The behavioural ecology of reindeer (*Rangifer tarandus*) during the last glaciation in Britain and its implications for human settlement, subsistence and mobility.

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Abstract

Reindeer was a major component of the subsistence strategies of human groups in northwest Europe during the last glaciation. Archaeological models of the subsistence strategies and related settlement patterns of those human groups are dependent upon assumptions about the nature of Devensian faunas, and, in particular, about the nature of reindeer behaviour. Previous attempts to reconstruct reindeer behaviour patterns have been based on direct comparison between the behaviour of modern reindeer populations and that of their prehistoric counterparts. Studies of modern species have indicated that many aspects of behaviour are not fixed, however, but are adaptive to environmental conditions. Changes in those conditions will result in corresponding alterations in patterns of behaviour.

The Devensian environments of Britain and northwest Europe are not comparable with any of the habitats of modern day reindeer populations. In order to build up a model of reindeer behavioural ecology which can be applied to Devensian environments, a detailed study is presented of the environmental factors which affect patterns of reindeer behaviour throughout their natural range and in all their known habitats.

In order to apply this model to the last glacial period in Britain, the seasonal distribution patterns of Devensian reindeer are analysed and the nature of Devensian environmental conditions are investigated. Existing zoo-archaeological techniques for the identification of seasonality are employed in the analysis of 28 Devensian faunal collections from both archaeological and geological sites. One previously unsubstantiated method of determining seasonality from shed reindeer antlers is tested against a modern sample and is found to be reliable. A new method of identifying seasonality in samples of juvenile reindeer bones is also developed and employed where possible.

Analysis of biological, lithological and geomorphological data, compiled from a wide variety of sources, enables the reconstruction of environmental conditions during several stages of the last glaciation. Models of reindeer behavioural ecology which are generated from these environmental reconstructions are tested against zoo-archaeological collections of known age and seasonality.

Finally, the behavioural models which are generated by this study are used to assess the potential for human settlement in Britain during the last glaciation and the range of subsistence strategies and settlement patterns which might have been adopted.
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I declare that this thesis was composed by me and is based upon my own work.

Nicola Murray
Introduction

1.1 Aims and assumptions

This study aims to investigate the behavioural ecology of reindeer during the last (Devensian) glaciation using a combination of ecological models and zoo-archaeological analyses. The behavioural models which are generated are used to assess the potential for human settlement in Britain during the last glaciation and the range of subsistence strategies and settlement patterns which might have been adopted.

Implicit to the arguments of this thesis are four primary assumptions; firstly that models of modern animal behavioural ecology may be applied to prehistoric settings; secondly that the patterns of seasonality which are observed in fossil assemblages represent seasonality in prehistoric animal behaviour; thirdly that reindeer was a major component of the subsistence strategies of early human groups in Britain and northwest Europe; and fourthly that changes in the distribution and behaviour patterns of Devensian reindeer may have been reflected in the subsistence strategies and settlement patterns of those early human groups.

The first assumption is common to many geological, palaeoecological and archaeological studies which attempt to make inferences about the past by reference to modern processes (Gould 1965, Gifford 1981, Binford 1981). The second assumption is also common to palaeoecological studies which are concerned with biogeography and is dependent upon an ability to eliminate taphonomic bias in zoo-archaeological material (Lyman 1982).

The third assumption is based on the results of recent studies which have shown that Palaeolithic subsistence strategies were built around the exploitation of four major herbivores - reindeer (Rangifer tarandus), red deer (Cervus elaphus), bison (Bison bison) and horse (Equus ferus) (Gamble 1986). Reindeer is of particular interest as it is a common prey species on many Palaeolithic sites and is often the major or dominant component of Palaeolithic faunal collections.

The fourth assumption is common to most studies of prehistoric subsistence strategies and their related settlement patterns. Most reconstructions of subsistence are dependent on the analysis of archaeofaunal collections and an attempt to interpret the relationship between the exploited fauna and the original extant community (Lyman 1982). Requisite analyses include an investigation of the taxonomic breadth of the prehistoric diet, the degree of selectivity involved in the predator-prey relationship and the possibility of seasonality in resource use scheduling. Before carrying out any of these analyses, however,
it is first necessary to understand the nature of the original extant faunal community, its
taxonomic diversity and any seasonal changes which may occur.

1.2 Overview of the study
Many reconstructions of Palaeolithic subsistence strategies and settlement patterns have
been dependent on interpretations of reindeer behaviour patterns. These studies, which are
discussed in Chapter 2, rely on direct comparison between the behaviour of modern
reindeer populations and that of their prehistoric counterparts. Studies of modern species
have indicated that many aspects of their behaviour are not fixed, however, but are adaptive
to environmental conditions. Changes in those conditions will result in corresponding
alterations in patterns of behaviour. The complex relationship between animals and their
environment is the subject of ecological science and one branch of this science, behavioural
ecology, is concerned with the study of adaptive behaviour in relation to ecological
circumstances (Krebs and Davies 1987). The Devensian environments of Britain and
northwest Europe are not comparable with any of the habitats of modern day reindeer
populations. In order to build up a model of reindeer behavioural ecology which can be
applied to Devensian environments, a detailed study has therefore been undertaken of the
environmental factors which affect patterns of reindeer behaviour throughout their natural
range and in all their known habitats (Chapter 3).

While a model of reindeer behavioural ecology can help to determine likely behaviour
patterns under given environmental circumstances, the seasonal distribution of reindeer can
only be assessed through the analysis of faunal remains from sites of known age. The zoo-
archaeological methods which have been used in this study are outlined in Chapter 4.

Faunal remains which date from the Devensian glaciation have been found in
numerous geological and archaeological deposits throughout Britain and northwest Europe.
The deposits have accumulated in river terraces, lake beds, and on cave floors, either
through natural processes or as a result of the predatory behaviour of carnivores, most
notably hyaenas, wolves and man. The faunal assemblages which have been considered in
this study are discussed in Chapter 5.

Environmental conditions underwent substantial periods of change throughout the last
 glaciation. Reconstructions of the environmental history of Britain may be built up using
many lines of evidence (Lowe and Walker 1984, Jones and Keen 1993) and have produced a
complicated picture of stadial and interstadial events. These events have been summarised
in Chapter 6. Environmental conditions during each of these periods are discussed in
Chapters 7 to 9 and the evidence for the distribution of reindeer populations is presented.
Likely behaviour patterns are then modelled on the basis of environmental evidence
relating to climate and vegetation.
Chapter 10 presents a discussion of human settlement in Britain during the Devensian glaciation in relation to the distribution of reindeer populations. Finally, the applicability of archaeological models of subsistence strategies and settlement patterns during the Devensian period in Britain is assessed in the light of new information on the behavioural ecology of Devensian reindeer.
2.1 Introduction
Over the last 20 years a great deal of archaeological research has been concerned with the investigation of synchronicity in archaeological patterning. One area of particular interest has been the identification of subsistence strategies and their related settlement patterns. Several studies have attempted to reconstruct Palaeolithic subsistence strategies and settlement patterns on a regional scale within Europe. Most of these studies have approached the problem through a combination of empirical analysis and ethnographic analogy. Patterns of site location, size and seasonality have been studied in relation to the environmental background and compared with models of settlement and subsistence derived from recent hunter-gatherers in North America and Eurasia.

A primary tool in the reconstruction of subsistence strategies is the analysis of faunal remains. In studies of Palaeolithic Europe one species, reindeer, has been of particular interest to archaeologists because of its predominance in the faunal collections from many Palaeolithic sites.

