, and the procedure was therefore abandoned.

However, even with the effects of rounding and measurement shift overcome, one still has to assess the significance of any peaks remaining on the Cosine Quantogram, bearing in mind that even one single peak could still have arisen by chance. Kendall's method was to make repeated analyses of a set of statistically similar data whose parameters varied stochastically. The values attained in each simulation could then be drawn on the quantogram of the true data, and the number of times any one peak was equalled or exceeded by the simulated data used in an assessment of the significance of that peak. The values of the simulated data runs were shown as short horizontal lines on the top left of each Cosine Quantogram.

The application of the method outlined above to horse teeth data from Devensian sites was begun on a sample from Kent's Cavern, the largest single set and the largest quantity known from any British Pleistocene site. As a check, and for any additional information which might be derived, a second sample, my next largest, was also tested, that from Wookey Hole. Quite apart from the rapid tail off in sample size of teeth from other sites, it was decided to limit examination to these two groups, as the method requires considerable computer time and the actual quantogramm construction tends to monopolise the graphics facilities. Analysis for each set considered upper premolar 2, molar 1, 2 and 3. Since upper premolar 3 and 4 could not be satisfactorily separated, it was decided to include those from Kent's Cavern as a group which should fail to display a quantum, as a check, since the difference in their initial lengths should obliterate any quantum produced in the wear of each when considered together. For all teeth, left and right specimens were considered separately, but upper molar 1 from Kent's Cavern was also examined in a pooled sample of left and right elements, again in the expectation that any quantum would thus be blurred. The investigation was continued on the set of upper tooth measurements from Wookey Hole Hyaena Den.

The results of this analysis are displayed in Figures 41-59. On the left of each figure is a histogram of the tooth crown heights, on the right the Cosine Quantogram. These figures were produced directly by the Sheffield computer using the graphics terminal facilities. The curve in black shows the peaks with 1/q in the horizontal axis plotted against Phi(r) in the vertical axis. The arrows which are in red (except in the case of Figure 59 where they are in green as a result of pen failure on the graph plotter) indicate the highest peaks in numerical order. The green horizontal bars in the top left hand corner of each quantogram are the levels attained by the highest peak in each simulated run on statistically similar data. A quick visual impression of the significance of each peak on the black curve may be obtained by seeing what proportion of the simulated peaks are exceeded by it. If a peak is higher than the majority of simulated peaks then it is likely to be significant. At the bottom of the diagram the various peaks attained by the black curve are listed, along with their altitudes, and a significance level at which the null hypothesis of no quantum may be rejected is given for the highest peak.

For convenience, the first quantum estimated for each tooth is abstracted and displayed in Table 33, which gives tooth, quantum, altitude, probability and sample size. In view of the long timescale of accumulation and the possible blurring of periodicity, it was decided to accept a 0.1 limit for hypothesis rejection, to avoid the possibility of not accepting evidence of periodicity when present but distorted. Thus any probability falling below 0.1 is taken to indicate a quantum in tooth wear, and the appropriate teeth marked accordingly in Table 33. Nine out of sixteen samples indicate periodicity in wear, a proportion which in Dr. Fieller's opinion suggests that a genuine quantum is being observed.

It was pointed out above that the demonstration of periodicity in wear was the subject of interest, rather than the estimation of the amount of annual wear itself. However, it is of some passing interest to see what the analysis suggests this wear to be. A number of the quanta produced vary between about 2.2 and 2.5 mm, whereas others vary between about 4.4 and 4.9 mm. These figures suggest that a quantum and either twice or half its value are being monitored. If the true figure is near to 2.5 then the original suggestion of around 3 mm per year may be supported.

It is not clear why the same tooth from different sides of the jaw should give different quanta and different probabilities of hypothesis rejection, particularly when sample sizes are so similar as in the case of upper molar 1 from Kent's Cavern. It is a reasonable assumption that the same overall population of horses is represented by each dental element: to assume otherwise would involve a very complicated explanation. It is possible that assymetry in wear produces such effects, but I simply have no data on this matter. The problem is clearly a suitable subject for further and more detailed investigation.

The horse tooth data may be considered to offer considerable support for the suggestion that these animals were present seasonally in Devensian Britain. The nature of the data would seem to render any expectation of more concrete proof, at higher levels of significance, unreasonable. Seasonal presence of horse clearly has important implications for the migration of other members of the animal community, man included.

5.10 The Rhinoceros

(i) Steppe Rhinoceros

Ipwichian deposits have produced relatively scanty remains of steppe rhinoceros (Tables 7, 23a, 23c, 23d and 23e). Only the open air site of Barrington (Fisher 1879; Hughes 1911; Gibbard and Stuart 1975) and the trap site of Joint mitnor (Sutcliffe 1960) have more than a handful or remains. The classic "hyaena den" of Tornewton Cave had such fragmentary material in the deposits assigned to the Ipswichian that Sutcliffe and Zeuner (1962: 134) listed only "a few specimens" under steppe rhinoceros, and the amount recovered from the deposits of Kirkdale Cave (Buckland 1822, 1823; Boylan 1972) was very similar. In fact, the low number of rhinoceros remains in Ipswichian sites of hyaena activity, together with their highly fragmentary nature, is soon apparent during examination of the available material, and parallels the evidence for other herbivores of the period, the reasons for which have been discussed above in section 5.2 (p106).

(ii) Woolly Rhinoceros

After the hyaena, and in conjunction with the horse, the woolly rhinoceros is one of the most common species found in British cave deposits of the last glaciation (Tables 18 and 23a). Every Devensian deposit which has hyaenas has also produced remains of this species, and in most instances the rhinoceros bones show evidence of considerable gnawing. Most of these specimens exhibit features in full agreement with the list of characteristics given by Sutcliffe (1970) for modern hyaena-damaged bones, as summarised in Chapter 4.1.1 and discussed further at the beginning of this chapter (section 5.2.1), and it is clear that the hyaena was an active agent in their state of preservation. Some typical examples of this damage are shown in Figure 26.

It is clear from the numbers of teeth listed in Tables 18 and 23a that portions of rhinoceros head were being carried into the caves. The head, together with the larger bones, would have been least touched by the other predators, lion included, and suitable only for a hyaena.

Although rhinoceros remains are abundant in Devensian deposits, and point clearly to the scavenging ability of the hyaenas, it must be emphasised that the condition of the specimens stands in marked contrast to those from Ipswichian sites. They are much less gnawed and damaged and much more complete, suggesting that while scavenging was important to Devensian hyaenas there was considerably less pressure upon them than acted on those of the Ipswichian, and that there was less need for them to consume virtually every scrap.

Since hyaenas are only likely to have been able to kill young rhinoceros, those incorporated in the deposits must come mainly from either natural mortality or the kills of other predators. Determining which predators presents a similar problem to that discussed for horse. Two avenues may be explored to resolve the issue, on the basis of limb bone evidence and that afforded by teeth.

Figures 60-63 show distributions of woolly rhinoceros limb shaft measurements. Since ungulate limbs tend to thicken with age, degree of thickness will afford some measure of both age at death and size, although it will not reveal whether large individuals were simply mature or very much older. Clearly, such measurements will also include effects of any sexual size difference. The data for humerus and femur shaft widths, in particular that for Pin Hole and Kent's Cavern, shows a tendency to bi-modality, and suggests two principal explanations. Firstly, it may point to selection by sex, such that the larger specimens, which are actually more common, represent old and perhaps solitary males, a target for lion and perhaps human predation. Secondly, it may point to two age ranges in the general population, with a group of large individuals representing natural mortalities plus a group of smaller ones representing animals taken by a predator, again perhaps lion or man. Since a number of the specimens in the smaller size group from Pin Hole were probably immature, the second explanation is preferred here. Thus we may be able to distinguish two sources of hyaena scavenging, while not being able to pinpoint the predator responsible for one of them.

Turning to dental evidence, Table 18 reveals that while rhinoceros teeth are well represented, they are by no means as common as horse teeth in Devensian deposits. For that reason, it is impracticable to adopt the same method of gauging age at death as was used for horse. Instead, the best sample, that from Kent's Cavern, will first be considered.

From Kent's Cavern, the distribution of upper third molar wear categories was recorded as shown in Table 61. While it is difficult to assign clear ages to these dental wear classes, it is likely that the last two categories in Table 61 would represent animals of at least middle age. Although there is no evident bimodality in the dental evidence as presented, the data are not inconsistent with the second interpretation given above to limb bone shaft thicknesses, and could be taken to support it.

Among the rhinoceros teeth from Kent's Cavern, 89 deciduous specimens were recorded. These could certainly have come from animals killed by hyaenas, particularly since a number were unworn and therefore from very young calves. It is worth emphasising the disparity between milk teeth and other juvenile body parts recovered at this site, as at others, which serves to indicate the extent to which young specimens may have been either completely consumed or simply not brought back (perhaps due in the latter event to consumption at the site of the kill). At the French site of Camiac, the material from which I was kindly allowed to examine at Bordeaux University by M. Lenoir, the excavator, only adult rhinoceros seem to have been deposited. The open-air context of this latter site, together with the number of flint implements found, suggests a site of human hunting where hyaenas later scavenged. The lack of juveniles at Camiac may suggest that young rhinoceros in Kent's Cavern and other British sites were not killed by man, who may have preferred to invest his labour in killing larger specimens. *Lion, hyaena and wolf* may therefore be offered as candidates for the role.

Turning briefly to other sites, the material from Coygan gives the impression of representing young and old rhinoceros, with few falling in between, as does the material from Pin Hole, Wookey Hole and King Arthur's Cave. These sites make up the only samples of adequate size, and of these only Kent's Cavern provides enough teeth of any one type for analysis. Thus the results should not be considered to be as reliable as those for horse, for example, although the amount of rhinoceros material in Devensian sites serves as some indication of the amount of scavengable meat available to a hyaena.

5.11 The Reindeer

The distribution of reindeer skeletal elements in various Devensian deposits is displayed in Tables 22, 23a, 23c, 23d and 23e. Although present in virtually every deposit, the remains of reindeer are often second in abundance to those of horse and woolly rhinoceros. Excluding Sandford Hill, where the reindeer remains appear to have resulted from natural trapping (section 3.3(i), p 51), the major exceptions to this are the sites of Pin Hole and Tornewton Reindeer Stratum. It is, however, dangerous to consider sample numbers alone as indicative of relative presence, particularly in the case of animals so different in robusticity as reindeer and rhinoceros, and it is possible that differential destruction of smaller, more easily consumed bones, may account for some features of this relative abundance. This point has been discussed in Section 5.2 of this chapter.

Most of the reindeer bones seen were too fragmentary to permit measurement, and the numbers of specimens suitable for such treatment insufficient for any estimation of sex ratio. Antler, since it is borne by both sexes, can be used in the determination of sex (Figure 67), but as discussed in Chapter 4.2.3 (p 96) the male and female growth cycles are out of phase. Any interpretation of sex ratios of reindeer in the deposit must take this into account, since females bear antler during the winter while the males do not. Unshed female antler would then point to winter occupation but not necessarily to selective predation on females, for instance, although it is possible that the males and females may have been separated during the winter.

In Chapter 4.3.7 (p 9 it was argued that the wolf may have concentrated on reindeer, being rather less able to exploit horse fully. As discussed, there is no modern evidence to suggest that wolves would have preyed on the two sexes differentially, at least averaged out over the year and considered over time. There is also no reason to assume that hyaenas would find one sex more vulnerable than the other, and the lion would have been unlikely to do so either, although the leopard may have found females a little easier to subdue. The young, sick and old would have formed a selected component for all predators. Overall, therefore, reindeer sexual distribution in a deposit should reflect availability near the site rather then selection.

Table 22 shows that in the case of most deposits other than Pin Hole and Tornewton Reindeer Stratum the largest component of sexable antler is of males and derives from cast specimens. Casting takes place at the beginning of November for males, following the October rut, and therefore points to an autumn presence at the sites. Significantly, this is the time of the year when the males are likely to be most vulnerable, following the exertions of the rut and consequent loss of condition. The compact adult fragments listed in Table 22, which would seem from their size to come from males, together with the occasional specimen of uncast compact male antler, would also point to a time close to, if not actually during, the rut.

Specimens of cast female antler listed in Table 22 point to reindeer presence in April and May. This evidence, together with that from cast male antler, could be held to support a theory of winter occupation of Britain, but that is unlikely to be correct. Winter presence would lead one to expect evidence of uncast female and juvenile antlers, since these are carried over winter and should occur among prey remains. Uncast female antler is in fact difficult to separate from uncast juvenile male antler, but the number of specimens in Table 22 which can be ascribed to either is small. There is no reason to assume that uncast but compact female or juvenile antler would be less preserved in the deposits, which argues that their small sample sizes are a realistic representation of true deposited proportions. The small samples of uncast specimens, together with the relatively few specimens of cast adult male antler, may represent no more than occasional attempts at overwintering in Britain. The evidence of modern reindeer movement, described in Chapter 4.2.3 (p96), clearly points to the possibility of such attempts, and the specimens recorded, after all, represent the animals which died in that attempt.

More liable to destruction than fully-formed antler, either in the deposits or by the teeth of a predator, would be the uncompacted summer antler of both males and females. Still encased in velvet, and nourished by a copious blood supply, this antler may have made an attractive snack for a hyaena able to digest the bone, and a good case can be argued for differential destruction of summer occupation evidence in this way. Thus the best preserved material is likely to be that from autumn and spring, with the unshed juvenile and female antler having been deposited elsewhere on the migration route. The interpretation of this preservation therefore requires some allowance to be made for the complexity of past reindeer activity.

As discussed at the beginning of this section, the precise predation pattern on reindeer at any one site should reflect local availability rather than predatory selection. The effects of scavenging would also reflect this availability, although destruction of young specimens remains a major problem for interpretation. It is therefore unlikely that reindeer remains could give much information on agents of primary predation. Sturdy (1972: 92) has suggested that human predation on reindeer in Germany may have concentrated on males, and if this were also true in Britain then remains scavenged from human kill sites could obviously reflect this pattern to some extent. However, the apparently low density of human occupation in Britain during this time argues for little effect from such activity.

Some idea of age range in adults and juveniles may be gained from tooth wear and bone fusion, although I am extremely reluctant to attempt any quantification of this kind of data in view of the fragility of reindeer remains and the bone consumption abilities of the larger predators. As Table 22 shows, only Pin Hole has provided any quantity of deciduous teeth, in addition to which the site has also produced a number of unfused limb bones. The Kent's Cavern sample also contains unfused material, although only one isolated deciduous tooth was seen, and most of the sites had some proportion of immature skeletal parts. Accepting that the very young were taken, these data point to successful predation on the less experienced animals, since non-fusion may indicate an age up to five years depending on the body part, but scarcely offers any great insight into predatory patterns. In the older age groups, wear on dentitions suggests a range of ages being taken, but again is difficult to interpret at face value. Of 46 reindeer mandibles seen from Kent's Cavern, for instance, the age distributions were as shown in Table 62.

The lack of unworn adult mandibles shown in Table 62 may simply be an artefact of deposition, or more probably, refers to reindeer absence from the area at that stage in their dental wear sequence. This is supported by the observation that of 210 isolated adult teeth from the site, only around 20 were unworn.

5.12 The Bison

Bison remains are recorded from almost every site where hyaena-accumulated bone has been found (Tables 11, 23, 23a, 23c, 23d and 23e), but in most of these cases the remains are extremely fragmentary. In line with the expectations of fragmentation put forward in the last chapter, the bison bones are most broken up in deposits of Ipswichian age, but even in Devensian sites whole bones are uncommon. Fortunately, from the point of view of size estimation, five sites have produced bison remains which are largely unbroken, at least in certain skeletal elements. From the Ipswichian period, the sites of Joint Mitnor (Sutcliffe 1960) and Barrington (Gibbard and Stuart 1975) provide evidence from a fissure trap and a river gravel context respectively, both with bison remains unaltered by hyaena action. From the Devensian period, the gravel pit site of Willments Pit, Isleworth (Coope and Angus 1975), the cave site of Banwell (Sutcliffe 1955) and the trap deposit of Windy Knoll (Dawkins 1875) again present assemblages of bison remains unaltered by hyaena destruction.