Reindeer was also a major component of the subsistence strategies of many recent northern hunters. Spiess (1979) has reviewed the ethnographic literature of these northern hunting communities and has shown that many varied subsistence strategies included reindeer as part of the resource base. Some communities were largely land-based, exploiting terrestrial mammals such as reindeer, moose and muskox. Other groups exploited riverine and marine resources including salmonids, seals and whales. Most hunters exploited a combination of resources, often on a seasonal or temporary basis. A few groups of northern hunters developed highly specialised subsistence strategies, however, which were based almost entirely on the exploitation of deer.Aside from the calorific value of reindeer meat and fat, the deer also provided skins for tents and clothing, and antler and bone for tools.

Archaeologists have drawn upon these ethnographic accounts of recent northern hunters to develop models of the subsistence strategies and settlement patterns of the Palaeolithic communities of northwest Europe. These models fall into two distinct groups which are referred to here as "Chipewyan-type" and "Broad-based models".

2.2 Chipewyan-type models
"Chipewyan-type" models draw their inspiration from ethnographic studies of specialised reindeer hunters such as the Chipewyan "Caribou-Eaters" of the barren-grounds of northwest Canada. The Chipewyan peoples were almost entirely dependent on the
exploitation of migratory herds of reindeer. Entire communities shifted camp several times each year and trekked over hundreds of miles of tundra in order to intercept the herds as they moved between their winter ranges and summer calving grounds.

Several archaeologists have suggested that similar long distance treks would have been required by reindeer-dependent peoples during the Palaeolithic period in Europe (Sturdy 1972, 1975, Bahn 1977, Gordon 1988). They have constructed "Chipewyan-type" models of herd-following which rely on several assumptions, concerning both reindeer behavioural ecology and the economic choices of human groups. A basic premise underpinning these models is the assumption that the behavioural ecology of Devensian reindeer was comparable to that of the highly gregarious barren-ground caribou of northern Canada and Alaska and the wild tundra reindeer of Eurasia. These reindeer regularly form large herds and migrate over distances of several hundred kilometres between winter ranges in the boreal forest and summer calving grounds on the open tundra plains. With regard to human subsistence strategies, the models also assume that the predominance of reindeer on many Palaeolithic sites implies an economic dependence on this species. This dependence is thought to have been so severe that Palaeolithic peoples were compelled to follow the reindeer herds on their long distance migrations across the tundra.

Such models are not new and have been proposed on several occasions in different regions of northwest Europe. One of the earliest herd-following models was proposed by Saint-Perier (1920) for the Pyrennean region of southwest France. Saint-Perier studied the seasonality of reindeer remains from Pyrennean cave sites and concluded that occupation of the caves was limited to the winter months. He proposed that the Magdalenian occupants quit the region in the summer months in order to follow migrating deer. A similar suggestion was made by Clark (1938) for the Lateglacial sites of the North European plain. Reindeer remains from these sites indicated a winter seasonality and Clark envisaged a pattern of seasonal movement of men and reindeer herds between winter camps on the North European plain and summer pastures in southern Britain.

These two regions, Germany and southwest France, have been the focus of more recent studies in which the herd-following models of Saint-Perier and Clark have been considerably elaborated. Sturdy (1972, 1975) has re-assessed the Lateglacial sites in the North German plain while Bahn (1977) and Gordon (1988) have re-considered the Magdalenian sites of southwest France. Sturdy and Gordon both re-analysed primary faunal data from archaeological sites for evidence of seasonality in reindeer distribution patterns. When they found evidence of single season presence at many of these sites, they concluded that reindeer were migratory and present in the region during only one season of the year. They then looked elsewhere for spring and summer sites which would fit into a pattern of long distance migration.
In contrast to Clark's model of Lateglacial reindeer herds migrating from winter pastures on the North German plain to summer ranges in southern Britain, Sturdy concluded that Lateglacial herds moved southwards into southern Germany and Switzerland. Faunal evidence from Ahrensburgian sites in northern Germany indicates that reindeer were present in the region during the winter. The Magdalenian settlements of southern Germany and Switzerland, however, have produced evidence for human presence during the spring and summer months. Sturdy concluded that the Ahrensburgian and Magdalenian assemblages of northern and southern Germany represented seasonal variants of a single cultural complex.

Gordon (1988) arrived at rather similar conclusions in his study of Magdalenian settlement patterns in France. From an analysis of reindeer seasonality at over 50 Magdalenian sites, Gordon identified a series of 8 annual ranges. Each of these ranges represents the total area exploited by a discrete population of reindeer. Gordon's fresh analysis of faunal remains is supported by earlier studies of cultural material undertaken by Paul Bahn (1977). Bahn proposed that reindeer herds wintered in the Pyrenees and Périgord and migrated over long distances to summer camps in areas such as the Atlantic littoral or the Mediterranean coast. Magdalenian hunting groups would have been compelled to follow these herds (Bahn, 1977, 250). Bahn based his arguments partly on existing faunal analyses and partly on the long distance movement of exotic artefacts such as decorative sea shells.

Bahn's model has been criticised on the grounds that artefact movement need not necessarily indicate the movement of human groups (White 1989). While exotic artefacts may appear on archaeological sites at some considerable distance from their point of origin, this may be the result of trading networks rather than the product of a herd-following strategy. Sturdy has also been criticised for linking together archaeological sites with very different artefact assemblages (Hahn 1979). While Sturdy considers these assemblage differences to be the product of seasonal variation in tool kits, many authors regard the Magdalenian and Ahrensburgian assemblages as representatives of quite separate cultural units (Hahn 1979, Weniger 1982, 1987). Gordon has been criticised on similar grounds (Pike-Tay 1991). In his study of French Magdalenian sites, Gordon recognised the long timescale of the Magdalenian industries but, when summarising his data, did not differentiate between earlier and later periods. All of his material was treated as part of a single cultural unit.

All three models have also been criticised on the grounds that they overemphasise man's dependence on reindeer as a resource and that they underestimate the adaptability of Palaeolithic hunting communities. Sturdy's assumption that the Lateglacial hunters of Germany were largely dependent on reindeer was based primarily on faunal evidence from
the site of Petersfels in southwest Germany. The faunal record at this site suggests that reindeer was the predominant prey species during the Lateglacial, although horse, fish, birds and small game were also available in some number. Sturdy dismisses these resources as insignificant and insufficient to support a human population during the winter. In contrast, Weniger (1982, 1987) has shown that southwest Germany was characterised by a rich grassland environment during the Lateglacial which supported an extremely rich fauna with ten species of ungulate and three species of carnivore. While reindeer is indeed the dominant prey species on many Magdalenian sites, horse-dominated sites are also common and other species were also exploited in smaller numbers.

Gordon (1988) recognised the existence of a similar rich and diverse ungulate fauna during the Lateglacial in southwest France and acknowledged the particular significance of horse in the Massif Central, Landes, Pyrenees and lower Rhône, bison and ibex (Capra ibex) in the Pyrenees and saiga antelope (Saiga tatarica) in the Gironde. By limiting his study to those sites which included reindeer remains, however, he was unable to assess the relative importance of these alternative species in the subsistence strategies of Magdalenian hunters.

Given an assumed dependence on reindeer, Sturdy, Bahn and Gordon proposed that herd-following was the most viable subsistence strategy available to Lateglacial hunters. Sturdy reviewed the alternative strategies of single season hunting and migration hunting. Single season hunting would have involved the exploitation of migratory herds of reindeer during one season only. Sturdy considered that this option would have been practicable only in situations where alternative dependable resources were available during the lean season of the year. Migration hunting would have required the interception of reindeer herds on the routes of their spring and autumn migrations. Sturdy also dismissed this option on the grounds that migration routes would have been too unpredictable and subject to rapid change. In contrast to the unpredictability of these options, Sturdy proposed that herd-following would have offered an assured and regular supply of food for Lateglacial hunting communities.

Despite Sturdy's reservations about the viability of single season hunting, ethnographic accounts of recent northern hunters furnish good evidence for the use of such strategies (Spiess 1979). One of the most notable examples is that of the "Caribou" Inuit who lived to the west of Hudson Bay in an area where few resources other than reindeer were available. Like the Chipewyan "Caribou-Eaters", Caribou Inuit were almost entirely dependent on reindeer. Rather than follow the migratory herds, however, the Caribou peoples lived in semi-permanent villages and hunted reindeer seasonally. They survived the lean seasons by storing large quantities of meat and by supplementing these stores with additional kills of caribou from small bands of sedentary deer which spent the winter on the tundra plains.
While herd-following was clearly not the only subsistence strategy available to Palaeolithic hunting communities, ethnographic evidence indicates that it was a viable strategy in recent times for certain communities in North America. The concept of herd-following has been widely criticised, however, by anthropologists who have suggested that the speed at which reindeer herds migrate makes it impossible for human groups to keep pace with them (Burch 1972, Spiess 1979). Gordon (1988) has recently clarified the distinction between "following" and "accompanying" herds. He acknowledges that it would be quite impossible for human groups to accompany the herds continuously, but suggests that herd following should be interpreted as the interception of herd movements throughout the course of their migrations.

The three models discussed above are all environmentally deterministic. They assume that Palaeolithic hunting communities were heavily dependent on reindeer and that herd-following was the only viable subsistence strategy available to them. More recent models have taken human adaptive behaviour into consideration and have reduced the environment from determinant to "possibilant". These alternative models of Palaeolithic subsistence strategies are based on the alternative strategies of storage and seasonal relocation. They also suggest that the utilisation of a wider resource base would have enabled Palaeolithic human groups to make a variety of adaptive choices in the formation of their subsistence strategies.

### 2.3 Broad-based models

Several major studies have re-assessed the Lateglacial data in southern Germany and southwest France. Hahn (1979) and Weniger (1982, 1987) have re-considered the Lateglacial sites in the Swabian Alb of southern Germany while White (1985) has re-analysed Upper Palaeolithic settlement patterns in the Périgord region of southwest France.

Weniger’s study was comprehensive and included the analysis of artefacts, faunal remains, seasonality indicators and the topographic location of 23 Magdalenian sites in and around the Swabian Alb. He classified these sites according to their size and the quantities of flint tools discovered. Subsequent analysis of the seasonality and topographic location of these sites enabled Weniger to generate a model of a flexible subsistence strategy based on the exploitation of reindeer and supplemented by the ungulate and small mammal faunas of this rich and varied environment. Weniger proposed that the Lateglacial hunting communities of the Swabian Alb would have moved camp several times during the year in order to exploit seasonally available resources. The territory covered by these movements would have been relatively small scale, however, in comparison with the vast distances proposed in Sturdy’s model.
Hahn has produced a rather similar model for the area based on an analysis of the flint assemblages. Both authors have also re-assessed the possible movement patterns of the Lateglacial reindeer populations and concluded that reindeer migrations in southwest Germany occurred on a much smaller scale than those proposed by Sturdy. Given the varied topography of the area, both authors proposed short-range migrations covering distances in the order of 50-100 km. While reindeer would not have been available in the Swabian Alb year-round, alternative resources such as horse were present and removed the necessity to follow the migrating herds.

White (1985) also analysed patterns of site location in his study of Upper Palaeolithic settlement in the Périgord region of southwest France. He suggested that Upper Palaeolithic hunters were operating a strategy of migration hunting, intercepting migrating herds of reindeer at predictable crossing points in valley "funnels". As with the more recent studies in the Swabian Alb, White concluded that reindeer were probably not long distance migrators but rather exploited the altitudinal differences in habitat provided by the varied topography of the Périgord region. While at least some reindeer would therefore have been available for exploitation year round, the diverse fauna of the area would also have permitted the exploitation of alternative species on a seasonal basis. A recent study of red deer seasonality in the southwest of France provides evidence in support of White's study, indicating that red deer hunting was a complimentary activity to the seasonal reindeer kills (Pike-Tay 1991).

These three studies have produced markedly different models of Palaeolithic subsistence strategies to the herd-following models proposed by Sturdy, Bahn and Gordon. They have also raised questions about the nature of reindeer behaviour in the areas concerned. While Sturdy, Bahn and Gordon suggest that Devensian reindeer herds may be compared with the barren-ground caribou of North America, Weniger, Hahn and White suggest that the movement patterns of reindeer in the extremely varied topography of the Swabian Alb and Périgord regions may have been rather different, involving relatively small scale territories and only short range movements, often on an altitudinal basis.

2.4 Reindeer behaviour and subsistence strategies
The nature of reindeer behaviour is crucial to each of the models described above as it defines the availability of the primary resource base. Two aspects of reindeer behaviour which are particularly important in the reconstruction of Palaeolithic subsistence strategies are group size and mobility (Spiess 1979).

Group size determines the appropriate techniques to use in hunting. Where animals form large herds they may be hunted through co-operative group activities, such as large scale drives and ambushes. Where animals regularly form small groups or live relatively
solitary lives individual hunting techniques will be required. The choice of hunting technique will obviously affect human social activity. Large scale hunts facilitate group activity and may require large numbers of people to drive and kill the animals and then to process the meat, fat and hides. In contrast, individual stalking may be carried out successfully by a lone hunter.

The mobility of an animal will affect resource scheduling strategies. Territorial animals which are present in an area year-round may be exploited at any season. Where a species is only seasonally present, however, it must be fitted into a resource use schedule. This may involve any of the subsistence strategies described above, including herd-following, storage or the seasonal exploitation of alternative resources.

2.5 Reconstructing reindeer behaviour
The models of reindeer behaviour discussed above have been derived through comparison with modern reindeer populations in North America and northern Eurasia. Eurasian reindeer and North American caribou belong to a single species, *Rangifer tarandus*, with a broad circumpolar distribution between 45 and 80°N. Seven subspecies have been identified, primarily on the basis of the morphology of the skull (Banfield 1961). Other characteristics such as pelage, overall size, and antler morphology have also been considered and the latter has been used as the basis for a further division of the species into two major taxonomic groups, Cylindricornis and Compressicornis (Jacobi 1931, Banfield 1961). Reindeer which belong to the group Cylindricornis have round antler beams in cross-section and tend to occur in tundra or mountain habitats, while those which belong to the group Compressicornis have flattened antler beams in cross-section and are usually associated with woodland environments. The current classification of reindeer subspecies is listed in Table 2.1. Recent taxonomic evidence suggests that the two most northerly subspecies, *R. t. platyrhynchus* and *R. t. pearyi*, are more closely related to one another than they are to other tundra reindeer and that they may therefore be considered as a third taxonomic grouping with a high arctic distribution (Roed 1985, Leader-Williams 1988).