Since bison show considerable sexual dimorphism, care must be exercised in any attempt to discern size changes. Fortunately the most robust bones, the metapodia, are also among the best indicators of sexual and general size differences, and these bones are particularly common in the sites mentioned above. Figures 64 and 65 show scatters of total length against distal thickness in bison metapodia from these and other sites, and reveal a number of features of interest. Firstly, on the basis of Willments material it would seem that the interglacial bison were generally larger than those of the last glaciation. Secondly, however, it is also clear that the Devensian bison exhibited a greater range of size variation, as evidenced by the metapodia from Kent's Cavern, Windy Knoll and Banwell. Thirdly, in view of the lack of grouping within the specimens from the three non-hyaena sites, it would seem that metacarpals offer a better indication of sexual dimorphism in this species than do metatarsals.

In a recent paper, Rackham (1978) has discussed the possibility of changing large vertebrate faunal communities during the course of the Devensian, including a lessened presence of bison following the Upton Warren interstadial. He has also suggested (pers. comm.) that the size variation in Devensian bison may be related to the presence of more than one population during that period, and may in itself be a further clue to undetected sequencing in deposition. Clearly, the Kent's Cavern deposits in particular cover a considerable portion of the Devensian.

The Lincolnshire sites of Tattershall Castle and Tattershall Thorpe, discussed by Rackham and claimed by him to show evidence of changing faunal communities over time, have radiocarbon dates in the region of 43,000 and 35,000 respectively (Rackham 1978: 1). At the former site reindeer are well represented by cast bull antler, while bison are abundant and horse and woolly rhinoceros are present in small quantities. At the latter site, bison and reindeer are absent, while horse and woolly rhinoceros are more common, but the faunal list is dominated by mammoth. On the basis of these differences between the two deposits, Rackham makes two major suggestions. Firstly, that the reindeer and bison were present at Tattersahll Castle in winter and summer respectively, and were not part of a single faunal assemblage at the site, and secondly that the change between the two sites reflects a change to more continental conditions with time, reflected in an increase of grazing species.

The problems of interpreting reindeer antler have been discussed in the section on that species, and clearly the recovery of bull antler cannot be taken to imply a solely winter presence. Female antler was found, although Rackham gives no indications of seasonal interpretations,[1] and clearly the shed male specimens could simply mean delayed movement from the area in the relatively mild autumns of the Upton Warren interstadial. In any event, material from a gravel pit, recovered as this was during gravel sorting, is likely to show, in the main, the more robust specimens. Reindeer and bison presence together during the summer is at least as likely as an interpretation.

Rackham's second point, of changing faunal communities with time is an interesting suggestion, and certainly the complete absence of bison and reindeer from Tattershall Thorpe is difficult to explain on face value. However, it should be noted that the Thorpe sample is much smaller than that from the Castle site, and that its composition tends to suggest a sorting by size as a plausible explanation for species proportions. While Rackham is undoubtedly correct in pointing out that we should not assume a single Devensian faunal community, neither should we assume identical conditions of deposition and preservation at two sites. It is therefore possible that the apparent changes between the two deposits reflects no more than differences in either conditions, with mammoth being particularly vulnerable to whatever processes operated at the later site, or post depositional sorting of the bone fragments by size. Certainly the bison material from Pin Hole cave does not show any indication of a sudden drop in bison presence equating with an increase in either horse or woolly rhinoceros (Figures 8, 10 and 11), and the site is arguably close enough to Lincolnshire to reflect a major change in faunal composition of the kind argued for there by Rackham.

The relatively sparse finds of bison from hyaena deposits preclude any attempt at assessment of predation pattern. The present-day evidence of hyaena and wolf predation upon the young, sick and old balanced by lion predation on adults in better condition seems unlikely to be far from the truth, however. To what extent the pattern of predation would have changed from Ipswichian to Devensian must remain unresolved, although it is probable that the lion may have taken less bison during the latter period, in view of the difficulties of concealment. With this predation load removed, it is conceivable that the bison may have increased their numbers somewhat, and that the subsequent competition for fodder may have been a factor in the apparent size decrease to which at least a part of the population was subject during the last glaciation. There may be a slight hint in Table 23a that bison were more available for scavenging during the Ipswichian in view of the higher proportion of their remains at Kirkdale.

The implications of these size variations for Upper Pleistocene bison evolution are not clear. Whether the two apparent size groups present in Britain during the Devensian represent two species or two sizes of the same species at two different times is unclear. Certainly the Willments Pit material, which has a radiocarbon date of 43,140 B.P. on associated material, may pre-date that from the other Devensian sites, but this is in no way certain. Ecologically, two species would seem unlikely and a size change response to harsh conditions is more probable, but the material recorded here was not examined with such problems in mind and no further resolution is therefore possible.

5.13 The Giant Deer

Most Ipswichian and Devensian sites have produced evidence of giant deer, as shown in Tables 8, 19, 23a, 23c, 23d and 23e, but the number of specimens is never large and the proportion of total specimens variable. The largest sample comes from Kent's Cavern, but since this is the largest of any British Upper Pleistocene faunal assemblage I am not inclined to attach any special significance to this fact.

Table 19 shows the specimens of giant deer preserved from the site of Kent's Cavern and housed in Torquay Museum. Cast antler suggests a spring presence of males in the vicinity, but cannot be more precise in the absence of knowledge about the shedding sequence in this species. Cast antler is known from a number of the Devensian sites, including Coygan, King Arthur's cave, and Wookey Hole. All pieces seen show signs of having been gnawed.

The most common giant deer specimens seen are teeth, usually isolated but occasionally in the jaw. At times other bones have been found, for instance astragali from Kirkdale in the Sedgwick Museum and a complete right metacarpal from Coygan in Cardiff Museum, but one has then to beware of misidentifications (the Coygan specimen was catalogued as <u>Bos primigenius</u>) and separation is not always easy.

In the case of the giant deer from Kent's Cavern, the lower M3 showed a range of wear stages from unworn through to very worn. Two mandibles with deciduous teeth still present point to young, although probably quite large, individuals, and most of the mandibles show clear gnawing traces. In Chapter 4.2.3 (p [illegible]) the likely vulnerability of giant deer was discussed, and it is clear that the Kent's sample may preserve the effect of a number of killing strategies: the young vulnerable to most predators, the middle aged females and males vulnerable through size and antler unwieldiness respectively, and the old. The latter category in particular may have been obtained from sources other than direct hunting.

Specimens from Ipswichian sites are too few to permit any assessment of the difference between exploitation of giant deer in the two periods. This is particularly unfortunate since this species is one of the few to have been preyed upon in both phases of the Upper Pleistocene of this country.

5.14 Other Cervids

Included in this category for the purposes of this study are red deer, giant red deer and fallow deer. The latter is found only in Ipswichian deposits, the giant red deer only in Devensian deposits, and the red deer in both. Only in the Ipswichian trap deposits of Joint Mitnor, Hoe Grange and Milton Hill do any of them occur in any quantity, and in sites of hyaena activity the sparse remains of all permit little evaluation of predation patterns for either period. In Devensian sites, there is considerable difficulty in distingusishing between remains of red deer, which is often large, and giant red deer, although the latter is only clearly present at Kent's Cavern and Tornewton Cave. Work in hand may clarify this matter (A. Lister pers. comm.), but since distinction is far from easy and criteria for doing so are still being established, I have adopted a similar stance to that taken on bear and avoided classifications beyond the most elementary. The material seen for these cervids is listed in Tables 9, 10, 21, 23a, 23c, 23d and 23e, with Devensian red and giant red deer remains shown together in the latter five tables.

There is little to be said regarding these species at present. Clearly, all would have presented attractive predation targets in varying degree, particularly the fallow deer, which on the evidence of Joint Mitnor and Hoe Grange was similar in size to modern specimens. The abundance of fallow deer in Ipswichian trap sites suggests that it may have been present in some numbers, and presumably found Zone II conditions to its liking.

The presence of red deer in Devensian deposits may reinforce the suggestion that much ungulate activity took place in Britain during the milder interstadial periods. Since size in modern populations seems closely dependent on environmental conditions, the size attained by Upper Pleistocene red deer points to more than adequate food supplies. It is possible that these animals mark unrecorded variation in faunal assemblage, and that they were not a constant feature of the total ungulate population. Any view based on this suggestion of faunal change should, however, bear in mind that red deer are an adaptable and competitive species. Modern-day judgement of red deer qualities tends to be based on sporting attributes, and insufficient allowance may thus be made for the deer's abilities to survive on poorer fodder.

The specimens of cast red deer antlers seen at a number of Devensian sites are of some interest (Table 21). Mature males cast in March, younger ones towards the end of April, pointing to spring presence. One could argue that this would be too early for the summer occupancy suggested on the basis of reindeer antler, but if the red deer were somewhat more prevalent during interstadial phases then the period March-April of each year may well have seen early immigrants. Of course some of the antler may come from giant red deer, for which the shedding sequence is unknown, but it may be quite reasonable to assume that this sequence was similar to that of red deer.

5.15 The Elephant and Hippopotamus

Elephant and hippopotamus are dealt with together not because of any particular similarities in their behaviour but because the remains of each are relatively scarce in the deposits. Both species present similar problems of size to a predator, and offer little in the way of insight into predation patterns beyond that discernible from the remains of other species.

Hippopotamus remains recorded from Ipswichian sites of hyaena activity in this study are entirely of teeth, and few in number (Table 23a). Adults are immune to predation, particularly when in the water, and exhibit determined defence of offspring. At Tornewton Cave, the Hyaena Stratum remains found consist of one tusk fragment and five deciduous teeth (Sutcliffe and Zeuner 1962 and personal observation). At Mother Grundy's Parlour (Dawkins and Mello 1879: 730), the remains of three individuals were found, all sub-adult. At Kirkdale, where again only a few individual teeth were found, Buckland (1823) makes no mention of the age of the animals, but his Plate 7 shows two teeth of young hippos together with a relatively worn premolar.

Sparse though it is, the available evidence suggests mainly juvenile hippopotamuses. In view of the apparent absence of man from Ipswichian Zone II, lion may have been the primary predator, the remains subsequently scavenged by hyaenas and wolves.

Elephant remains are similarly confined almost entirely to teeth and tusk fragments as shown in Tables 12, 20, 23a, 23c, 23d and 23e. The numbers of specimens from some sites run into double figures, particularly in the case of Devensian mammoths from Kent's Cavern and Wookey Hole, and in theory some idea of age range at death should be possible in view of the replacement sequence of elephant teeth. Two factors conspire, however, to prevent this reconstruction. Firstly, the difficulty of identifying individual teeth, and of thus interpreting their place in the eruption sequence, and secondly the extremely fragile nature of fossil elephant teeth. Inadequate curation over the years since recovery has reduced many specimens from most sites to a series of platelets, from which little other than species may be deduced.

One feature of interest, shown in Table 20 particularly, is the number of juvenile specimens represented. It is conceivable that robusticity may have something to do with this, with the larger teeth being more easily broken in handling owing to their considerable weight, but the bias towards juveniles may still be significant. As in the case of hippopotamus, this may therefore reflect predatory selection of the young, again by lion, although in the case of mammoth man may also have played some considerable part in the killing. For him, the thick hide and subcutaneous fat may have been an important resource, to say nothing of the veritable mountain of food which the carcase of an adult would present. To see the hyaena scavenging kills of mammoth calves from lions and kills of adults from man may be close to the truth, in which case one would expect there to have been rather more juvenile elephants presented in Ipswichian deposits, in view of human absence. Once again, however, the fragmentary nature of the interglacial material prevents such an examination.

5.16 Faunal Change, Sea Level and Isolation

In Chapter 3 I pointed out that the appearance of horse, woolly rhinoceros and mammoth in deposits assignable to Ipswichian III/IV suggests either early movement from the Continent prior to the full onset of glacial conditions or movement southwards from an interglacial refuge area in Scotland. Stuart (1976: 242) has suggested the latter alternative as more likely, a view with which I am inclined to agree although certain difficulties remain.

The Scottish refugium view is supported by the apparently late drop in sea level following oxygen-isotope stage 5e (Figure 4), which suggests isolation from the Continent until into the Devensian period. Also, the later Ipswichian deposits containing mammoth, horse and even woolly rhinoceros have neither reindeer nor, perhaps more significantly, hyaena. Had the late Ipswichian animals emigrated from the Continent, one would at least expect hyaena to have accompanied them, although reindeer may not have been present in areas from which such movements might take place. The general lack of bone cave deposits assignable to other than Ipswichian Zone II does, as discussed in Chapter 3, point to and support hyaena absence from Zones III and IV (Table 24).

The arguments against this view are that any species which spent Zone II in Scotland would itself have been accompanied by hyaenas, and would therefore have brought this predator back into Britain in Zones III and IV when they moved south. None of these three ungulates, however, are likely to have been as easy for a hyaena to take as such species as fallow deer, reindeer and Devensian horse which do appear in cave deposits. The pre-Devensian horses were, as discussed, probably considerably larger than those of the last glaciation, and any hyaenas which moved towards the north of the country during Zone II may not have found conditions particularly easy or more to their advantage.

Other ungulate species would also have been present in Scotland, but there is no information on the vegetation there at that time. Although arguably less dense than that further south, the Zone II vegetation of the north may still have been sufficient to impede the cursorial hunting habits of the hyaena, and together with the possible predominance there of larger ungulates may have curtailed hyaena activity and so prevented the establishment of a population able to re-colonise England in Zone III.

Again, resolution of this problem is difficult. The strongest argument in favour of the view that hyaenas became locally extinct following Ipswichian Zone II remains, however: the general lack of cave deposits assignable to other than Zone II. This should prove testable, both by further excavations and by work in hand, such as that at Bacon Hole (Stringer 1975), and by possible extentions to the radiocarbon timescale discussed briefly in Chapter 3. Should debated sites which Sutcliffe (1976) argues are pre-Ipswichian prove to be so then the force of the argument presented here will be diminished, although a considerable hiatus between presently known Ipswichian cave deposits and those of the Devensian might still be implied, particularly by the hyaena data. The considerable differences in dental proportions between the hyaena population of the two periods, and the absence of intermediate groups, point to a real separation.

CHAPTER 6. Discussion and Conclusions

This study has attempted, primarily, to integrate fossil material and modern ethological data in an assessment of predator-prey interactions during the British Upper Pleistocene. Much of the material has lain unexamined in museums for decades, and but for the stimulus offered by modern ethological results would no doubt have continued to do so. Poorly recorded though much of this material may be, it remains suitable for examinations of the kind undertaken here, where the aim is sufficiently broad to exploit the chronological span of the evidence. Indeed, it would seem advisable to frame questions related to the nature of the material, rather than to dismiss it as useless or expect it to support more detailed investigation than it can bear. With this latter caveat in mind, I have avoided quantifications which give no more than spurious impressions of accuracy, a common feature in archaeozoological reports where number estimations are involved, for instance, as discussed in Chapter 2.

It will be convenient and useful to discuss conclusions in two ways, firstly with specific reference to Upper Pleistocene Britain and then more generally to highlight aspects of the study which are of wider relevance.