Within this broad holarctic distribution reindeer inhabit a wide variety of environments. The most southerly populations are found in the boreal forest zone where they inhabit bogs, open meadows and alpine tundra areas. In the far north of their distribution, reindeer live in polar desert conditions on the high arctic islands of the Canadian Arctic Archipelago and Svalbard. Between these extremes are the rolling open tundra plains which are home to the barren-ground caribou of Canada and Alaska and the wild tundra herds of northern Eurasia.

1. While the terms reindeer and caribou are both acceptable English language names for the species *Rangifer tarandus*, the term reindeer will be used throughout this text except in those circumstances where specific mention is made to North American populations.

10
<table>
<thead>
<tr>
<th>Latin Name</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Rangifer tarandus</em></td>
<td>Reindeer or caribou</td>
</tr>
<tr>
<td>Group Compressicornis:</td>
<td></td>
</tr>
<tr>
<td><em>R. t. fennicus</em></td>
<td>Forest reindeer</td>
</tr>
<tr>
<td><em>R. t. caribou</em></td>
<td>Woodland caribou</td>
</tr>
<tr>
<td>Group Cylindricornis</td>
<td></td>
</tr>
<tr>
<td><em>R. t. tarandus</em></td>
<td>Tundra reindeer</td>
</tr>
<tr>
<td><em>R. t. groenlandicus</em></td>
<td>Barren-ground caribou</td>
</tr>
<tr>
<td><em>R. t. granti</em></td>
<td></td>
</tr>
<tr>
<td>High Arctic subspecies</td>
<td></td>
</tr>
<tr>
<td><em>R. t. pearyi</em></td>
<td>Peary caribou</td>
</tr>
<tr>
<td><em>R. t. platyrhynchus</em></td>
<td>Svalbard reindeer</td>
</tr>
</tbody>
</table>

Table 2.1 Taxonomic classification of extant subspecies of *Rangifer tarandus*.

Reindeer behaviour patterns vary considerably from one population to another. In the high arctic archipelagos two subspecies of deer, *R. t. platyrhynchus* and *R. t. pearyi*, form relatively small and sedentary populations. Population size may number a few hundred individuals but group size will rarely exceed two or three animals. As has already been discussed, this is in marked contrast to the barren-ground caribou of Canada and Alaska (*R. t. groenlandicus* and *R. t. granti*) and the wild tundra populations of Eurasia (*R. t. tarandus*). These populations regularly form large herds, occasionally numbering tens of thousands of animals, and undertake long distance migrations between winter pastures and summer calving grounds. The distances involved in these bi-annual migrations may cover several hundreds of kilometres and take the reindeer from winter range in the boreal forest to summer pastures on the open tundra plains. The behaviour patterns of woodland reindeer (*R. t. caribou* and *R. t. fennicus*) fall between these two extremes. Like the high arctic populations, woodland reindeer are relatively solitary animals and rarely form large herds. They are less sedentary than their northern counterparts, however, and undertake short range movements within the forests, often on an altitudinal basis.

In attempting to reconstruct the behaviour patterns of Devensian reindeer, archaeologists have used two rather different methods. Some archaeologists have attempted to predict behaviour patterns on the basis of topographic conditions while others have used taxonomy as a guide to behavioural patterns.
2.5.1 Topography

Most reconstructions of reindeer behaviour which make reference to environmental conditions concentrate on the effects of topography. This is the case with Sturdy’s reconstruction of the range of Lateglacial migrations in northern Germany. Sturdy based his discussion on the assumption that migration is essential to the health of a reindeer herd and that all reindeer populations are therefore migratory. From his review of the literature, Sturdy concluded that the distance involved in these migrations is a function of the heterogeneity of the environment. He argued that reindeer seek out a variety of habitats throughout the year in order to secure different conditions of snow cover, vegetation and temperature. The distance between habitat types would therefore equate with the distance involved in reindeer migrations. In the case of the North European plain, Sturdy argued that the homogeneity of the topography would have resulted in long distance migrations.

Several authors have followed Sturdy’s reasoning in their discussions of reindeer behaviour (eg Bahn, Hahn, Weniger). While the ecological arguments behind Sturdy’s discussion of reindeer migration are sound, there is a fundamental flaw in his model which stems from the primary assumption that all reindeer migrate. Migration may be defined as the seasonal movement of an animal population from one area to another. In many situations, however, reindeer do not form large groups, and, while they may be individually mobile, do not undertake unidirectional movements which might be termed migration. Before attempting to understand the environmental factors involved in migration, therefore, it is first necessary to consider the factors involved in large group formation. The role of the environment in determining these two aspects of reindeer behaviour will be discussed in further detail in Chapter 3.

2.5.2 Taxonomy

A second method of reconstructing Devensian reindeer behaviour has involved the use of taxonomic evidence. In his taxonomic classification of the species, Banfield (1961) noted a behavioural distinction between the woodland and tundra reindeer subspecies with regard to their degree of gregariousness and the range of their annual movements. He summarised this distinction as follows:

Cylindricornis: "Gregarious, generally perform extensive seasonal migrations to taiga; however, some populations perform only local or altitudinal migrations and do not reach forested regions in winter. Shows little wariness..." (1961, 43)

Compressicornis: "Only moderately gregarious; live in small bands. Undertake local seasonal migrations, often altitudinal; individually more wary..." (1961, 70).
These summaries were only intended to give an overall appreciation of the behaviour of the various subspecies and do not cover the great range of behavioural variation which may be observed both within and between the taxonomic groupings. Several archaeologists have attempted to use this taxonomic distinction, however, in their analyses of Quaternary reindeer.

In order to understand the subspecific affiliation of fossil material archaeologists have attempted to assign fossil antlers to one or other of the taxonomic groupings, Cylindricornis or Compressicornis. Bouchud (1966) used this distinction in his analysis of reindeer remains from Middle and Upper Palaeolithic sites in the Périgord region of southwest France. From his study of antler morphology, complimented by the biometric analysis of reindeer astragali, Bouchud concluded that both tundra and woodland forms were present in the region during the Middle Devensian period. More recently, Gordon (1988), also working in the southwest of France, has used the same distinction in antler form to determine the behaviour of reindeer populations during the Magdalenian period. Gordon found examples of Cylindricornis reindeer antler in Magdalenian art and assumed that the populations represented by these paintings would have behaved in much the same way as their modern day counterparts on the barren-grounds of Canada (R. t. groenlandicus). He proposed tundra type behavioural characteristics for these Late Devensian reindeer populations, involving both large herd formation and long distance migration.

The use of taxonomy to reconstruct behaviour patterns relies upon two assumptions; that taxonomic affiliation can be established from fossil antlers and that animal behaviour is genetically linked to these taxonomic characters. In the case of the former assumption it is now generally accepted that reindeer antler is of little taxonomic value (Bubenik 1975). Patterns of antler growth vary as much with age, sex and overall health as they do from one subspecies to another. While Banfield's distinctions between the antlers of woodland and tundra subspecies are valid generalisations, there is nonetheless a large degree of overlap between the antler forms of each group. Banfield himself acknowledged this and concluded that

"racial characteristics in reindeer antlers could only be described in the broadest of terms. Observed individual variation among populations prohibited one from placing too much weight on particular antler formations." (1961, 24).

Perhaps of more critical importance to the taxonomic approach to behavioural reconstruction is the assumption that behavioural traits are inherited as fixed attributes in the same manner as physiological characteristics. Some aspects of animal behaviour are clearly instinctive, resulting in identical responses to given environmental stimuli in all
individuals of the species. The prone response in infant red deer and the follower response in neonatal reindeer are examples of such innate behaviour patterns amongst cervids (Lent 1974). Many aspects of animal behaviour are not fixed, however, but are adaptive to environmental conditions. Changes in those conditions will result in corresponding alterations in patterns of animal behaviour.

The taxonomic approach to the reconstruction of reindeer behaviour does not take into account such environmentally conditioned behavioural changes, but rather considers behaviour as a series of fixed attributes. The fallacy of this assumption may be illustrated by examples from modern populations which do not fit into Banfield's behavioural classification scheme. The caribou populations of the tundra and boreal forest environments of Newfoundland, for example, have been assigned to the group Compressicornis on the basis of skeletal evidence. Their annual long distance migrations between winter ranges and summer calving grounds are more akin to the behaviour characteristics of the barren-ground caribou, however, than they are to the more sedentary patterns of other Compressicornis populations (Bergerud 1974a).

A similar transformation of behaviour types has been observed by Baskin (1986) amongst wild tundra reindeer in the former USSR. Groups of wild reindeer are regularly transplanted to forest environments to replenish local populations. The transplanted animals, which are highly gregarious in the tundra environment, disperse rapidly when moved to the taiga and are frequently lost by herdsmen. Such dispersed behaviour is more typical of the woodland subspecies adapted to enclosed forest environments.

2.5.3 Behavioural ecology

Many aspects of reindeer behaviour are clearly adaptive to environmental conditions. As the Devensian environments of Europe are not directly comparable with any of the habitats of modern day reindeer populations it is not possible to draw simple analogies between the behaviour pattern of Devensian reindeer and those of their modern day counterparts. The complex relationship between animal behaviour and environmental conditions can be modelled, however. In order to build up a model of reindeer behavioural ecology which can be applied to Devensian environments, it is necessary to examine the environmental factors which affect patterns of reindeer behaviour throughout their natural range and in all their known habitats.
3.1 Introduction
This study of the behavioural ecology of reindeer has concentrated on wild populations in their natural habitats. In addition to the seven subspecies listed in Table 2.1, herds of domesticated reindeer are also found throughout northern Eurasia and have been introduced into North America and onto the subantarctic island of South Georgia. Some of these herds have been bred for their meat, others for use as draught animals and some have been allowed to roam freely and interbreed with wild populations. Because of the great influence of man on the behaviour of these domestic populations they have not been included in this study of behavioural ecology, although their life histories have been considered in the study of zoo-archaeological methods (Chapter 4).

Modern populations of reindeer have been the subject of intensive research. Much of this research has been restricted to individual populations, but some researchers have attempted cross-population comparisons. A great deal of the literature which has been included in this study is concerned with populations of Canadian and North American reindeer. While reindeer populations in northern Eurasia have also been intensively studied, much of the literature is only published in Russian and translations are not yet available. Wherever possible, however, Eurasian sources have also been consulted. This study has concentrated on two areas of reindeer behavioural ecology which are of particular relevance to man - social behaviour and movement patterns.

3.2 The social organisation of reindeer
Reindeer have an open social system with no fixed group structure (Lent 1966, White et al 1981). Group size fluctuates continually, reflecting the adaptive choices and conflicting interests of the individual animals. The basic social unit is the mother and calf pair (Miller et al 1975). The mother-infant bond is strong and while weaning may occur at three to four months, calves will often remain with their mothers until the birth of the new calf the following year. Yearlings are usually repulsed by their mothers at the time of parturition (Epsmark 1975) but in woodland environments yearlings occasionally remain with the new mother-calf pair into their second year of life (Shoesmith and Storey 1977).

Woodland caribou are essentially solitary animals and average group size rarely rises above two or three individuals. In contrast, tundra reindeer regularly form small bands and occasionally form large herds numbering tens of thousands of individuals (Banfield 1954, Kelsall 1968, Egorov 1967). These large aggregations are only temporary phenomena, however, created by the convergence of smaller bands. The formation of large aggregations
occurs on post-calving grounds, during the rut and during the annual long distance migrations between summer pastures and winter ranges (Miller 1974).

As with other ungulates in open environments, three types of groupings regularly occur amongst tundra reindeer - these are nursery groups, bachelor groups and solitary mature males (Estes 1974). Nursery groups comprise cows, calves and occasional yearlings. Bachelor groups include groups of juvenile, subadult and adult males. In addition mixed groups are formed at certain times of year, most notably during the rut and migration (Miller 1974). The size and structure of these bands and herds is very fluid but there is some indication of long-term bonding between individuals. Radio-tracking of caribou bulls by aerial survey has shown that certain animals regularly remain together and return to the same group after a separation of hours or days (Miller et al 1975).

While reindeer social behaviour varies greatly from one area to another, annual fluctuations in group size and structure occur amongst all populations. Patterns of social organisation have no single adaptive function but are the product of multiple selective pressures. In the case of reindeer the five principal factors governing the formation of groups are foraging conditions, predation, harassment by biting flies, breeding strategies and migration (Table 3.1, White et al 1981).

3.2.1 Reindeer foraging strategies and group size

Foraging conditions vary both latitudinally and seasonally. Reindeer have adapted to a highly seasonal environment where plant growth may be limited to two months of the year and where plant diversity is a fraction of that of more temperate regions (Bliss et al 1981, Klein 1986). Annual plant productivity is also limited and site specific, decreasing markedly with latitude. The above-ground standing crop of vascular plants decreases from approximately 225 to 50 gm/m² from alpine and low arctic to high arctic regions (White et al 1981).

The drop in plant productivity with increasing latitude is mirrored by a decline in reindeer group size and density. Mean summer feeding group sizes of 40 individuals in the sub-arctic alpine tundra environment of Hardangervidda in Norway may be contrasted with a mean of 9.3 individuals in the high arctic conditions of the Queen Elizabeth Islands (Miller et al 1977, White et al 1981). As both populations are subject to predation by wolves (Canis lupus) (see discussion below on the effects of predation on group size) the marked difference in group size is therefore not attributable to the effects of predation and may be interpreted as a function of increasing resource patchiness along the latitudinal-altitudinal gradient.

While concentrations of high plant productivity may be found throughout the subarctic and arctic regions, the patchiness of the vegetation becomes more pronounced at
<table>
<thead>
<tr>
<th>Season</th>
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<th>Habitat</th>
<th>Group size</th>
<th>Source</th>
</tr>
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<tbody>
<tr>
<td>Postcalving females + calves</td>
<td>Svalbard</td>
<td>78°N</td>
<td>Open, no predators</td>
<td>7.3</td>
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<td></td>
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<td>Shoesmith &amp; Storey 1977</td>
</tr>
<tr>
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<td>Open, predators</td>
<td>45.8</td>
<td>Egorov 1967</td>
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<td>11.5</td>
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<td></td>
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<td>54-56°N</td>
<td>Closed, predators</td>
<td>3.2</td>
<td>Shoesmith &amp; Storey 1977</td>
</tr>
<tr>
<td></td>
<td>Alberta</td>
<td>57°N</td>
<td>Closed, predators</td>
<td>5.4</td>
<td>Fuller &amp; Keith 1981</td>
</tr>
</tbody>
</table>

Table 3.1 Mean group size in reindeer in relation to season, latitude and habitat type.
the climatic extremes. Skogland (1980) has shown that reindeer population density is highly correlated with the above-ground standing crop of live vascular plants, indicating that reindeer actively select the most productive patches in their environment. As patch size decreases along the latitudinal-altitudinal gradient each patch will facilitate exploitation by fewer individuals.