6.1 Upper Pleistocene Britain

1. Perhaps contrary to expectations, it is likely that conditions during the Ipswichian were less favourable to the hyaena than those of the Devensian. The evidence of age at death derived from tooth wear categories (Chapter 5.4(iv) (p 141) strongly supports

this suggestion, with Devensian hyaenas tending to live longer than their Ipswichian counterparts, and may even explain the confinement of hyaenas to Zone II of the interglacial, since with such a high death rate among young adults the population may have been incapable of sustaining itself.

2. Most of the major cave assemblages of bone in Upper Pleistocene Britain appear to have accumulated through the activities of hyaenas.

The extent of damage to the bones supports and amplifies the conclusions derived from tooth wear in Upper Pleistocene hyaenas. The greater extent of damage seen in Ipswichian specimens, together with the variation in body part among identified bones between the two periods, in itself argues that interglacial hyaenas found life more arduous than their Devensian descendants.

3. Pleistocene hyaenas were generally larger than modern-day representatives of the species and showed some interesting differences in dental and bodily proportions (Chapter 5.4, pp 13[illegible] - 1[illegible]). These differences may have been related to prey defence tactics and to problems of consumption for hyaenas faced with prey adapted to extreme cold. The variations in dental proportions seen between hyaenas of Ipswichian and Devensian times may owe much to this latter factor, as suggested by Kurtén (1969a). It is interesting, however, and should be emphasised, that the vastly greater incidence of bone-gnawing in Ipswichian deposits would tend to reinforce my interpretation of hyaena tooth wear in relation to age at death, since if wear were largely dependent on chewing then the Ipswichian animals should have

the more worn teeth.

4. While scanty by comparison with the remains of hyaena, the available evidence suggests that both lion and wolf were smaller during the Devensian than in the Ipswichian, although this change is less clear in the case of the wolf (Chapter 5.5, 5.6, pp145 -151). These two species would seem to have fared better during the interglacial conditions than did the hyaena. It is probable that the lion was primarily adapted to hunting large prey, perhaps taken cooperatively, and it is possible that the great size attained by these cats was disadvantageous during colder periods with less vegetational cover. However, since the deep-sea core evidence now reveals the true extent of Pleistocene glacial cycles, this interpretation of relative adaptiveness may require some amendment (see also below, point 6).

The wolf is likely to have always existed in smaller social groups than the hyaena, and to have been unable to raise the numbers essential for consistent success in horse hunting. It may also have struck a better balance of numbers in relation to prey and vegetational conditions than did the hyaena during the Ipswichian.

5. The absence of horse from Zone II of the Ipswichian is seen to be a real feature and not an artefact of poor excavation (Chapter 3.2(i) p 37). The horseless-hippopotamus stratum seen at so many Ipswichian sites resulted from the presence of hyaenas being confined to Zone II, since only then were these predators around to act as the necessary agents of accumulation.

6. Only at Coygan does the evidence point to direct hyaena predation on horse (Chapter 5.9(ii) (p158). At all other sites with sufficient evidence for examination there is a tendency to sexual parity in horse remains. Since wolf is unlikely to have been a major horse predator, the most probable sources of horse carcases at these other sites are lion kills, human kills or scavenging from natural horse deaths. The horse remains from Paviland Cave suggest that man may have tended to take younger horses, thereby narrowing the choice of agencies at remaining sites to lion or natural mortality. It is difficult to clarify this further, but one should guard against the assumption that the choice is <u>either</u> lion or normal mortality. Clearly any animal not killed by a predator will die eventually, but in the presence of predators it is less likely to enjoy an old age of increasing infirmity. Since it is apparent that Serengeti hyaenas obtain a good living exploiting lion kills, that lions kill whatever zebra are available, and that in a Serengeti-type ecosystem those available will tend to be older than those in a Ngorongoro-type one, then inevitably the age range of zebra scavenged from lions on the plain will tend to resemble normal mortality among old animals. The difficulty in a palaeontological reconstruction is that differential destruction will tend to remove the other large component of prey, the young.

If horse remains at Devensian sites were in large part derived from lion kills, then this predator may have been the major killing agent of the period, justifying the view that its importance is inversely related to its frequency in the deposits.

7. Pleistocene horses do indeed become smaller over time, and while horse remains do not clarify the position of sites such as Crayford and Ilford within the British sequence they do suggest that a major size decrease occurred some time prior to the Devensian (Chapter 5.9(i) (p154).

8. Seasonal presence during the Devensian is suggested by three lines of evidence. Firstly, the remains of female reindeer antler indicate a summer and spring occupation, and the adult specimens may point to autumn movements and to occasional overwintering in Britain more than to consistent winter occupation (Chapter 5.11 (p181)). Secondly, the evidence from horse teeth strongly suggests a periodicity in dental wear, a feature best explained by seasonal appearance (Chapter 5.9(iv) (p166)). The evidence of climate and conditions derived from geomorphological and botanical studies, as outlined in Chapter 3.3(ii) (p 53), indicates that a summer movement into Britain would have been most likely. Thirdly, the number of bear remains found in deposits with copious hyaena debris suggests the winter absence of the latter species, permitting bears to den without interference (Chapter 5.8 (p152)). To what extent this interdigitating of occupational evidence differed during the Ipswichian is difficult to establish, since the hyaenas were clearly consuming more of the bones which lay in the caves: bear is less common in Ipswichian deposits, but that is only to be expected.

It is also worth emphasising, as I pointed out in Chapter 5.9(iv) (p168) when discussing the horse evidence, that the demonstration of significant peaks in tooth wear suggests a relatively short seasonal appearance in Britain, which is of general importance. If horses were present for a short time, this could be because they arrived late in the summer and moved early, but it could also point to the broader pattern of faunal movement. Absence of any portion of the ungulate population would have been important for the predators. Climatic inferences discussed in Chapter 3.3(ii) (p53) suggest cold winters, but it is difficult to know their duration and at what points in the year immigration would have been possible and emigration imperative.

9. The second aim of the study given in Chapter 1 (p1) was stated to be a correction of the misleading impression of human activity in Upper Pleistocene Britain. In the light of the evidence of bone-accumulation by modern and fossil hyaenas discussed in Chapter 4.1.1 (p) and Chapter 5.2 (p), it is clear that human activity in this area at that time has indeed been misinterpreted. That man was present in Britain at various stages during this period is undisputed, but much of the evidence taken to indicate his economic emphasis and development has come from material accumulated largely through the action of hyaenas. Such evidence cannot be used in an analysis of the economic exploitation patterns of Upper Palaeolithic man.

However, human presence in Britain during the Upper Pleistocene may have reached its apex during the Later Upper Palaeolithic, by which time the number of other major predators may have been substantially reduced. Unequivocal evidence of this shift in relative presence of human and non- human predators is nevertheless difficult to establish in the face of poorly stratified material, and points to the shortcomings of the data once greater resolution is attempted. A number of major hyaena accumulations may be dated to before the Devensian maximum, on the basis of archaeological, palynological, sedimentological and absolute chronological information, as discussed in Chapter 3.3(i) (p 42), but at Pin Hole Cave, Creswell, hyaena remains are recorded from very high in the deposits in levels also producing Later Upper Palaeolithic tools. Further excavation in good deposits is needed to clarify this matter. In view of the seasonality in horse, reindeer and hyaena appearance, it would be reasonable to assume that man was also a migrant visitor, since the winter vegetation would certainly not have supported him if the herbivores found it inadequate. Further evidence for man's seasonal presence comes from the paucity of artefacts themselves, which do not support interpretations of overwintering and the consequent engagement in maintenance activities of the kind implied by the vast quantities of lithic debris found in many South-West France sites where winter occupation is indicated.

10. Evidence for seasonality emphasises that events recorded in Britain were simply one part of the annual round of activities of the men and animals represented. This aspect of observation via the archaeological and palaeontological record has recently been pointed out by Gamble (1978) with particular reference to contemporaneous events in the Swabian Alb, and finds many parallels with the approach adopted by Sturdy (1972, 1975) and Bahn (1977). Gamble (1978: 182) emphasises the non-commitment of human groups to a single adaptive strategy, quoting Thomson (1939) whose classic study of seasonal variability in activity and artefact form seems to have taken so long

to permeate archaeological thought. In precisely the same manner, predator behaviour in terms of social cohesiveness, group size and concomitant hunting strategy is likely to have altered with season and prey availability. These animals have been shown to have considerable behavioural repertoires, with the flexibility to adapt to periodic variation in food supply.

Precisely where ungulates spending the Devensian summer in Britain would have moved to during the winter is difficult to say, but migration into the plains of the then uncovered areas of the North Sea and the Channel is likely, together with a certain amount of occupation of the Continent. (It will be of interest to see what seasonal indications are available from the Jersey site of La Cotte (McBurney and Callow 1971) when the faunal remains are eventually published.) These movements may have resulted in relatively closer bunching of ungulates in some areas as a result of coalescence from dispersed summer feeding grounds, and are likely to have produced a very different prey population from that of the summer. Prey deaths from natural causes may have increased at this time, and the need to hunt may have been reduced as a result of carrion availability. Looser predator social structures may therefore have been adopted, following the lessened need for large hunting group size and the numbers adequate to defend territory and kills. The extent of change in social behaviour will have varied considerably from area to area, however, and in some regions of the winter territory it is possible that increased predator density would have had the reverse effect, leading to tight social order and organised group hunting. While prediction of these events in specific detail is therefore probably not possible, it should be emphasised that consideration of such matters is not empty speculation but an attempt to apply the logical consequences of observed modern behaviour and deduced climatic variation to an interpretation of past events.

11. The use of large mammals as environmental indicators has now largely been abandoned. Nevertheless, the temptation to consider the range of species present in different periods as indicators of vegetation and climatic conditions is difficult to avoid. It is easy to produce a series of circular arguments in this area of study, however, such as the assumption that the presence of a number of species in a deposit points to their contemporaneity and therefore indicates no faunal succession, which in turn indicates no major shift in vegetation which in turn would support the view of no faunal change. These kind of arguments are even more seductive in the absence of much detailed stratigraphy.

The major shift to grazing species in the Devensian is clear enough: horse, mammoth, woolly rhinoceros and bison were all well suited to the available fodder, and reindeer will also consume a wider range of vegetation than they are at times given credit for. Within the Devensian, absence of species such as mammoth, woolly rhinoceros, hyaena and lion following the glacial maximum, or at least a drop in their numbers, has been suggested by Campbell (1977) and may well be substantially correct, although difficult to demonstrate clearly. Other shifts in faunal composition within the Devensian are even less clear. The presence of horse alone may have enabled the ruminant herbivores to make a fuller utilisation of the vegetation, and may well have ensured a diverse fauna existing on a relatively narrow range of plants. Rackham's suggestion for change to a more steppe-like fauna in Lincolnshire, with a marked absence of bison and increase in horse, woolly rhinoceros and mammoth over this time, is not well supported by the evidence from Creswell, and while he may be partially correct the evidence, as I pointed out, may owe more to taphonomic factors than to actual change in overall species presence, and is perhaps not well suited to test such suggestions.

6.2 Predator-prey Interactions in a Wider Context

As discussed in Chapter 1.2(b) (p 2), predators have only been considered in relation to man in studies of early hominids, where the recognition of ecological similarities between the two have resulted in suggestions of possible behavioural parallels. It is now possible to give an answer to the question posed by the third aim of the study set out in Chapter 1 (p 1), and to suggest that these ecological similarities do indeed give a measure of insight into the behaviour of later Pleistocene man but of a somewhat different nature to that afforded for early hominids. Whereas the Lower Pleistocene human groups may have aspects of their behavioural evolution explained by comparative studies of carnivores, it is likely that by the Upper Pleistocene the behavioural patterns and social interaction of man owed more to stimulus from within the developed human behavioural repertoire. That view need not in any way deny the important initial effect of predatory activity upon the evolution of that repertoire, but suggests that the admittedly complex but comparatively limited behavioural range of the predators offers little insight into human response by the time that Homo sapiens appeared. Instead, the predators of the Upper Pleistocene inform on man through their activities as his competitors. Man lived out this period in an environment of which large carnivores were an integral and prominent part, and for all his abilities and evolutionary development their presence must have impinged upon him.

Human groups shared with the large predators an interest in similar resources, and certainly made use of the same occupation sites at times. In periods of environmental stress they operated under similar constraints, having to move with the ungulate herds on their seasonal migrations, needing to maintain minimum food intake to combat the cold and having at times to tackle animals much larger than the individual group members. The extent of competition between man and these predators, and the nature of interactions, are matters for discussion not assumption, and are as relevant to an understanding of Pleistocene man as stone tool studies, cave sediment analysis or absolute dating. The proper study of mankind is not, never has been and cannot become a study simply of man alone. This is true for the present, when the mechanisms of human heredity would be little understood without, for example, the parallel study of Drosophila flies, and must be even more so for attempts to unravel the past, when man stood in closer contact with his immediate environment. Equally, it would be unwise to investigate Pleistocene palaeoecology without a consideration of the part played by man.

The relative consumption rates of the large predators are highly relevant to studies of human palaeoeconomy and subsistence. From Table 34a it may be seen that a single man and one individual from each of the large predator species would require between them approximately 70 prey animals of 100 kg live weight simply to supply food needs each year. Of this total, man would need just five animals. Any study which assumed a specific cull rate of the prey population in order to estimate human numbers but which failed to take this simple fact into account could overestimate the human population by fourteen times. The precise error would depend upon the number of predator species in competition for the resource, and on the numbers of animals involved, so that in the absence of figures for predator biomass it would not even be possible to apply the appropriate correction factor. Since, as Kruuk (1975) showed in the case of present day lion and hyaena numbers in the Ngorongoro Crater, predator proportions may fluctuate considerably, it is clear that attempts to model human population size on the basis of prey culling rates can be no more than guesses in the face of so many variables. This limitation applies equally to biomass estimates for any predator, which is why no such calculations have been attempted in this study.

Failure to consider predator competition is one criticism which can be levelled at the work of Sturdy (1972, 1975) on Late Pleistocene reindeer-based human economies in northern Europe. The activities of wolves alone could have done much to alter the killing rate which the reindeer suffered, and the estimations of human numbers would then require considerable revision.

Gamble (1979) also failed to take adequate account of predator activity in his study of south German Upper Pleistocene human activity, in this case with respect to the agency of deposit accumulation (Chapter 5.3(iv), p 133). Taken together, the studies of Sturdy and Gamble highlight a curious oversight on the part of people explicitly interested in examining man-animal relationships. While emphasising the need to consider more than just sequences of stone tools these works in fact concentrate on only two items in a triangular relationshiop, man and his prey, overlooking the interactions between man and predators and the predators and the prey.

Caveats to quantification not withstanding it may still be worth asking what the data presently available for the Pleistocene imply in terms of relative abundances of man and large predators. The evidence presented in this study for seasonal occupation of Devensian Britain amplifies that of Sturdy (1972, 1975) for northern Europe and Bahn (1977) and Speiss (1979) for South-West France. Migration may indeed have been a very general human behavioural phenomenon, and implies that even the densest of human occupation layers and site conglomerations may belie the true numbers involved at any one time. Looking even more widely, the apparently late movement of early man into the temperate zones (Isaac 1975a, 1975b) and the later movements into the the arctic areas (Campbell 1972; Klein 1971, 1975), together with the late movement into Australia (White and O'Connell 1979) and the New World (Klein 1975), also point to low human Pleistocene density. Little population pressure may have existed to cause search for new territories.

Maglio (1975) has pointed out that large predators also make a comparatively late movement into the temperate zones, and although chronological resolution at this period is relatively coarse, it is likely that man, lion, leopard, hyaena and wolf all appear at around the same time. The crucial point here, in the absence of knowledge about true relative densities, is that if all these species were present in roughly equal numbers, all perhaps at a low density, then any one of them, including man, was only one predator among many. At this early stage man may have been somewhat disadvantaged still in his ability to compete, and his behavioural repertoire may have continued to undergo selection as a result of pressure from this direction.