The productivity of the environment varies not only with latitude but also with season. In the highly seasonal environments of the subarctic and arctic regions snow cover may effectively reduce food availability for up to nine months of the year and restrict reindeer autumn and winter diet to evergreen shrubs and lichens (Bergerud 1972, Skogland 1984a). Reindeer forage beneath the snow by digging craters with their forefeet. Both the depth and hardness of snow will affect their success in feeding.

The density and specific gravity of snow cover changes throughout the winter season (Formosov 1964). Several factors may influence this metamorphosis including wind, rainfall and temperature. Hard compact snow forms under several conditions. Drifting snow which is driven by the wind in the form of a fine dust forms hard and compact crusts on the surface. In late winter partial thawing and subsequent re-freezing also gives rise to compacted crusts and layers within the snow. In continental forests compaction is less common as the forest canopy protects the snow cover from winds and temperature fluctuations. As a result forest snow cover is often deep and soft making movement difficult. In more open areas depth of snow is greatly affected by strong winds which create deep dunes in depressions and corresponding snow-free areas on exposed hills and ridges.

Reindeer can crater through snow up to 65 cm deep but will usually seek lesser depths (Pruitt 1959, Kelsall 1968, Stardom 1975). More important than snow depth, however, is the degree of compaction of snow cover which greatly affects an animal's ability to dig through it. Reindeer have a relatively high threshold of tolerance to digging through compact snow but will avoid areas with a hardness above 25-29 kg cm\(^{-2}\) (La Perriere and Lent 1977, Skogland 1978). Snow depth and compaction affect reindeer group size in exactly the same manner as variable plant productivity by altering the patchiness of the environment. Reindeer respond to increasing resource patchiness by aggregating in the most productive patches. This is reflected by an increase in average group size as the winter progresses, particularly during winters with a heavy snow cover (Fuller and Keith 1981, Shoesmith and Storey 1977, Helle 1981, Stardom 1975).

### 3.2.2 Effects of predation on reindeer social organisation

Modern reindeer populations are subject to predation by a number of carnivorous animals, most notably wolves, wolverines (*Gulo gulo*), lynx (*Felix lynx*), brown bear (*Ursus arctos*), and arctic fox (*Alopex lagopus*) (Egorov 1967, Kelsall 1968). Wolf is the major threat to
reindeer, but wolverine, lynx, fox and bear will also take young calves or scavenge from abandoned kills.

A major function of animal social behaviour is related to the avoidance of predation. Ungulates have evolved physical characteristics which help them to outrun their predators but have also adapted their behaviour patterns in an attempt to minimise the risk of predation. The avoidance strategies which are adopted by prey species are largely determined by their environment.

In closed environments such as forests it has been suggested that dispersal is the best survival strategy against predation (Hirth 1977). The predator's visibility is greatly reduced by trees and successful predation is largely a matter of chance. Reindeer populations in woodland environments have adapted their social behaviour accordingly and are largely solitary animals, occasionally forming groups of three or four individuals.

In contrast to the solitary behaviour patterns of woodland populations, reindeer in tundra environments regularly form large bands. Such clumped social behaviour is thought to be an adaptation to predation in open environments (Bergerud 1974a, Cumming 1975). While clumping increases the visibility of the group, it reduces individual vulnerability in a number of ways. Increased awareness is the most obvious advantage of clumping; the larger the group size the greater is the group's ability to detect predators. This also has an advantageous effect on feeding efficiency. With increasing group size there is a reduction in the level of individual alertness which allows greater time for foraging (Skoog 1968). Aside from increasing overall awareness, clumping also reduces the risk of predation by creating confusion. Predators usually isolate a single individual when hunting. When reindeer are subject to an attack by predators they react by swarming and milling about. The resultant confusion reduces the predators ability to isolate an individual animal, thereby reducing their hunting success.

The key role of predation in determining group size may be illustrated by the behaviour patterns of reindeer in areas where predation does not occur. High arctic populations of Svalbard reindeer live in an open environment devoid of predators or biting flies. Despite the open terrain average group sizes are similar to those of woodland caribou, rarely numbering more than two or three individuals (Gossow 1980).

3.2.3 Group size during the fly season
Parasitic flies are a major problem for reindeer during the summer. The fly season lasts for three to four weeks in July and August and is a period of intense misery for reindeer (Banfield 1954). The most prevalent parasites are warble flies (*Oedamagen* *a* *taran* *d* *i*) and nosebot flies (*Cephenomyia trompe*). The former lay their eggs on the skin and, once hatched, the larvae bore their way through the hide and spend the remainder of their life
cycle in the flesh. Nosebot flies deposit their larvae in the nasal passages of the deer where they grow into maturity before being coughed or sneezed out by their host. Nosebot flies make breathing difficult and can cause severe debilitation. Together with bloodsucking mosquitoes (Culicidae), warble flies and nosebot flies form massive swarms in the warm, still days of July and August. Reindeer have adopted several behavioural traits which help to lessen the impact of these parasitic creatures. Fly activity is temperature dependent, requiring a temperature of at least 13 to 17°C for gad flies, midges, nosebot and warble flies and 7°C for mosquitoes (White et al 1981). Reindeer respond to fly harassment by seeking cooler areas and windy ridges, by dispersing into the forests or by milling together in large aggregations. The former methods are all avoidance tactics related to fly activity. Aggregation in groups reduces fly harassment by diluting the number of attacks on each individual animal. This tactic reaches a level of diminishing returns, however, in groups of more than 2500 animals (Duncan and Vigne 1979, White et al 1981). Aggregation in groups above that number causes pronounced interference with feeding.

Bergerud (1974a) has summarised the effect of fly harassment on reindeer aggregation and movement patterns in different environments. These are listed in Table 3.2.

The effects of predation and biting insects on group size are most marked in the calving strategies adopted by reindeer populations in different environments. All reindeer populations exhibit synchrony in the timing of parturition, a behavioural trait which swamps potential predators with an abundance of neonatal prey. Predators often seek out the smallest and most vulnerable individual within a population. Animals which are born within a few weeks of each other and which are all of roughly equal size are less vulnerable than those which are born over a period of several months.

Populations of woodland caribou respond to the vulnerability of parturition in closed environments by calving individually in the forest. Average group sizes reach an annual minimum during parturition as animals disperse into areas of dense cover. In contrast, reindeer populations in open environments which are subject to attack by wolves and biting insects form large aggregations during parturition. Tundra reindeer usually select high, open terrain for calving. While individual cows are dispersed at the time of calving they join together with other cow-calf pairs to form nursery bands within hours of parturition. A common feature of these calving grounds is the almost total segregation of the sexes. While a few yearling males may be found on the edge of the calving area, no mature males enter the calving grounds and the herd remains segregated for a period of several days (Bergerud 1974a, Lent 1966, Kelsall 1968). Within a few days the nursery bands begin to coalesce and males and barren cows join the nursing females to form large post-calving aggregations. These mixed groups may number between a few hundred and
several thousand individuals and several theories have been proposed to explain their formation.