Studies of modern predator interactions, however, suggest that competition between man and the large carnivores is unlikely to have involved a "tooth and claw" struggle in relation to either resource emphasis or direct conflict. Large carnivores have evolved behavioural patterns which minimise such problems of coexistence and there is every reason to suppose that man would have done so also. By the Upper Pleistocene, if not considerably earlier, he is likely to have come to terms with the danger posed by these animals and to have developed techniques for both defence and, when necessary, offence. The example of the Nunamiut Eskimos' respect for the wolf discussed by Stephenson and Ahgook (1975) shows that in situations of real competition for resources man and predator can still coexist without animosity. Only when his domestic stock is attacked, or his leisure-time hunting threatened, does man seem impelled to react harshly to predators. Lower, Middle and perhaps even Upper Pleistocene hominids should possibly best be considered as low density predators making an adequate living from the share of the ungulate biomass available to them, unable to make greater inroads into the game than any of their competitors and not concerned to do so. To envisage man as a rapidly and constantly evolving species may involve an overestimation of his importance as a member of the Pleistocene fauna, a reaction perhaps to the acquisition of modern technology and the aura of superiority which it lends. Stripped of gadgetry and placed in a more "natural" setting man is in many ways simply another competent predator, provided that he has some equipment to make up for his physical deficiences. An over concern with that equipment, the stone tools, may play a large part in biasing our view of man, when in fact we are simply looking at the debris of the one Pleistocene predator which happened to make and discard implements. It is worth considering what the quantities of tools and waste flakes found at even the most prolific sites may mean in terms of annual discard over the total period of possible occupation, and acknowledging how misleading such accumulations may therefore be.

In Chapter 5.3(iii)(p 122) I discussed the apparent increase in human numbers in Britain following the Devensian maximum, and suggested that increasing ability to cope with harsh conditions might have something to so with this later influx. A broad view of the later Upper Pleistocene, however, may suggest a general increase in human numbers coinciding with a decrease in predator remains on a virtually world-wide scale. The relatively rapid movement of man through the American continent at or about this time may owe much to demographic pressures, and it is tempting to correlate this with the extinction of many of the large predators in the New World (Martin and

Wright 1967; Kurtén and Anderson 1980). I hesitate to point to cause and effect in this difficult area of study, but the decrease in large predators in both the Old and New World would have made a substantially greater proportion of the surplus ungulate biomass available to man than would otherwise have been the case, despite the parallel loss of ungulate species which occurred. It is worth briefly considering the phenomenon of Late Pleistocene predator extinctions area by area on a world-wide basis.

In post-glacial Europe, only the wolf continued to offer man serious competition for food on the hoof. By the Upper Pleistocene, man's ability to cope with the rigours of the climate was probably considerable, and the attainment of an Eskimo-like technology is quite likely. It is therefore difficult to point to increases in technological or intellectual abilities which would then explain either LUP expansion in Britain or the extinction of the predators. Rather, it may make better sense simply to suggest that a sudden increase in food supplies following the extinction of competitors provided a stimulus to further human movements as a result of increased numbers.

But such a view must take account of the predator extinctions and attempt to explain them, not simply accept their occurrence. Two major mechanisms for extinction may be put forward, direct human activity and "natural" causes, the latter implying no direct human involvement. Of the two, the latter would appear the most reasonable, because it may be in turn related to the ungulate extinctions of the time. A drop in prey species numbers would tend to produce a reaction among predatory species which could well explain the observed extinctions, whereas placing the burden of carnivore disappearance directly on man fails to account for ungulate losses. The first casualties of such changed circumstances would be the species most adapted to hunting the extinct ungulates and least able to alter their predatory techniques. In the face of such pressures, man and wolf could be predicted to stand the best chances of survival, since these two predators are clearly the ones with the social behaviour patterns best adapted to cushioning such blows. Of course, man's technology gives him a further advantage: it is conceivable that he may have been the prime mover in these ungulate extinctions, inflicting irrecoverable damage on both prey and predator populations in the process, but the advantages which the wolf has in dealing with such difficulties would remain. In fact explaining ungulate extinctions lies at the heart of the problem whatever mechanism is favoured, but an insistence on clear explanations of this phenomenon may defeat insight. If instead we simply accept that ungulates became extinct, then the drop in prey diversity and biomass is likely to have produced a parallel drop in predator diversity and biomass which we may think of as the output from an imperfectly observed system.

In America, the events of the Late Pleistocene are rather more complex. Although a number of predators including sabre-toothed cats, the American lion and the dire wolf became extinct at this time (Martin 1967; Martin and Wright 1967; Kurtén and Anderson 1980), man and wolf continued to be faced with competition from the puma and the jaguar at least. The great size of the American land mass may explain many features of this increased predator population complexity when compared with Europe, since the larger ecosystem may be expected to have a greater degree of elasticity. Niches for exploitation are therefore more likely in such circumstances, and a greater range of predators to be expected. Furthermore, we should not expect precisely similar events in the two areas so far discussed, or identical responses on the part of the fauna. Whether the same causes of extinction operated in both America and Europe is far from clear. The model proposed by Martin (1973; Mosiman and Martin 1975), whereby man decimated the American fauna within 1000 years of his arrival there at about 12,000 b.p., would certainly explain the demise of so many predators, but is perhaps a trifle extreme in its claims. Kurtén and Anderson (1980: 362) have recently discussed this view, and pointed to a number of difficulties: the model ignores natural predation, disease, weather and the hardships of implied rapid movement by the human groups. It also fails as an explanation if migration to America was earlier than the assumed date of 12,000 b.p., requires an extremely high annual growth rate among the human groups, and is supported by no positive evidence in the form of massive kill sites. Only mammoth and bison figure in known butchery sites to any extent.

In both Africa and Asia, the number of predators which exist to the present day remains high, particularly by comparison with Europe (Martin 1966; Schaller 1967; Guggisberg 1975; Sankhala 1978). In neither continent is the evidence for human presence during the Pleistocene very extensive, taking into account timespans for even the largest occupation levels, and it is possible that man was there in less density than elsewhere in the Old World. This seems particularly true of the Middle and Upper Pleistocene. As Isaac (1975a) has pointed out, however, prior to the Lower-Middle Pleistocene boundary at around 750,000 B.P. Africa and the tropics may well have been the main home of the hominids. It is conceivable that only at that time did pressure from competing predators act as a major factor in man's adaptive radiation to the temperate zones. The parallel movement of other predators (Maglio 1975) at this time may have resulted from similar pressures on them, bearing in mind the suggestion made above that any one predator could be seen as a small part of the carivore biomass with all the other species in competition with it. Continued competition from large predators, and the consequent reduction in food available, may have prevented human numbers from expanding greatly in Africa, even in the face of the great ungulate biomass available. Sustained pressures on African hominids by competitors may offer some insight into the apparently early appearances of modern man now being claimed for that continent (Rightmire 1979). It is possible that the apparently stable environment of Africa may have offered more challenges to a developing hominid than the more obviously rigorous setting of Pleistocene Europe, and that once more we are misled by the artefactual evidence into a false sense of the importance of certain areas and finds. It would be worthwhile to reconsider the Eurocentric view of later human evolution which often prevails, and to seek fresh insight from Africa.

The issue of Pleistocene faunal extinctions in Australia is one of considerable interest, but one on which I am unqualified to offer much in the way of comment. The majority of the species relevant to arguments of overkill versus natural mortality in this part of the world are large marsupials (Merrilees 1967) with which I have no familiarity. However, in a recent discussion on the problem of human involvement in megafaunal extermination there, Gillespie et al (1978) draw attention to the considerable overlap now established for radiocarbon dates of human presence and continued large marsupial existence. A point worth underlining from their study is that one of the large marsupial predators to continue in the presence of at least aboriginal man is the Tasmanian wolf, Thylacinus cf. cynocephalus, the last known specimen of which was recorded on film in the nineteen thirties. Although in no way related to the modern wolf, it is possible that the convergent evolutionary trends which operated to cause sufficient physical similarities with the wolf may also have acted on its behavioural abilities. It is therefore conceivable that the survival of this species resulted from similar factors to those favouring the wolf.

The views expressed above do not contradict the observation made by Pilbeam (1967) that it would be a mistake to tie man down to a particular exploitation strategy during the Pleistocene, since with his technological ability he could have extended his range of food choice beyond that dictated by his basic physical characteristics. Man's hunting choice would still have been governed by factors of availability, and if a number of predators were exploiting the same prey as him then some limits were imposed on his selection. To see man as able to exploit a change in circumstances which made more food available, or evolving as a result of pressures from his ecological competitors, does not mean that his abilities must be considered falsely curtailed by the scheme proposed above. The point to reiterate here is that man may have evolved as a result of pressures from competitors, but that for much of the time he in all probability existed quite comfortably with his own exploitation strategies, making an adequate living. It would be a great mistake to envisage man as a creature constantly striving to evolve, seeking greater and greater control of his environment and the relentless elimination of competition. So far as we know, no other predator exerts useful energy in the cause of totally eliminating other carnivores, and the case of the Eskimo view of the wolf referred to above (p 202) suggests that only twentieth century western man may have developed this urge. The complexities of human culture may be no more than an expression of the "overrun" in a system which evolved to deal with the intricacies of organisation at an order of magnitude lower, as emphasised recently by Lewin (1979).

Studies of predator palaeoecology have further significance for Palaeolithic and later archaeology which must give additional cause for concern about interpretations of excavated evidence. Firstly, in view of the increasing emphasis on faunal analysis of archaeological material and the investigation of human palaeoeconomies over the past decade or so, the difficulties of interpreting predator-accumulated bone assemblages are worth underlining. As I have stressed, the relatively greater predictability of predator behaviour makes it easier to assess the past behaviour and exploitation strategy of these species in given circumstances than that of man, and to suggest probable traces of this activity to be found in the fossil record. Yet it clearly remains difficult to achieve this goal of predator behaviour reconstruction in practice, and one is often left with a number of possible interpretations with no clear means of resolution.

Much of this difficulty stems from differential consumption and scavenging activity, as well as poor recovery, but in the case of human behaviour the problems of distant kills, butchery practice and joint selection are likely to introduce similar factors of bias. These observations suggest that even more obstacles lie in the path of the archaeologist seeking to interpret past human behaviour than await the palaeontologist dealing with animals, and argue for considerable thought to be given to reconstructions which utilise number estimates, age structure, sex ratios, and species composition.

Secondly, it is apparent that many of the instances of tool manufacture claimed for early hominids are based upon objects actually fashioned by carnivore activity. It is abundantly clear that the determined attack on suggestions of hyaena bone-accumulating mounted by Dart (1956) were motivated by concern over the position of his osteodentokeratic theory of australopithecine behaviour, and the later work of Brain (1967a, 1967b) and Sutcliffe (1970) have revealed the questionability of Dart's stance. There is sufficient evidence of the bone tool making capacities of man, in the form of undoubted implements, to require little support of the dubious kind offered by Dart's colleague Kitching (1963), in some of his more extreme interpretations of hyaena-damaged bones from Pin Hole Cave.

These latter problems have arisen from a common fallacy where bone shaping and damage are concerned, the notion that regularity and consistency in pattern denote intentional fabrication. What Dart and his followers have failed to realise is that while human activity can undoubtedly fashion implements of bone to a template, so the physical properties of the bone will also determine the form of the finished product to an extent. These properties will continue to have an influence when the forming agency lacks specific goals but operates on the bone in a consistent manner. A large predator eating a bone will do most damage to the most vulnerable parts of the bone first, and if complete consumption is halted then the finished products will have an impressively similar appearance. Failure to take these factors into account would lead to the labelling of virtually any predator's discarded bone as human manufacture. Such mistakes are by no means confined to the examination of Palaeolithic bone debris, since precisely this error can be observed in the report on faunal remains from the Bronze and Iron Age site of Dinkha Tepe, northwestern Iran (Gilbert and Steinfeld 1977). In their figures 4 and 5 the authors show two bones, a sheep or goat metapodial and a distal bovine tibia, with breakages and wear precisely like that from Kirkdale Cave, an undoubted hyaena den, and modern hyaena dens in East Africa (Sutcliffe 1970). In fact the bovine tibia shown in their figure looks almost identical to one from Kirkdale which Buckland (1823) compared with another from Bristol Zoo which had been deliberately fed to a hyaena. The Dinkha Tepe faunal sample contained dogs, and such damage would certainly not be beyond the capabilites of a canid. A quotation form the report is rather revealing, "Our criteria in identifying tools are such characteristics as abrasion, polish, retouch, and *conspicuous and repetitive breaks*. Broken tools were discarded, *and were often badly gnawed, probably by household dogs, so that identification was often difficult*". (my emphasis). This quotation would suggest some failure on the part of the authors to think through the implications of their findings fully. It should be apparent that the view advocated in this study does not rule out the possibility of early hominid bone tool-making activity, nor reject out of hand the possibility of bone tools on sites of later periods, but merely seeks to point out the dangers of an unquestioning assumption of human involvement and the clear evidence for potential error in such an assumption.

6.3 Methodology and Future Research

In assessing the validity of the foregoing conclusions and the study as a whole, one must have regard to the degree of precision aimed for. At the risk of repetition and special pleading, the intention here has been to cover a broad span of the Upper Pleistocene of Britain, and to make best use of the data collected here to date which has precisely that property. The foregoing conclusions represent an attempt to evaluate both the specific observations made on this data and some of the wider inferences which may be drawn from them. The integration of modern ethological observations has permitted a set of predictions about the evidence to be found in specific past environmental circumstances, and the discussion of the fossil material shows the broad agreement with expectations which has been found. The application of these results to an evaluation of human and predator adaptive radiation is a brief foray into the kind of investigations which must be attempted if palaeoecological studies of Pleistocene mammals are to achieve advances beyond extended species cataloguing.

It is notable that while the specific conclusions relate in the main to the large predators, the general points discussed show a greater emphasis on the importance of predator palaeoecology for hominid studies. I take the view that studies of Pleistocene predators are of interest and value in their own right, and need no such support for their continuance, but the applications to archaeological research cannot be overstressed. As a guard against misinterpretation and as a means of insight into palaeoecosystems in operation, predator-prey relationships are as fundamental to the study of man as any other method which the archaeologist routinely employes to examine the past. Wobst (1974) has emphasised the need for an alternative to overly particularistic research strategies in palaeolithic archaeology and for the necessity of developing general models. The development of a fuller model of human and animal evolution and adaptive radiation would be a very worthwhile goal for such a revised strategy. While recent studies such as that of Cahen *et al* (1979) may serve a useful purpose in demonstrating the inadequacies of many existing notions of tool typology and curation, one must wonder how the reconstruction of perhaps a few hours activity in the lives of a small group of Belgian palaeoliths can be integrated into a wider view of human evolution.

It is clear that the discussion of predator-prey interactions presented here has pointed to greater complexities than can perhaps ever be recovered or tested, however good the material evidence may become. This should be stressed and borne in mind as a constant limiter to reconstruction. It is abundantly clear in the writings of Schaller, Mech, Kruuk and others, that an understanding of all the details of a modern ecosystem is likely to prove illusory, even with the benefits of first-hand information. How likely is it that we can then reconstruct a palaeoecosystem, imperfectly observed as it is as a result of numerous factors? The one advantage which the palaeontologist has is a time perspective, the emphasis, once again, on the broad trend. While Occam's razor may be of general utility in scientific reasoning, and the simplest explanation consistent with all the evidence to be preferred in each individual decision, it seems likely that when considering palaeoecosystems one should start with an assumption of greater complexity than that observable, if only to avoid simplistic interpretations.

Turning finally to the prospects of further research on the British material, it is clear that for the present study the stratigraphic and environmental information presently available is only just adequate. As soon as one attempts closer resolution of specific issues it becomes inadequate, as is clearly the case with relative abundances of predators, prey and man following the Devensian maximum, for instance. It is unlikely that further progress can be made in studies of British Upper Pleistocene predator and prey interactions and behaviour, that of man included, with the present data alone. The next step must therefore be the recovery of large samples of well stratified remains, from sites of both human and predator activity and from deposits containing botanical and sedimentological material amenable to dating and environmental reconstruction techniques. This is particularly crucial for the Devensian, and while material from all periods within this phase would be worth examining, the main points for emphasis should perhaps be the

BIBLIOGRAPHY

Allen, E., Rutter, J. G. 1946-48. *Gower Caves*. Swansea

Ardrey, R. 1961. *African Genesis.* London: Collins

Ardrey, R. 1966. *The Territorial Imperative*. New York: Atheneum

Ardrey, R. 1970. *The Social Contract*. New York: Atheneum

Ardrey, R. 1976. *The Hunting Hypothesis*. New York: Atheneum

Armstrong, A. L. 1929. Excavations at Creswell Crags, the Pin Hole Cave 1925-28. *Transactions of the Hunter Archaeological Society*. 3: 332-4

Bahn, P. 1977. Seasonal migration in south-west France during the late glacial period. *Journal of Archaeological Science*. 4: 245-57

Bahn, P. 1978. The unacceptable face of the west European Upper Palaeolithic. *Antiquity*. 52: 183-92

Baker, R. R. 1978. *The Evolutionary Ecology of Animal Migration*. London: Hodder and Stoughton

Balch, H. E. 1914. *Wookey Hole*. London: Oxford University Press

Balch, H. E. 1947. *Mendip-The Great Cave of Wookey Hole*. 3rd. ed. Bristol: John Wright and Sons

Balch, H. E. 1948. *Mendip-its Swallet Caves and Rock Shelters*. 2nd. ed. Bristol: John Wright and Sons

Balch, H. E. 1938-53. *Exploration of the Badger Hole at Wookey Hole*. 2 volume unpublished diary of excavations, Wells Museum.

Balikci, A. 1968. The Netsilik Eskimos: adaptive processes. In *Man The Hunter*, eds. R. B. Lee and I. de Vore, 78-82 Chicago: Aldine

Banfield, A. W. F. 1954. *Preliminary Investigation of the Barren Ground Caribou*. Canadian Wildlife Service, Wildlife Management *Bulletin, Ser I, 10A* and 10B

Bannikov, A. G. (ed.) 1967. *Biology of the Saiga*. Jerusalem: Israel Program for Scientific Translation

Barmintsev, J. N. 1974. Horse breeding in the Soviet Union. *Veterinary Medical Review*. 3: 226-40

Barrington, N., Stanton, W. 1976. *Mendip. The Complete Caves and a View of the Hills*. Cheddar: Barton Productions

Bearder, S. K. 1975. Inter-relationship between hyaenas and their competitors in the Transvaal lowveld. *Nuwe Reeks Publication University of Pretoria*. 97: 39-48

Bearder, S. K. 1977. Feeding habits of spotted hyaenas in a woodland habitat. East African Wildlife Journal. 15: 263-80

Bell, F. G. 1969. The occurrence of southern, steppe and halophyte elements in Weichselian (last-glacial) floras from southern Britain. New Phytologist. 68: 913-22

Bell, R. H. V. 1971. A grazing system in the Serengeti. Scientific American. 225: 86-93

Bemrose, H. H. A., Newton, E. T. 1905. On an ossiferous cavern of Pleistocene age at Hoe Grange Quarry, Longcliffe, near Brassington (Derbyshire). Quarterly Journal of the Geological Society of London. 61: 43-63

Bertram, B. C. R. 1975. Social factors influencing reproduction in wild lions. Journal of Zoology, London. 177: 463-82

Beynon, F., Dowie, H. G., Ogilvie, A. H. 1929. Report on the excavations in Kent's Cavern, 1926-29. Transactions and Proceedings of the Torquay Natural History Society. 5: 237-42

Bilsborough, A. 1972. Cranial morphology of Neanderthal man. Nature. 237: 351-2

Bilsborough, A. 1976. Patterns of evolution in Middle Pleistocene hominids. Journal of Human Evolution. 5: 423-39

Binford, L. R. 1972. Contemporary model building: paradigms and the current state of palaeolithic research. In Models in Archaeology, ed. D. L. Clarke, 109-66 London: Methuen

Binford, L. R. 1973. Interassemblage variability. The Mousterian and the "functional" argument. In The Explanation of Culture Change, ed. A. C. Renfrew, 227-54 London: Duckworth

Binford, L. R. 1974. Forty-seven trips. Paper presented at the Australian Institute of Aboriginal Studies Biennial Conference, Canberra, Australia

Binford, L. R. 1978. Nunamiut Ethnoarchaeology. New York: Academic Press

Binford, L. R. 1979. Organisation and formation processes: looking at curated technologies. Journal of Anthropological Research. 35(3): 255-73

Bordes, F. 1972. A Tale of Two Caves. New York: Harper and Row

Bordes, F., Laville, H., Lumley, H. de, Miskovsky, J.C., Paquereau, M.M., Pillard, B., Prat, F., Renault-Miskovsky, J. 1972. Le Wurmien II. Tentative de corrélations entre le Lanquedoc méditerraneen (l'Hortus) et le Périgord (Combe-Grenal). In Etudes Quaternaires Memoire no. 1, ed. H. de Lumley, 353-62

Bordes, F., Prat, F. 1965. Observations sur les faunes du Riss et du Wurm en Dordogne. L'Anthropologie. 69: 31-46

Borsuk-Bialynicka, M. 1973. Studies on the Pleistocene rhinoceros *Coelodonta antiquitatis* (Blumenbach). *Academie Polonaise des Sciences Institut de Paleozoologie*. 29: 94pp. + plates

Bouchud, J. 1966. *Essai sur le Renne et la climatologie du Paleolithique moyen et supérieur*. Périgueux: Imprimerie Magne

Bouchud, J. 1970. Les apports de la paléontologie du Quatenaire à la connaissance de l'homme fossile. In *L'Homme de Cro-Magnon*, ed. G. Camps and G. Olivier, 213-18 Paris: Arts et Metiers Graphiques

Bouchud, J. 1975. Etude de la faune de l'Abri Pataud. In *Excavation of the Abri Pataud Les Eyzies (Dordogne)*, ed. H. L. Movius, 69-153 Cambridge, Massachusetts: Peabody Museum, Harvard University Bulletin No. 30

Boule, M. 1906. Les grands chats des cavernes. *Annales de Paléontologie*. 1: 69-95

Boule, M. 1911-13. L homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie*. 6: 109-197; 7: 21-56, 85-192; 8: 1-67

Bowen, D. Q. 1970. The palaeoenvironment of the 'Red Lady" of Paviland. *Antiquity*. 44: 134-6

Bowen, D. Q. 1979a. Quaternary correlations. *Nature*. 277: 171-2

Bowen, D. Q. 1979b. Reply to Mangerud *et al*. *Nature*. 279: 108

Boylan, P. J. 1972. The scientific significance of the Kirkdale Cave hyaenas. *Annual Report of the Yorkshire Philosophical Society* . (for 1971) 38-47

Boylan, P. J. 1977. *The Ice Age in Yorkshire and Humberside*. York: York Museum

Brace, C. L. 1978. Review of *The Hunting Hypothesis*, R. Ardrey. *American Anthropologist*. 80: 172-3

Brain, C. K. 1967a. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Scientific Papers of the Namib Desert Research Station*. 32: 1-11

Brain, C. K. 1967b. Bone weathering and the problem of bone pseudo-tools. *South African Journal of Science*. 63: 97-9

Brain, C. K. 1970. New finds at the Swartkrans australopithecine site. *Nature*. 225: 1112-1119

Brain, C. K. 1974. Some suggested procedures in the analysis of bone accumulations from Southern African Quaternary sites. *Annals of the Transvaal Museum*. 29: 1-8

Brain, C. K. 1975a. An introduction to the South African australopthecine bone accumulations. In *Archaeozoological Studies*, ed. A. T. Clayson, 109-119 Amsterdam, Oxford: North Holland Publishing Company

Brain, C. K. 1975b. An interpretation of the bone assemblage from the Kromdraai australopthecine site, South Africa. In Paleoanthropology: Morphology and Paleoecology, ed. R. H. Tuttle, 225-43 The Hague, Paris: Mouton; Chicago: Aldine

Brain, C. K. 1976a. Some principles in the interpretation of bone accumulations associated with man. In Human Origins: Louis Leakey and the East African Evidence, ed. G. Ll. Isaac and E. R. McCowan, 97-116 Menlo Park, California: W. A. Benjamin Inc.

Brain, C. K. 1976b. A re-interpretation of the Swartkrans site and its remains. South African Journal of Science. 72: 141-6

Brander, A. A. D. 1927. Wild Animals in Central India. London

Brose, D. S. and Wolpoff, M. H. 1971. Early Upper Palaeolithic man and late Middle Palaeolithic tools. American Anthropologist. 73: 1156-94

Buckland, W. Rev. 1822. Account of an assemblage of fossil teeth and bones of elephant, hippopotamus, bear, tiger and hyaena and sixteen other animals discovered in a cave at Kirkdale, Yorkshire in the year 1821: with a comparative view of five similar caverns in various parts of England, and others on the Continent. Philosophical Transactions of the Royal Society London. 1: 171-236

Buckland, W. Rev. 1823. Reliquae Diluvianae. London: John Murray

Busk, G. 1872. On the organic remains of the Brixham cave. Proceedings of the Royal Society. 20: 514-24

Busk, G. 1873. Report on the exploration of the Brixham cave. Philosophical Transactions of the Royal Society.

Busk, G. 1875. List of mammalian remains collected by the Rev. J. M. Mello in the Rock Fissure cavern in Creswell Crags, Derbyshire. Quarterly Journal of the Geological Society. 31: 683-91

Butzer, K. W. 1972. Environment and Archaeology. 2nd. ed. London: Methuen

Cahen, D., Keeley, L. H., Noten, F. L. van. 1979. Stone tools, toolkits and human behaviour in prehistory. Current Anthropology. 20(4): 661-83

Calkin, J. B., Green, J. F. N. 1949. Palaeoliths and terraces near Bournemouth. Proceedings of the Prehistoric Society. 15: 29-37

Campbell, B. G. 1962. The systematics of man. Nature. 194: 225-32

Campbell, B. G. 1967. Human Evolution. London: Heinemann

Campbell, B. G. 1972. Man for all seasons. In Sexual Selection and the Descent of Man, ed. B. G. Campbell, 40-58 Chicago: Aldine

Campbell, J. B. 1969. Excavations at Creswell Crags: preliminary report. *Derbyshire Archaeological Journal*. 89: 47-52

Campbell, J. B. 1971. *The Upper Palaeolithic of Britain*. Unpublished D.Phil. Thesis, Oxford University

Campbell, J. B. 1977. *The Upper Palaeolithic of Britain*. 2 vols. Oxford: Clarendon Press

Campbell, J. B. , Sampson, C. G. 1971. A new analysis of Kent's Cavern, Devonshire, England. *University of Oregon Anthropological Papers*. 3: 40pp

Casteel, R. W. 1977. Characterisation of faunal assemblages and the minimum number of individuals determined from paired elements: continuing problems in archaeology. *Journal of Archaeological Science*. 4: 125-34

Catt, J. A. 1980. Till facies associated with the Devensian glacial maximum in Eastern England. *Quaternary Newsletter*. 30: 4-10

Chandler, R. H. , Leach, A. L. 1912. Report of an excursion to the lower Tertiary section and the Pleistocene river drifts near Erith. *Proceedings of the Geological Association*. 23: 183-90

Chaplin, R. E. 1971. *The Study of Animal Bones from Archaeological Sites*. New York: Seminar Press

Chapman, N., Chapman, D. 1978. *Fallow Deer*. (2nd. revised edition). British Deer Society

Clegg, J. 1964-70. Excavations at Coygan Cave near Laugharne. *Carmarthenshire Antiquary*. 5-6: 13-20

CLIMAP Project. 1976. The surface of the Ice-Age Earth. *Science*. 191: 1131-7

Clutton-Brock, T. H., Albon, S. D., Gibson, R. M., Guiness, F. E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Animal Behaviour* . 27; 211-25

Collins, D., Collins, A. 1970. Excavations at Oldbury in Kent: cultural evidence for Last Glaciatial occupation in Britain. *Bulletin of the Institute of Archaeology*. 8-9: 151-76

Coombs, W. P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quarterly Review of Biology*. 53: 393-418

Coope, G. R. 1974. Interglacial coleoptera from Bobbitshole, Ipswich, Suffolk. *Journal of the Geological Society*. 130: 333-40

Coope, G. R., Angus, R. B. 1975. An ecological study of a temperate interlude in the middle of the last Glaciation, based on fossil coleoptera from Isleworth, Middlesex. *Journal of Animal Ecology*. 44: 365-391

Corruccini, R. S. 1975. Multivariate analysis in biological anthropology: some considerations. *Journal of Human Evolution*. 4: 1-19

Cottle, J. 1829. The Oreston Caves. Folio Edition

Coxon, P., Hall, A.R., Lister, A., Stuart, A.J. 1980. New evidence on the vertebrate fauna, stratigraphy and palaeobotany of the interglacial deposits at Swanton Morley, Norfolk. Geological Magazine. 6: 525-46

Dart, R. A. 1956. Myth of the bone accumulating hyaena. American Anthropologist. 58: 40-62

Dart, R. A. 1957. The Makapansgat australopithecine osteodentokeratic culture. In Third Pan-African Congress on Prehistory 1955, ed. J. D. Clark, 146-71 London: Chatto and Windus

Dart, R. A. 1958. Bone tools and porcupine gnawing. American Anthropologist. 60: 715-24

Dart, R. A. 1959. Further light on australopithecine humeral and femoral weapons. American Journal of Physical Anthropology. 17: 87-93

Dart, R. A. 1962. The continuity and originality of the australopithecine osteodentokeratic culture. In Actes du IVe Congres Panafrican de Prehistoire et de l'Etude Quaternaire. Section III, 27-41 ed. G. Mortelmans and J. Neuquin

Davies, A. J. 1926. Notes on Upper Palaeolithic implements from some Mendip Caves. Proceedings of the University of Bristol Spelaeological Society. 2: 261-73

Davies, H. N. 1907. Supplementary notes of the Clevedon bone-cave and gravel. Proceedings of the Bristol Naturalists Society. IV Series 1(3): 188-90

Davis, J. W. 1882. On the exploration of a fissure in the mountain limestone at Raygill. Report of the British Association for the Advancement of Science. 1881: 645-6

Dawkins, W. Boyd. 1862. On a hyaena den at Wookey Hole, near Wells. Quarterly Journal of the Geological Society. 18: 115-26

Dawkins, W. Boyd. 1863a. On a hyaena den at Wookey Hole, near Wells. Quarterly Journal of the Geological Society. 19: 260-74

Dawkins, W. Boyd. 1863b. Wookey Hole hyaena den. Proceedings of the Somersetshire Archaeological and Natural History Society. 11: 196-219

Dawkins, W. Boyd. 1865. On the dentition of Hyaena spelaea, and its varieties with notes on the recent species. Natural History Review. New series V: 80-96

Dawkins, W. Boyd. 1866. On the dentition of Rhinoceros leptorhinus Owen. Proceedings of the Royal Society of London. 15: 106-7

Dawkins, W. Boyd. 1867. On the dentition of Rhinocerus leptorhinus Owen. Quarterly Journal of the Geological Society of London. 23: 213-27