Bergerud (1974a) suggests that post-calving aggregations are largely a function of predation in open environments, while Miller (1974) believes that the aggregations play an important role in the re-socialisation of winter foraging bands which are broken during the spring migration. Both of these suggestions may have a functional role in the formation of post-calving aggregations. Evidence from tundra-wintering populations of reindeer in the northeastern Northwest Territories of Canada, however, suggests that harassing insects are the most likely cause of large group formation during the post-calving period (Calef and Heard 1980). Three herds of reindeer inhabit the northeastern Northwest Territories. These populations occupy similar calving grounds to the main tundra populations of North America in high and exposed terrain but the large-scale post-calving aggregations of their southern counterparts are not known. While predators occur throughout the summer range, mosquitos emerge later than on the main barren-land ranges and never in such large numbers. A similar absence of post-calving aggregations may be observed amongst Peary caribou in the high arctic where biting flies are rare or absent. It appears, therefore, that while clumping is a function of predation in open environments, large scale post-calving aggregations of caribou are a behavioural adaptation to harassing insects during the short fly season in July and August.

### Table 3.2 Summary of reindeer behaviour in response to fly harassment under differing environmental conditions (from Bergerud 1974a).

<table>
<thead>
<tr>
<th>Terrain</th>
<th>Aggregation</th>
<th>Movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest cover</td>
<td>small</td>
<td>quite sedentary</td>
</tr>
<tr>
<td>No forest cover but wind-swept ridges</td>
<td>moderate</td>
<td>quite sedentary</td>
</tr>
<tr>
<td>No forest cover and discontinuous wind-swept terrain</td>
<td>large</td>
<td>continuous movement</td>
</tr>
</tbody>
</table>

3.2.4 Reindeer breeding strategies

Reindeer mate in the autumn during a short and highly synchronous rut. Reindeer have a polygynous mating system where males attempt to defend a group of females from the attentions of other stags. Dominance hierarchies amongst stags are determined by a combination of display and sparring and occasionally by true fights. As with all other
aspects of reindeer social organisation, the rutting group is not a fixed unit but rather an open association of individuals. The precise structure of the group will change as females join and leave the company (Lent 1965a, Bergerud 1973, 1974b).

Group size varies greatly during the rut from one environment to another but, even amongst the most dispersed populations, average group size increases as oestrous females actively seek out and associate with males. Amongst migratory populations group size may range from 2 to 1000 animals (Lent 1965a). The general trend amongst tundra populations is towards fairly large rutting groups, however, usually scattered over a tundra clearing. Similar studies of rutting behaviour amongst woodland populations indicate that average rutting companies may range in size from very small associations of two or three individuals in closed canopy habitat to larger bands numbering in the region of 40 to 70 animals in more openly forested areas (Fuller and Keith 1981, Bergerud 1973). Bergerud (1973) has suggested that group size during the rut is largely a function of habitat type. Open habitat facilitates greater contact between individuals than closed canopy forest, thereby encouraging the formation of larger breeding groups. Another factor which could influence rutting group size is the adult sex ratio. Bergerud (1974b) has found that average group size increases in response to a decline in the ratio of adult males to females. As females initiate much of the movement in rutting groups and actively seek out males during oestrus, a decline in the number of males within a population could lead to the formation of larger aggregations.

3.2.5 Herd formation amongst migratory tundra reindeer

Animal migration involves the movement of populations from one habitat to another according to the seasons. Many populations of reindeer undertake migrations between winter and summer pastures. The most remarkable migrations are those of the barren-ground caribou of North America and the tundra reindeer of Eurasia (Banfield 1954, Egorov 1967, Kelsall 1968, Geller and Borzhanov 1984). Amongst these populations large scale migrations occur twice annually in the spring and autumn. Spring migrations are usually rapid and direct movements, led by pregnant females anxious to reach tundra calving grounds before the time of parturition. The autumn migration is usually less direct and purposeful and initially involves a leisurely drift from the tundra to the tree line. After the rut the migration becomes more directional and the herds move rapidly into the boreal forest where they disperse to form smaller winter bands.

Tundra reindeer usually migrate over traditional routes often following the same paths and making the same river crossings from one year to the next. Group size during migrations may range from isolated small bands to massive herds sometimes numbering tens of thousands of animals. Large aggregations are usually formed at bottle-necks such as
river crossings but, having amassed, the herds often remain together and may be found moving along well-worn trails in single file.

This migratory movement of entire populations has led many people to regard the herd as the basic unit of reindeer social organisation. Skoog (1968) has defined a herd as a breeding unit which shares the same calving ground over a period of several years. This definition has been generally accepted amongst North American ecologists and the geographical names of calving grounds are widely used to refer to discrete reindeer populations. As with all other aspects of reindeer social organisation, however, large herd formation is a temporary phenomenon reflecting opportunistic behaviour. Amongst the tundra populations small bands of reindeer regularly remain distinct from the main herds and do not join the autumn migrations. Large herd formation and the use of a communal calving ground is also restricted to certain environmental circumstances and specific times of year. The term "herd" is therefore of limited use when discussing the social behaviour of reindeer and should only be applied in those contexts where herd formation occurs. The use of the broader term "population" is used here to describe those animals which share a common gene pool and which form a discrete breeding unit.

3.3 Reindeer movement patterns

Much has been written about the migratory habits of reindeer and their ceaseless nomadic movements. As with reindeer social organisation, however, it is extremely difficult to generalise about reindeer movement patterns. Some populations perform extensive long distance migrations, others move altitudinally to exploit seasonally available resources, and some wander nomadically throughout their annual cycle. In attempting to model reindeer movement patterns it is necessary to distinguish between two different levels of movement, nomadism and migration.

Nomadism involves a ceaseless wandering in search of pasture and is thought to be an adaptational response to environments in which resource density is highly unpredictable in both time and space (Wiens 1976). Nomadic animals have no fixed territories and do not attempt to defend their living space. With no territorial boundaries individuals may cover vast tracts of countryside in search of the most productive areas. Each individual or group moves according to its own needs and, consequently, nomadic movements show no fixed overall pattern. In contrast to the seemingly random nature of nomadism, migrations are direct and purposeful movements of entire populations. Migrational movements need not cover long distances but involve a population shift from one habitat to another. Some populations of reindeer perform both forms of movement but many are purely nomadic.

While the nomadic movements of reindeer often appear to be highly random the direction of these movements is greatly influenced by a number of environmental factors.
The most significant factor influencing reindeer distribution patterns is the availability of forage, but harassing insects and the location of suitable calving grounds also play a role in determining annual movement patterns.

3.3.1 The seasonal availability of forage
Reindeer have adapted to the patchy and unpredictable distribution of resources in northern environments by developing a generalist foraging strategy. They are both browsers and grazers and include a wide diversity of plant species in their diet (White et al. 1981). The most important plant groups include broad-leaved evergreen and deciduous shrubs, lichens, grasses, sedges and fungi (Bergerud 1972). Forage availability varies considerably, however, across the latitudinal gradient from the more productive environments of the boreal forest to the polar deserts of the arctic archipelagos (Klein 1986). This restriction in forage availability is particularly noticeable in the winter diet. Amongst populations wintering in boreal forest habitats arboreal lichens form the staple dietary component. Towards the northern end of their distribution, however, the availability of lichens declines and they are largely replaced in the winter diet by a combination of willows (Salix spp) and mosses.

Forage availability varies not only latitudinally, however, but also with the seasonal cycle. The short summer growing season limits the availability of many plant species to two or three months of the year, while the long months of winter snow cover restrict foraging activity to areas where reindeer can forage effectively by cratering through the snow.