Dawkins, W. Boyd. 1868. On the dentition of *Rhinoceros* etruscus Falconer. *Quarterly Journal of the Geological Society of London.* 24: 207-18

Dawkins, W. B. 1871. On the discovery of the glutton (*Gulo* luscus) in Britain. *Quarterly Journal of the Geological Society.* 27: 406-10

Dawkins, W. Boyd. 1874. *Cave Hunting.* London: Macmillan

Dawkins, W. Boyd. 1875. The mammalia found at Windy Knoll. *Quarterly Journal of the Geological Society of London.* 31: 246

Dawkins, W. Boyd. 1876. On the mammalia and traces of man found in the Robin-Hood Cave. *Quarterly Journal of the Geological Society.* 32: 245-58

Dawkins, W. B. 1877. On the mammal-fauna of the caves of Creswell Crags. *Quarterly Journal of the Geological Society.* 33: 589-612

Dawkins, W. Boyd. 1880. *Early Man in Britain.* London: Macmillan

Dawkins, W. B., Mello, J. M. 1879. Further discoveries in the Creswell Crags. *Quarterly Journal of the Geological Society of London.* 35: 724-35

Dawkins, W. B., Oakley, H. W. 1877. Proboscidea. In *Cassell's Natural History* Vol 2, ed. P. M. Duncan, 273-91 London: Cassell Petter and Galpin

Dawkins, W. Boyd., Sanford, W. Aysford. 1866-72. *British Pleistocene Mammalia vol I: British Pleistocene Felidae.* London: Palaeontographical Society

Delap, P. 1977. *Red Deer.* 2nd. revised ed. British Deer Society

Delpech, F. 1972. Etude paléoclimatique des faunes aurignaciennes et périgordiennes du gisement du Roc de Combe (Payngnac, Lot). *Quaternaria.* 16: 247-54

Delpech, F. 1975. Les faunes du Paléolithique supérieur dans le sud-ouest de la France. *Thèse de doctorat d'Etat ès Sciences Naturelles Bordeaux.* 479, 374pp, 159 tab, 98pl

Dennell, R. W. 1979. Prehistoric diet and nutrition: some food for thought. *World Archaeology.* 11(2): 121-35

Destombes, J. P., Shephard-Thorn, E. R., Redding, J. H. 1975. A buried valley sytem in the Strait of Dover. *Philosophical Transactions of the Royal Society of London.* A 279: 243-56

Donovan, D. T. 1954. A bibliography of the Palaeolithic and Pleistocene sites of the Mendip, Bath and Bristol area. *Proceedings of the University of Bristol Spelaeological Society.* 7(1): 23-34

Donovan, D. T. 1955. The Pleistocene deposits at Gough's Cave, Cheddar, including an account of recent excavations. *Proceedings of the University of Bristol Spelaeological Society.* 7(2): 76-102

Dreisch, A. von den. 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*. Peabody Museum Bulletin 1. Peabody Museum of Archaeology and Ethnology, Harvard University

Eaton, R. L. 1970. The predatory sequence, with emphasis on killing behaviour and its ontogeny, in the cheetah (*Acinonyx jubatus* Schreber). *Zeitschrift fur Tierpsychologie*. 27: 492-504

Elliot, J. P., Cowan, I. Mc. 1978. Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. *Canadian Journal of Zoology*. 56(8): 1726-34

Eloff, F. C. 1973. Ecology and behaviour of the Kalahari lion, *Panthera leo vernayi* (Roberts 1929). In *Proceedings of the 1st International Conference on the Ecology, Behaviour and Conservation of the World's Cats*, ed. R. L. Eaton, 90-126 Winston, Oregon: World Wildlife Safari

Ewer, R. F. 1973. *The Carnivores*. London: Weidenfeld and Nicolson

Fink, J., Kukla, G. J. 1976. Pleistocene climates in Central Europe: at least 17 interglacials after the Olduvai event. *Quaternary Research*. 7(3): 363-71

Fisher, O. 1879. On a mammaliferous deposit at Barrington, near Cambridge. *Quarterly Journal of the Geological Society*. 35: 670-7

Fletcher, T. J. 1974. The timing of reproduction in red deer (*Cervus elaphus*) in relation to latitude. *Journal of Zoology, London*. 172: 363-7

Fox, M. W. (ed.) 1975. *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. New York, London: Van Nostrand Reinold

Franks, J. W. 1960. Interglacial deposits at Trafalgar Square, London. *New Phytologist*. 54: 145-52

Frison, G. C. 1978. *Prehistoric Hunters of the High Plains*. New York, London: Academic Press

Gamble, C. 1978. Resource exploitation and the spatial patterning of hunter-gatherers: a case study. *British Archaeological Reports*. 47: 153-85

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

Garrod, D. A. E. 1926. *The Upper Palaeolithic Age in Britain*. Oxford

Gates, W. L. 1976. Modelling the Ice-Age climate. *Science*. 191: 1138-44

Geist, V. 1971. *Mountain Sheep*. Chicago: University of Chicago Press

Gibbard, P. L., Stuart, A. J. 1975. Flora and vertebrate fauna of the Barrington Beds. *Geological Magazine*. 112(5): 493-501

Gilbert, A. S., Steinfeld, P. 1977. Faunal remains from Dinkla Tepe, northwestern Iran. *Journal of Field Archaeology*. 4 (3): 329-51

Gilbertson, D. D., Hawkins, A. B. 1974. Upper Pleistocene deposits and land forms at Holly Lane, Clevedon, Somerset. *Proceedings of the University of Bristol Spelaeological Society*. 13(3): 349-60

Gillespie, R., Horton, D. R., Ladd, P., Macumber, P. G., Rich, T. H., Thorne, R., Wright, R. V. S. 1978. Lancefield Swamp and the extinction of the Australian megafauna. *Science* 200: 1044-8

Girling, M. A. 1974. Evidence from Lincolnshire of the age and intensity of the mid-Devensian temperate episode. *Nature*. 250: 270

Girling, M. A. 1977. Tattershall and Kirby-on-Bain. In *Yorkshire and Lincolnshire Guidebook for Excursion C7, X INQUA Conference*, ed. J. A. Catt, 19-21

Goddard, J. 1967. Home range, behaviour and recruitment rates of two black rhinoceros populations. *East African Wildlife Journal*. 5: 133-50

Goodall, J., van Lawick, H. 1970. *Innocent Killers*. London: Collins

Gould, S. J. 1974. The origin and function of "bizarre" structures: antler size and skull size in the "Irish Elk", *Megaloceros giganteus*. *Evolution*. 28: 191-220

Grigson, C. 1978. The Late Glacial and Early Flandrian ungulates of England and Wales - an interim review. In *The Effect of Man on the Landscape: the Lowland Zone*, ed. S. Limbrey and J. G. Evans, 46-56 Council for British Archaeology Report 21

Grimes, W. F., Cowley, L. F. 1935. Coygan Cave, Llansadyrnin. *Archaeologia Cambrensis*. 90: 95-111

Groves, C. P. 1974. *Horses, Asses and Zebras in the Wild*. London: David and Charles

Guggisberg, C, A. W. 1966. *S.O.S. Rhino*. London: Andre Deutsch

Guggisberg, C. A. W. 1975. *Wild Cats of the Wild*. London: David and Charles

Guiness, F. E., Clutton-Brock, T. H., Albon, S. D. 1978. Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology*. 47: 817-32

Guthrie, R. D. 1967. Differential preservation and recovery of large mammal remains in Alaska. *Journal of Paleontology*. 41: 243-6

Guthrie, R. D. 1968. Paleoecology of the large-mammal community in interior Alaska during the late Pleistocene. *American Midland Naturalist*. 79: 346-63

Gwynne, M. D., Bell, R. H. V. 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. *Nature*. 220: 390-3

Haldane, J. B. S. 1956. The argument from animals to men: an examination of its validity for anthropology. *Journal of the Royal Anthropological Institute of Great Britain and Ireland*. 86: 1-14

Hall, R. L., Sharp, H. S. 1978. *Wolf and Man. Evolution in Parallel*. New York: Academic Press

Harbottle, G., Sayre, E. V., Stoenner, R. W. 1979. Carbon-14 dating of small samples by proportional counting. *Science*. 206: 683-5

Harris, S. 1978. Age determination in the red fox (*Vulpes vulpes*) - an evaluation of technique efficiency as applied to a sample of suburban foxes. *Journal of Zoology*. 184(1): 91-117

Harrison, G. A., Weiner, J. S., Tanner, J. M., Barnicot, N. A. 1977. *Human Biology*. 2nd. ed. Oxford: Clarendon

Harrison, R. A. 1977. The Uphill Quarry Caves, Weston Super Mare, a reappraisal. *Proceedings of the University of Bristol Spelaeological Society*. 14(3): 233-54

Hays, J. D., Imbrie, J., Shackleton, N. J. 1976. Variations in the Earth's orbit: pacemaker of the Ice Ages. *Science*. 194: 1121-32

Heath, T. 1879. *An Abstract Description and History of the Bone Caves of Creswell Crags*. Derby: Wilkins and Ellis

Hewer, T. F. 1926. King Arthur's Cave. *Proceedings of the University of Bristol Spelaeological Society*. 2: 221-8

Hicks, H. 1884. On some researches in bone caves of Wales. *Proceedings of the Geological Association*. 9: 1-21

Hicks, H. 1885a. Results of researches in some bone caves in North Wales (Ffynnon Beuno and Cae Gwyn). *Proceedings of the Geological Association*. 10: 3-19

Hicks, H. 1885b. On the Ffynnon Beuno and Cae Gwyn bone caves, North Wales. *Geological Magazine*. 11: 510-13

Hicks, H. 1886a. Results of some recent researches in some bone-caves in North Wales. *Quarterly Journal of the Geological Society*. 42: 3-11

Hicks, H. 1886b. On the Ffynnon Beuno and Cae Gwyn Caves. *Geological Magazine*. 11: 566-71

Hicks, H. 1888. On the Cae Gwyn Cave, North Wales. *Quarterly Journal of the Geological Society*. 44: 562-77

Hicks, H., Davies, W. 1886. Results of recent researches in some bone caves in North Wales (Ffynnon Beuno and Cae Gwyn) with a note on the animal remains. *Quarterly Journal of the Geological Society*. 42: 319

Hicks, H., Rance, C. E. de. 1888. On the Cae Gwyn Cave in North Wales. *Quarterly Journal of the Geological Society*. 44: 561-77

Higgs, E. S. (ed.) 1972. *Papers in Economic Prehistory*. Cambridge: Cambridge University Press

Higgs, E. S. (ed.) 1975. *Palaeoeconomy*. Cambridge: Cambridge University Press

Higgs, E. S., Jarman, M. R,. 1969. The origins of agriculture: a reconsideration. *Antiquity*. 43: 31-41

Higgs, E. S., Jarman, M. R. 1975. Palaeoeconomy. In *Palaeoeconomy*, ed. E.S. Higgs, 1-7 Cambridge: Cambridge University Press

Higgs, E. S., Vita-Finzi, C. 1972. Prehistoric economies: a territorial approach. In *Papers in Economic Prehistory*, ed. E. S. Higgs, 27-36 Cambridge: Cambridge University Press

Hollingworth, S. E., Allison, J., Godwin, H. 1950. Interglacial deposits from Histon Road, Cambridge. *Quarterly Journal of the Geological Society*. 105: 495-509

Howells, W. W. 1974. Neanderthal: names, hypotheses, and scientific method. *American Anthropologist*. 76: 24-38

Howells, W. W. 1975. Neanderthal man: facts and figures. In *Paleoanthropology: Morphology and Paleoecology*, ed. R. H. Tuttle, 389-407 The Hague, Paris: Mouton; Chicago: Aldine

Howells, W. W. 1976. Explaining modern man: evolutionists versus migrationists. *Journal of Human Evolution*. 5: 477-95

Hughes, T. M. 1887. On the drifts of the Vale of Clwyd and their relations to the caves and cave deposits. *Quarterly Journal of the Geological Society of London*. 43: 73-120

Hughes, T. M. 1911. Excursion to Cambridge and Barrington. *Proceedings of the Geological Association*. 22: 268-78

Huxley, J. S. 1931. The relative size of antlers in deer. *Proceedings of the Zoological Society*. 1931: 819-64

Huxley, J. S. 1932. *Problems of Relative Growth*. London

Isaac, G, Ll. 1970. The diet of early man: aspects of archaeological evidence from lower and middle Pleistocene sites in Africa. *World Archaeology*. 2: 278-99

Isaac, G. Ll. 1975a. Stratigraphy and cultural patterns in East Africa during the middle ranges of Pleistocene time. In *After the Australopithecines*, ed. K. W. Butzer and G. Ll. Isaac, 495-542 The Hague, Paris: Mouton

Isaac, G. Ll. 1975b. Sorting out the muddle in the middle: an anthropologist's post-conference appraisal. In *After the Austalopithecines*, ed. K. W. Butzer and G. Ll. Isaac, 875-87 The Hague: Mouton

Jackson, J. W. 1937. Schedule of cave finds. *Caves and Caving*. 1(1): 18-21

Jackson, J. W. 1938. Centenary account of Victoria Cave, Settle. *Caves and Caving*. 1: 169-74

Janis, C. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution*. 30: 757-74

Jarman, M. R., Wilkinson, P. F. 1972. Criteria of animal domestication. In *Papers in Economic Prehistory*, ed. E. S. Higgs, 83-96 Cambridge: Cambridge University Press

Jelinek, J. 1975. *The Evolution of Man*. New York, London, Sydney, Toronto: Hamlyn

Jenkinson, R. D. S. 1978. *The Archaeological Caves and Rock Shelters in the Creswell Crags Area*. Creswell Crags Visitor Centre Research Report No. 1. Nottinghamshire County Council

John, B. S. 1971. The "Red Lady" of Paviland: a comment. *Antiquity*. 45: 141-44

Johnston, H. Sir. 1903. *British Mammals*. London: Hutchinson

Keeley, L. H., Newcomer, M. H. 1977. Microwear analysis of experimental flint tools: a test case. *Journal of Archaeological Science*. 4: 29-62

Kelsall, J. P. 1968. *The Caribou*. Ottawa: Canadian Wildlife Service, Queen's Printer

Kendall, D. G. 1974. Hunting quanta. *Philosophical Transactions of the Royal Society*. A 276: 231-76

Kennard, A. S. 1944. The Crayford brickearths. *Proceedings of the Geological Association*. 55(3): 121-69

King, G. E. 1976a. Society and territory in human evolution. *Journal of Human Evolution*. 5: 323-32

King, G. E. 1976b. Socioterritorial units and interspecific competition: modern carnivores and early hominids. *Journal of Anthropological Research*. 32: 276-84

Kitching, J. W. 1963. *Bone, Tooth and Horn Tools of Palaeolithic Man, An Account of the Osteodontokeratic Discoveries in the Pin Hole Cave, Derbyshire*. Manchester: Manchester University Press

Klein, R. G. 1971. The Pleistocene prehistory of Siberia. *Quaternary Research*. 1: 133-61

Klein, R. G. 1974. A provisional statement on terminal Pleistocene mammalian extinctions in the Cape biotic zone (Southern Cape Province, South Africa). *South African Archaeological Society Goodwin Series*. 2: 39-45

Klein, R. G. 1975. The relevance of Old World archaeology to the first entry of man into the New World. *Quaternary Research*. 5: 391-4

Klein, R. G. 1979. Environmental and ecological implications of large mammals from Upper Pleistocene and Holocene sites in southern Africa. Paper given at *Towards a Better Understanding of the Upper Pleistocene in Sub-Saharan Africa*, Southern African Association of Archaeologists Workshop in Stellenbosch, 27-29 June 1979.

Klinghammer, E. 1978. *The Behaviour and Ecology of Wolves*. New York: Garland

Kominz, M. A., Pisias, N. G. 1979. Pleistocene climate: deterministic or stochastic? *Science*. 204: 171-3

Kowalski, K. 1967. The Pleistocene extinction of mammals in Europe. In *Pleistocene Extinctions: The Search for A Cause*, ed. P. S. Martin and H. E. Wright, 349-64 New Haven: Yale University Press

Krantz, G. S. 1968. A new method of counting mammal bones. *American Journal of Archaeology*. 72: 286-8

Kruuk, H. 1971. Interactions between populations of spotted hyaenas (*Crocuta crocuta* Erxleben) and their prey species. In *Animal Populations in Relation to their Food Resources*, ed. A. Watson, 359-74 Oxford, Edinburgh: Blackwell Scientific Publications

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

Kruuk, H. 1975. *Hyaena*. London: Oxford University Press

Kukla, G. J. 1975. Loess stratigraphy of Central Europe. In *After the Australopithecines*, ed. K. W. Butzer and G. Ll. Isaac, 99-188 The Hague, Paris: Mouton

Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zoologica Fennica*. 76: 1-122

Kurtén, B. 1954. Population dynamics and evolution. *Evolution*. 8: 75-81

Kurtén, B. 1955a. Sex dimorphism and size trends in the Cave Bear, *Ursus spelaeus* Rosenmuller and Heinroth. *Acta Zoologica Fennica*. 90: 1-48

Kurtén, B. 1955b. Contribution to the history of a mutation during 1,000,000 years. *Evolution*. 9: 107-18

Kurtén, B. 1956. The status and affinities of *Hyaena sinensis* Owen and *Hyaena ultima* Matsumoto. *American Museum Novitates*. 1764: 1-48

Kurtén, B. 1957a. A case of Darwinian selection in bears. *Evolution*. 4: 412-16

Kurtén, B. 1957b. The bears and hyaenas of the interglacials. *Quaternaria*. 4: 69-81

Kurtén, B. 1958. Life and death of the Pleistocene Cave Bear. A study in paleoecology. *Acta Zoologica Fennica*. 95: 1-59

Kurtén, B. 1959. On the bears of the Holsteinian Interglacial. *Stockholm Contributions in Geology*. 2: 73-102

Kurtén, B. 1963. The cave hyaena, an essay in statistics. In *Science in Archaeology*, ed. D. Brothwell and E. Higgs, 1st. ed. , 224-34 London: Thames and Hudson

Kurtén, B. 1964. The evolution of the polar bear, *Ursus maritimus* Phipps. *Acta Zoologica Fennica*. 108

Kurtén, B. 1967. Some quantitative approaches to dental microevolution. *Journal of Dental Research*. 46: 817-28

Kurtén, B. 1968a. *Pleistocene Mammals of Europe*. London: Weidenfeld and Nicolson

Kurtén, B. 1968b. Fossil Reste von Hyänen und Bären (Carnivora) aus den Travertinen von Weimar-Ehringsdorf. *Abhandlungen des Zentralen Geologischen Instituts Heft*. 23: 465-84

Kurtén, B. 1969a. Evolution at the population level: a statistical approach. In *Science in Archaeology*, 2nd. ed., ed. D. Brothwell and E. S. Higgs, 661-8 London: Thames and Hudson

Kurtén, B. 1969b. Cave bears. *Studies in Speleology*. 2(1): 13-24 + plates

Kurtén, B. 1972. The cave bear. *Scientific American*. 226(3): 60-72

Kurtén, B. 1973a. Fossil glutton (*Gulo gulo* L.) from Tornewton Cave, South Devon. *Societas Scientiarum Fennica Commentationes Biologicae*. 66: 8pp

Kurtén, B. 1973b. Transberingian relationships of *Ursus arctos* Linne (brown and grizzly bears). *Societas Scientiarum Fennica Commentationes Biologicae*. 65: 10pp

Kurtén, B. 1973c. Geographic variation in size in the puma (*Felis concolor*). *Societas Scientiarum Fennica Commentationes Biologicae*. 63: 8pp

Kurtén, B. 1976. *The Cave Bear Story: Life and Death of a Vanished Animal*. Columbia: Columbia University Press

Kurtén, B., Anderson, E. 1980. *Pleistocene Mammals of North America*. New York: Columbia University Press

Laing, R. 1889. On the bone caves of Creswell and the discovery of an extinct Pliocene feline (*Felis brevlostris*) new to Great Britain. *Report of the British Association*. 582-4

Laughlin, W. S. 1968. Hunting: an integrated biobehaviour system and its evolutionary importance. In *Man the Hunter*, ed. R. B. Lee and I. de Vore, 304-320 Chicago: Aldine

Laws, R. M., Parker, I. S. C., Johnstone, R. C. B. 1975. *Elephants and their Habitats*. London: Oxford University Press

Leakey, R. E. F., Lewin, R. 1977. *Origins*. London: MacDonald and Jane's

Lee, R. B., de Vore, I. (eds.) 1968. *Man the Hunter*. Chicago: Aldine

Leuthold, W., Leuthold, B. M. 1975. Patterns of social grouping in ungulates of Tsavo National Park, Kenya. *Journal of Zoology, London*. 175: 405-20

Lewin, R. 1979. An ancient cultural revolution. *New Scientist*. 83: 352-5

Lowe, H. J. 1922-3. The excavation products of Kent's Cavern and their distribution. *Transaction and Proceedings of the Torquay Natural History Society*. 4(1): 6-9

Lowe, U. P. W. 1961. A discussion on the history, present status and future conservation of red deer (*Cervus elaphus* L.) in Scotland. In *Ecology and Management of Wild Grazing Animals in Temperate Zones*, ed. F.Bourliere, 99-40 Paris: Sociètè Nationale de Protéction de la Nature

Lumley, H. de. (ed.) 1976. *La Préhistoire Française: Tome 1. Les Civilizations Paläeolithiques and Mésolithiques de la France*. Paris: Edition du Centre National de la Recherche Scientifique

Maglio, V. J. 1975. Pleistocene faunal evolution in Africa and Eurasia. In *After the Australopithecines*, ed. K. W. Butzer amd G. Ll. Isaac, 419-76 The Hague, Paris: Mouton

Mangerud, J., Soustegaard, E., Sgrup, H. O. 1979. Correlation of the Eemian (interglacial) stage and the deep-sea oxygen-isotope stratigraphy. *Nature*. 277: 189-92

Martin, P. S. 1966. Africa and Pleistocene overkill. *Nature*. 212: 339-42

Martin, P. S. 1967. Prehistoric overkill. In *Pleistocene Extinctions: The Search for a Cause*, ed. P. S. Martin and H. E. Wright, 75-120 New Haven: Yale University Press

Martin, P. S. 1973. The discovery of America. *Science*. 179: 969-74

Martin, P. S., Wright, H. E. 1967. eds. *Pleistocene Extinctions: The Search for a Cause*. New Haven: Yale University Press

Mathews, L. H. 1939. Bionomics of the spotted hyaena. *Proceedings of the Zoological Society of London*. A 109: 43-56

McBurney, C. B. M. 1961. Two soundings in the Badger Hole near Wookey Hole in 1958, and their bearings on the Palaeolithic finds of the late H.E. Balch. *Report of the Wells Natural History and Archaeology Society* 1961: 19-27

McBurney, C. B. M., Callow, P. 1971. The Cambridge excavations in the Cotte de St. Brelade, Jersey - a preliminary report. *Proceedings of the Prehistoric Society*. 37: 167-207

Mech, L. D. 1970. The Wolf. New York: Natural History Press

Megaw, J.V.S., Simpson, D.D.A. 1979. Introduction to British Prehistory. Leicester: Leicester University Press

Mellars, P. A. 1969. The chronology of Mousterian industries in the Perigord region of south-west France. Proceedings of the Prehistoric Society. 35: 134-71

Mellars, P. A. 1973. The character of the Middle-Upper Palaeolithic transition in south-west France. In The Explanation of Culture Change: Models in Prehistory ed. A. C. Renfrew, 255-76. London: Duckworth

Mellars, P. A. 1974. The Palaeolithic and Mesolithic. In British Prehistory, ed. A. C. Renfrew, 41-99 London: Duckworth

Mello, J. M. 1875. On some bone caves in Creswell Crags. Quarterly Journal of the Geological Society. 31: 679-83

Mello, J. M. 1876. The bone caves of Creswell Crags; 2nd. Paper. Quarterly Journal of the Geological Society. 32: 240-44

Mello, J. M. 1877. The bone-caves of Creswell Crags: 3rd paper. Quarterly Journal of the Geological Society. 33: 579-88

Merrilees, D. 1968. Man the destroyer: Late Quaternary changes in Australian marsupial fauna. Journal of the Royal Society of Western Australia. 51: 1-24

Milne, J. A., MacRae, J. C., Spence, A. M., Wilson, S. 1976. Intake and digestion of hill-land vegetation by the red deer and the sheep. Nature. 263: 763-4

Mitchell, G. F., Penny, L. F., Shotton, F. W., West, R. G. 1973. A correlation of Quaternary deposits in the British Isles. Special Report of the Geological Society of London, 4: 99p

Moir, J. R., Hopwood, A. T. 1939. Excavations at Brunden, Suffolk (1935-7). Proceedings of the Prehistoric Society. 5: 1-32

Molleson, T., Burleigh, R. 1978. A new date for Goat's Hole Cave. Antiquity. 52: 143-5

Morgan, A. 1973. Late Pleistocene environmental changes indicated by fossil insect faunas of the English Midlands. Boreas. 2(4): 173-212

Morgan, A. V. 1973. The Pleistocene geology of the area north and west of Wolverhampton, Staffordshire, England. Philosophical Transactions of the Royal Society of London. A 279: 243-56

Morgan, W. Ll. 1913. Bacon Hole, Gower. Archaeologia Cambrensis. 13: 173-80

Morris, D. 1967. The Naked Ape. New York: McGraw-Hill

Mosiman, J.E., Martin, P.S. 1975. Simulating overkill by Paleoindians. American Scientist. 63: 304-13

Murchison, C. (ed.) 1868. Palaeontological Memoirs and Notes of the Late Hugh Falconer. Vols 1 and 2 London: Hardwicke

Murie, A, 1944. The Wolves of Mount McKinley. Fauna of the National Parks of the United States Series, no. 5

Newton, E. T. 1879. Notes on some fossil remains of Emys lutaria from the Norfolk coast. Geological Magazine. 6: 304-6

Nobis, G. 1971. Vom Wildpferd zum Hauspferd. Koln, Wien: Bohlau Verlag

Nobis, G. 1974. The origin, domestication and early history of domestic horses. Veterinary Medical Review. 3: 211-25

Norris, G. 1962. Some glacial deposits and their relation to the Hippopotamus-bearing beds at Barrington, Cambridgeshire. Geological Magazine. 99: 97-118

Oakley, K. P. 1968. The date of the "Red Lady" of Paviland. Antiquity. 42: 306-7

Ohel, M. Y. 1979. The Clactonian: an independent complex or an integral part of the Acheulian? Current Anthropology. 20(4): 685-726

Olsen, S. J. 1960. Post-cranial and skeletal characters of Bison and Bos. Papers of the Peabody Museum, Harvard University. 35(4) 12pp + figs.

Owen, R. 1846. A History of British Fossil Mammals and Birds. London: John Van Voorst

Palmer, L. S., Hinton, M. A. C. 1929. Some gravel deposits at Walton near Clevedon. Proceedings of the University of Bristol Spelaeological Society. 3: 154-61

Parker, W. K., Parker, T. J. 1877. The land carnivora. In Cassell's Natural History. Vol 2., ed. P. M. Duncan, 1-208 London: Cassell, Petter and Galpin

Parkin, D. W., Shackleton, N. J. 1973. Trade wind and temperate correlations down a deep-sea core off the Saharan coast. Nature. 245: 455-7

Parry, R. F. 1928. Excavations at the caves, Cheddar. Proceedings of the Somerset Archaeological and Natural History Society. 74: 102-21

Parry, R. F. 1930. Excavations at Cheddar. Proceedings of the Somerset Archaeological and Natural History Society. 76: 46-62

Paterson, T. T., Tebbutt, C. F. 1947. Studies in the Palaeolithic succession in England, no. 3. Palaeoliths from St. Neots, Huntingdonshire. Proceedings of the Prehistoric Society. 13: 37-46

Payne, S. 1972. On the interpretation of bone samples from archaeological sites. In Papers in Economic Prehistory, ed. E. S. Higgs, 65-81 Cambridge: Cambridge University Press

Pengelly, W. 1865-80. Reports 1-16 of the Committee for Exploring Kent's Cavern, Devonshire. Report of the British Association for the Advancement of Science.

Pengelly, W. 1871. The Ash Hole and Bench bone-caverns at Brixham, South Devon. Transactions of the Devonshire Association for the Advancement of Science, Literature and Art. 4: 73-80

Pengelly, W. 1872. Literature of the Oreston Caves. Transactions of the Devonshire Association for the Advancement of Science, Literature and Art. 1872

Pennington, W. 1977. The Late Devensian flora and vegetation of Britain. Philosphical Transactions of the Royal Society. B, 280: 247-71

Percival, A, B. 1924. A Game Ranger's Note Book. London: Nisbet

Pfeiffer, J. E. 1970. The Emergence of Man. London: Thomas Nelson

Pfizenmayer, E. W. 1939. Siberian Man and Mammoth. London, Glasgow: Blackie

Phillips, L. 1972. Pleistocene Vegetational History and Geology in Norfolk. Unpublished PhD Thesis: University of Cambridge

Phillips, L. 1974. Vegetational history of the Ipswichian/Eemian interglaical in Britain and Continental Europe. New Phytologist. 73: 589-604

Piennar, U. de V. 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. Kodoe. 12: 108-76

Pilbeam, D. 1967. Review article. Proceedings of the Prehistoric Society. 33: 457-462

Pilbeam, D. R. 1975. Middle Pleistocene hominids. In After the Australopithecines, ed. K. W. Butzer and G. Ll. Isaac, 809-56 The Hague, Paris: Mouton

Powers, R., Stringer, C. B. 1975. Palaeolithic cave art fauna. Studies in Spelaeology. 2: 266-98

Pruitt, W. O. 1959. Snow as a factor in the winter ecology of the barren-ground Caribou. Arctic. 12(3)

Pulliainen, E. 1965. Studies on the wolf (Canis lupus L.) in Finland. Annals Zoologica Fennica. 2: 215-59

Pulliainen, E. 1975. Wolf ecology in northern Europe. In The Wild Canids, ed. M. W. Fox, 292-9 New York, London: Van Nostrand Reinold

Pyke, M. 1970. Man and Food. London: Weidenfeld and Nicolson

Racey, P. A., Skinner, J. D. 1979. Endocrine aspects of sexual mimicry in spotted hyaenas, Crocuta crocuta. Journal of Zoology. 187: 315-26

Rackham, D. J. 1978. Evidence for changing vertebrate communities in the Middle Devensian. Quaternary Newsletter. 25: 1-3

Rausch, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. American Zoologist. 7: 253-65

Reynolds, S. H. 1902. The Cave Hyaena. British Pleistocene Mammalia Vol. II(1). London: Palaeontographical Society

Reynolds, S. H. 1906. The Bears. British Pleistocene Mammalia Vol. II(2). London: Palaeontographical Society

Reynolds, S. H. 1907. A bone-cave at Walton near Clevedon. Proceedings of the Bristol Naturalists Society. IV Series. 1(3): 183-8

Reynolds, S. H. 1909. The Canids. British Pleistocene Mammalia Vol. II(3). London: Palaeontographical Society

Rightmire, G. P. 1975. Problems in the study of later Pleistocene man in Africa. American Anthropologist. 77: 28-52

Rightmire, G. P. 1979. Implications of the Border Cave skeletal remains for later Pleistocene human evolution. Current Anthropology. 20(1): 23-35

Roe, D. A. 1968. A Gazeteer of British Lower and Middle Palaeolithic Sites. London: Oxford University Press

Roe, F. G. 1972. The North American Buffalo. Newton Abbott: David and Charles

Rowlands, B. M. 1971. Radiocarbon evidence of the age of an Irish Sea glaciation in the Vale of Clwyd. Nature: Physical Science. 230: 9-11

Rutter, J. 1829. Delineation of the North-Western Division of the County of Somerset and of its Antediluvian Bone-caverns. London: Longman, Rees

Sahlins, M. D. 1968. Notes on the original affluent society. In Man the Hunter, eds. R. B. Lee and I. de Vore, 85-89 Chicago: Aldine

Sanford, W. A. 1867. On the Pleistocene Mammalia of Somerset. Catalogue of bones in the Museum of the Archaeological and Natural History Society at Taunton. No. 1 - Felis. Proceedings of the Somersetshire Archaeological and Natural History Society. 14

Sankhala, K. 1978. Tiger!. London: Collins

Savage, R. J. G. 1969. Pleistocene mammal faunas. Proceedings of the University of Bristol Spelaeological Society. 12(1): 57-62

Schaller, G. B. 1967. The Deer and the Tiger: a Study of Wildlife in India. Chicago, London: University of Chicago Press

Schaller, G. B. 1972. The Serengeti Lion. Chicago, London: University of Chicago Press

Schaller, G. B., Lowther, G. R. 1969. The relevance of carnivore behaviour to the study of early hominids. *S. W. Journal of Anthropology*. 25: 307-41

Seber, G. A. F. 1973. *The Estimation of Animal Abundance and Related Parameters*. London: Griffin

Selous, F. C. 1907. *A Hunter's Wanderings in Africa*. 5th ed. London: Macmillan

Shackleton, N. J. 1969. The last interglacial in the marine and terrestial records. *Proceedings of the Royal Society of London*. B 174: 135-54

Shackleton, N. J. 1975. The stratigraphic record of deep-sea cores, and its implications for the assessment of glacials, interglacials, stadials, and interstadials in the Mid-Pleistocene. In *After the Australopithecines*, ed. K. W. Butzer and G. Ll. Isaac, 1-24 The Hague, Paris: Mouton

Shackleton, N. J., Opdyke, N. D. 1976. Oxygen-isotope and paleomagnetic stratigraphy of Pacific V28-239 Late Pliocene to Latest Pleistocene. *Geological Society of America Memoir*. 145: 449-64

Shotton, F. W. 1977. The Devensian stage: its development, limits and substages. *Philosophical Transactions of the Royal Society*. B 280: 107-18

Shotton, F. W., Sutcliffe, A. J., West, R. G. 1962. The fauna and flora from the brick pit at Lexden, Essex. *Essex Naturalist*. 31: 15-22

Silver, I. A. 1969. The ageing of domestic animals. In *Science in Archaeology*, ed. D. Brothwell and E. Higgs, 283-302 London: Thames and Hudson

Simpson, G. G. 1941. Large Pleistocene felines of North America. *American Museum Novitates*. 1136: 1-27

Simpson, G. G. 1950. *Horses*. London: Oxford University Press.

Sinclair, H. M. 1953. The diet of Canadian Indians and Eskimos. *Proceedings of the Nutrition Society*. 12: 69

Sollas, W. J. 1913. Paviland Cave, an Aurignacian station in Wales. *Journal of the Royal Anthropological Institute*. 43: 325-74

Sparks, B. W. 1952. Notes on some Pleistocene sections at Barrington, Cambridgeshire. *Geological Magazine*. 89: 163-74

Sparks, B. W., West, R. G. 1960. The Palaeoecology of the interglacial deposits at Histon Road, Cambridge. *Eiszeitalter und Gegenwart*. 10: 123-43

Sparks, B. W., West, R. G,. 1963. The interglacial deposits at Stutton, Suffolk. *Proceedings of the Geological Association*. 74: 419-81

Sparks, B. W., West, R. G. 1968. Interglacial deposits at Wortwell, Norfolk. *Geological Magazine*. 105: 471-81

Sparks, B. W., West, R. G. 1970. Late Pleistocene deposits at Wretton, Norfolk, 1. Ipswichian interglacial deposits. *Philosophical Transactions of the Royal Society*. B 258: 1-30

Speiss, A. E. 1979. *Reindeer and Caribou Hunters*. New York, San Francisco, London: Academic Press

Spinage, C. A. 1973. A review of the age determination of mammals by means of teeth, with especial reference to Africa. *East African Wildlife Journal*. 4: 165-87

Stefansson, V. 1923. *Hunters of the Great North*. London: Harrap

Stephenson, R. O., Ahgook, R. T. 1975. The Eskimo hunter's view of wolf ecology and behaviour. In *The Wild Canids*, ed. M. W. Fox, 286-91 New York, London

Straus, W. L., Cave, A. J. E. 1957. Pathology and posture of Neanderthal man. *Quarterly Review of Biology*. 32: 348-63

Straw, A. 1979. An Early Devensian glaciation in Eastern England? *Quaternary Newsletter*. 28: 18-24

Straw, A. 1980. An Early Devensian glaciation in Eastern England reiterated. *Quaternary Newsletter*. 31: 18-23

Stringer, C. B. 1974. Population relationships of later Pleistocene hominids: a multivariate study of available crania. *Journal of Archaeological Science*. 1: 317-42

Stringer, C. B. 1975. A preliminary report on new excavations at Bacon Hole Cave. *Gower*. 26: 32-7

Stringer, C. B. 1979. Review of *The Upper Palaeolithic of Britain*, by J. B. Campbell. *Journal of Archaeological Science*. 6: 105

Stuart, A. J. 1974. Pleistocene history of the British vertebrate fauna. *Biological Reviews of the Cambridge Philosophical Society*. 49: 225-66

Stuart, A. J. 1976. The history of the mammal fauna during the Ipswichian/last interglacial in England. *Philosphical Transactions of the Royal Society*. B 276: 221-50

Stuart, A. J. 1977. The vertebrates of the last cold stage in Britain and Ireland. *Philosophical Transactions of the Royal Society*. B 280: 295-312

Sturdy, D. A. 1972. *Reindeer Economies in Late Ice Age Europe*. Unpublished PhD dissertation, Cambridge University

Sturdy, D. A. 1975. Some reindeer economies in prehistoric Europe. In *Palaeoeconomy*, ed. E. S. Higgs, 55-95 Cambridge: Cambridge University Press

Sutcliffe, A. J. 1955. Banwell bone cave. *Journal of the Axbridge Caving Group*. 2: 35-41

Sutcliffe, A. J. 1957. Cave Fauna and Cave Sediments. Unpublished PhD Thesis: University of London

Sutcliffe, A. J. 1960. Joint Mitnor Cave, Buckfastleigh. Transactions of Torquay Natural History Society. 13: 1-28

Sutcliffe, A. J. 1969. Adaptation of spotted hyaenas to living in the British Isles. Bulletin of the Mammal Society of Great Britain. 31: 10-14

Sutcliffe, A. J. 1970. Spotted hyaena: crusher, gnawer, digester and collector of bones. Nature. 227: 1110-3

Sutcliffe, A. J. 1975. A hazard in the interpretation of glacial-interglacial sequences. Quaternary Newsletter. 17: 1-3

Sutcliffe, A. J. 1976. Reply from Anthony J. Sutcliffe (to points raised by West (1976) to Sutcliffe (1975)). Quaternary Newsletter. 18: 1-7

Sutcliffe, A. J. 1978. Unpublished manuscript.

Sutcliffe, A. J., Bowen, D. Q. 1973. Preliminary report on excavations in Minchin Hole - April-May 1973. Newsletter of the William Pengelly Cave Studies Trust. 21: 12-25

Sutcliffe, A. J., Kowalski, K. 1976. Pleistocene rodents of the British Isles. Bulletin of the British Museum (Natural History) Geology. 27(2): 33-147

Sutcliffe, A. J., Zeuner, F. E. 1962. Excavations in the Torbryan caves, Devonshire. 1. Tornewton Cave. Proceedings of Devonshire Exploration Society. 5: 127-45

Swinscow, T. D. V. 1977. Statistics at Square One. London: British Medical Association

Symonds, W. S. 1871. On the contents of a hyaena's den on the Great Doward, Whitchurch, Ross. Geological Magazine. 1871: 432-8

Synge, F. M. 1977. Records of sea levels during the Late Devensian. Philosphical Transactions of the Royal Society. B 280: 211-28

Taylor, H. 1928. King Arthur's Cave near Whitchurch, Ross-on-Wye. 2nd Report. Proceedings of the University of Bristol Spelaeological Society. 3: 59-83

Thacker, A. G. 1914-5. Report on the mammalian remains found in King Arthur's Cave, Herefordshire. 5th Report of the Public Museum Committee of the City of Gloucester.

Thom, B. G. 1973. The dilemma of high interstadial sea levels during the last glaciation. Progress in Geography. 5: 167-246

Thompson, P. R. 1976. A behaviour model for Australopithecus africanus. Journal of Human Evolution. 5: 547-58

Thomson, D. F. 1939. The seasonal factor in human culture. Proceedings of the Prehistoric Society. 36: 1-37

Tiddeman, R. H. 1876. Third report of the Victoria Cave Exploration Committee. Report of the British Association for the Advancement of Science. 1875: 166-75

Tratman, E. K. 1963. Gough's Old Cave, Cheddar, Somerset. Proceedings of the University of Bristol Spelaeological Society. 9(1): 7-21

Tratman, E. K. 1964. Picken's Hole, Crook Peak, Somerset. A Pleistocene site. Proceedings of the University of Bristol Spelaeological Society. 10(2): 112-15

Tratman, E. K., Donovan, D. T., Campbell, J. B. 1971. The Hyaena den (Wookey Hole) Mendip Hills, Somerset. Proceedings of the University of Bristol Spelaeological Society. 12: 245-79

Turnbull-Kemp, P. 1967. The Leopard. London: Bailey Brothers and Swinfen

Turner, C. 1975. Der Einfluss grosser Mammalier auf die interglaziale Vegetation. Quartärpaläontologie. 1: 13-19

Turner, C., West, R. G. 1968. The subdivision and zonation of interglacial periods. Eiszeitalter und Gegenwart. 19: 93-101

Ucko, P. J., Rosenfeld, A. 1967. Palaeolithic Cave Art. London: Weidenfeld and Nicholson

Verheyen, R. 1951. Contribution à l'etude éthologique des mammifères du Parc National de l'Upemba. Bruxelles: Institut des Parcs Nationaux du Congo Belge

Vernon-Harcourt, W. 1829. On the discovery of fossil bones in a marl pit near North Cliff. Philosophical Magazine. 2(6): 225-32

Vesey-Fitzgerald, D. F. 1960. Grazing succession among East African game animals. Journal of Mammalogy. 41: 161-72

Vita-Finzi, C., Higgs, E. S. 1970. Prehistoric economy in the Mount Carmel area of Palestine : site catchment analysis. Proceedings of the Prehistoric Society. 36: 1-37

Walker, E. P. (ed.) 1964. Mammals of the World. Vol. 2. Baltimore: John Hopkins Press

Walvius, M. R. 1961. A discussion of the size of recent red deer (Cervus elaphus) compared with prehistoric specimens. Beaufortia Series of Miscellaneous publications, Zoological Museum, Amsterdam. 97(9): 75-82

Watson, E. 1977. The periglacial environment of Great Britain during the Devensian. Philosophical Transactions of the Royal Society. B 280: 183-98

West, R. G. 1957. Interglacial deposits at Bobbitshole, Ipswich. Philosophical Transactions of the Royal Society. B 241: 1-31

West, R. G. 1969. Pollen analysis from interglacial deposits at Aveley and Grays. Proceedings of the Geological Association. 80: 271-82

West, R. G. 1972. Relative land-sea-level changes in south-eastern England during the Pleistocene. Philosophical Transactions of the Royal Society of London. A 272: 87-98

West, R. G. 1976. The British glacial-interglacial sequence. Quaternary Newsletter. 18: 1

West, R. G. 1977a. Early and Middle Devensian flora and vegetation. Philosophical Transactions of the Royal Society. B 280: 229-46

West, R. G. 1977b. Pleistocene Geology and Biology. 2nd. ed. London, New York: Longmans

West, R. G., Dickson, C. A., Catt, J. A., Weir, A. H., Sparks, B. W. 1974. Late Pleistocene deposits at Wretton, Norfolk. II. Devensian deposits. Philosophical Transactions of the Royal Society of London. B 267: 337-420

West, R. G., Lambert, C. A., Sparks, B. W. 1964. Interglacial deposits at Ilford, Essex. Philosophical Transactions of the Royal Society. B 247: 185-212

West, R. G., Sparks, B. W. 1960. Coastal interglacial deposits of the English Channel. Philosophical Transactions of the Royal Society. B 243: 95-133

Whidbey, J. 1821. A further account of some fossil bones discovered in caverns enclosed (sic) in the limestone rocks at Plymouth. By Joseph Whidbey Esq. In a letter addressed to Sir Everard Home, Bart, V. P. R. S. Philosphical Transactions of the Royal Society. 39: 133ff.

Whidbey, J. 1823. On some fossil bones discovered in caverns in the limestone quarries of Oreston. By Joseph Whidbey Esq. F. R. S. In a letter addressed to John Barrow Esq. F. R. S. To which is added, a description of the bones by Mr William Clift, Conservator of the Museum of the College of Surgeons. Philosophical Transactions of the Royal Society. 1823. 41: 78-90+plates

White, J. P., O'Connell, J. F. 1979. Australian prehistory: new aspects of antiquity. Science. 203: 21-8

Widger, J. L. 1892. The Torbryan Caves. Torquay Directory. 15th June, 1892

Wilkinson, P. F. 1975. The relevance of musk ox exploitation to the study of prehistoric animal economies. In Palaeoeconomy, ed. E. S. Higgs, 9-53 Cambridge: Cambridge University Press

Wilson, E., Reynolds, S. H. 1901. Uphill bone caves. Proceedings of the British Naturalists Society. 9(3): 152-60

Wobst, H. M. 1974. Boundary conditions for palaeolithic social systems: a simulation approach. American Antiquity. 39(2): 147-178

Wojtusiak, K. 1953. Szczatki Iwa Jaskiniowego (Felis spelaea Goldfuss) z jaskini Wierzchowskiej Gornej. Acta Geologica Polonica . 3: 573-92

Woodburn, J. 1968. An introduction to Hadza ecology. In *Man the Hunter*, eds. R. B. Lee and I. de Vore, 49-55 Chicago: Aldine

Woodward, H., Davies, W. 1874. Notes on the Pleistocene deposits yielding mammalian remains in the vicinity of Ilford, Essex. *Geological Magazine*. 11: 90-98

Wright, B. S. 1960. Predation on big game in East Africa. *Journal of Wildlife Management*. 24(1): 1-15

Wymer, J. J. 1968. *Lower Palaeolithic Archaeology in Britain*. London: Oxford University Press

Young, S. P., Goldman, E. A. 1944. *The Wolves of North America*. Vol. II. New York: Dover

Zeuner, F. E. 1945. New reconstruction of the woolly rhinoceros and Merk′s rhinoceros. *Proceedings of the Linnaean Society of London*. 156: 183-95

Zimen, E. 1976. On the regulation of pack size in wolves. *Zeitschrift für Tierpsychologie*. 40: 300-41