Reindeer have adapted to the seasonal limitations on forage availability by actively selecting the highest quality forage as and when it becomes available (Skogland 1984a). Although lichens represent the staple winter component of many reindeer diets, they quickly lose their place as the preferred forage once new green plant growth appears at the onset of the summer growing season. Lichens are a rich source of carbohydrate but are very low in proteins. Experiments have shown that reindeer which are fed on lichens ad libitum will eventually lose weight (Courtwright 1959). In contrast to the low protein value of lichens, the young shoots of green vascular plants are a rich source of nitrogen, the main building block of proteins. Skogland (1980, 1984a) has shown that reindeer actively select these vascular plants as they begin to emerge during the summer months and concentrate their foraging activity in habitats with high proportions of green phytomass at an early stage of growth.

The timing of new plant growth is largely dependent on the progression of snow melt and will therefore vary according to the nature of habitat relief. In alpine environments the steep relief gradient and the wide variation in aspect combine to create a wide range of
micro-climates. Such environments produce a diverse and varied plant community mosaic with a relatively predictable pattern of growth. South facing slopes with a steep gradient allowing rapid run-off will promote earlier plant growth than north facing slopes with a gentler relief gradient. Reindeer populations in alpine environments have been shown to follow a predictable pattern of seasonal movement which allows them to exploit the most productive summer habitats (Skogland 1980, 1984a). In tundra environments the relative absence of relief promotes a less diverse floral community and areas of rich new plant growth are spread more evenly throughout the summer range. Patterns of movement in tundra environments during the summer months are therefore more opportunistic and less predictable than those of alpine populations.

In woodland habitats reindeer also seek out new green plant growth during the spring and early summer (Bergerud 1972, Helle 1980, 1981). Snow melt occurs earliest in lightly stocked areas or clearings within the forest where increased sunlight penetration also encourages the development of a rich understorey. Spring movements within forest environments are therefore directed away from the mature forests of the winter range towards more open areas such as bogs, clearings, lake shores or areas of alpine tundra above the tree line.

In the high arctic archipelago of Svalbard, hydrological conditions change over very short distances and, as a result, different plant associations lie juxtaposed within a fine mosaic (Tyler and Oritsland 1989). The full sequence of phenological progression occurs within distances of a few metres and this may explain why Svalbard reindeer are essentially sedentary animals.

With the onset of plant senescence at the end of the summer growing season reindeer again alter their foraging preferences to include a higher proportion of non-vascular plants. While lichens and mosses have a general distribution throughout most northern habitats the long months of winter snow cover nonetheless place severe restrictions on winter forage availability. The principal effect of winter snow cover is to increase the patchiness of resource distribution. This is reflected in reindeer foraging behaviour by an increase in the size of the winter range (Table 3.3).

As with group size, the depth and hardness of snow have a considerable effect on reindeer distribution patterns. In open environments reindeer seek out exposed hills and ridges which have been swept free of snow by the wind. The intervening hollows and valleys are avoided, however, as they are rapidly filled with drifting snow which is too deep for reindeer to crater through (Jakimchuk and McCourt 1975, Skogland 1978, Punsvik et al 1980). In forested areas the availability of arboreal lichens obviates the necessity to crater for food and enables reindeer to tolerate greater depths of snow (Edwards and Ritcey 1959, Stardom 1975). Indeed increasing snow depths bring fresh supplies of
<table>
<thead>
<tr>
<th>Population</th>
<th>Summer</th>
<th>Winter</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hardangervidda, Norway</td>
<td>320 km²</td>
<td>1270 km²</td>
<td>Skogland 1984a</td>
</tr>
<tr>
<td>Northeast Alberta (males)</td>
<td>65 km²</td>
<td>335 km²</td>
<td>Fuller &amp; Keith 1981</td>
</tr>
<tr>
<td>Northeast Alberta (females)</td>
<td>77 km²</td>
<td>137 km²</td>
<td>Fuller &amp; Keith 1981</td>
</tr>
</tbody>
</table>

Table 3.3 Seasonal fluctuations in range size in two reindeer populations.

Lichens within the reach of browsing deer. The most luxuriant and accessible lichen pastures grow in moderately stocked, mature forests which are selected by reindeer as preferred winter range (Bloomfield 1980). The forest canopy also protects the snow cover from wind exposure, however, and hence from the formation of hard crusts. During winters with a heavy snow fall the lack of wind exposure may result in the formation of great depths of soft snow which cannot support an animal's weight and which may effectively prohibit movement. Under such conditions reindeer distribution is restricted to open areas within the forest such as frozen lakes or bogs.

3.3.2 Harassing insects
Parasitic insects also affect the distribution patterns of reindeer during the short fly season in July and August. Severe fly harassment has a significant effect on reindeer foraging behaviour, limiting their ability to forage effectively and causing considerable distress. Reindeer attempt to minimise the effects of fly harassment by taking evasive action. As insects are inactive at high wind speeds (more than 6 metres per second) and at temperatures below 7°C, reindeer actively seek out exposed hills and ridges where the wind velocity is high, or move to cooler areas such as snow beds, lakes and coastal waters where fly activity is reduced (White et al 1981, Walsh et al 1992).

3.3.3 The distribution of calving grounds
A third factor governing the annual movement patterns of reindeer is the distribution of suitable calving grounds. The selection of a suitable area for calving is dependent on the nature of the habitat. In woodland habitats reindeer have adopted an anti-predator strategy which involves concealing the young in isolated hiding places (Shoesmith and Storey 1977, Helle 1980, 1981). The cows are dispersed at the time of parturition in areas of dense forest cover. Island environments which offer the additional escape route of open water are also
sought by many woodland populations (Bergerud et al 1990). In contrast, reindeer in open environments have adopted an anti-predator strategy which involves swamping the predator with a superabundance of neonatal prey (Skogland 1985). Calving takes place in a well-defined open and coverless area and cow-calf pairs join together to form maternal bands within a few hours of birth.

Tundra calving grounds are usually located on the highest and least hospitable terrain available, where snow and ice is late-lying and where the flora is impoverished and late-developing (Kelsall 1968, Calef and Heard 1980). A positive correlation has been observed between zones of greatest snow cover and areas of concentrated calving (Eastland et al 1989). It has been suggested that the selection of these areas may be influenced both by nutritional requirements and predator-avoidance strategies.

Delayed snow-melt results in the late onset of new plant growth. As a result, pregnant females arrive at the snow-bound calving grounds just as the earliest spring growth is beginning to appear and at a time when forage nutrient levels are at their highest. The selection of late-lying snow areas can therefore be seen to be nutritionally advantageous for pregnant and lactating females.

The selection of snow fields in high and broken terrain may also form part of an anti-predator strategy. Wolves are relatively immobile at this time of year, being restricted to their own denning sites (Kelsall 1968). The latter are generally located in dry, well drained terrain away from areas of wet, melting snow which makes travel difficult. Kelsall has further suggested that late-lying snow and ice on calving grounds may inhibit the early activity of biting insects, thus reducing the likelihood of harassment to the developing calf.

Tundra calving grounds are used repeatedly each year and historical records show that barren-ground caribou have returned to the same grounds over a period of several decades (Banfield 1954, Kelsall 1968). Many of the barren-ground populations take their name from the geographical location of these calving grounds. The Kaminuriak population of the Canadian Northwest Territories, for example, derives its name from the traditional calving grounds around Kaminuriak Lake. A similar loyalty to calving grounds has been recorded amongst woodland caribou populations. Individual animals have been found to return to the same location over a period of several years (Shoesmith and Storey 1977). Miller et al (1977) have demonstrated that the Peary caribou of the Canadian archipelago make extensive inter-island movements between winter and summer ranges and suggest that this may also be explained by a strong affinity to traditional calving grounds.

The use of traditional calving grounds amongst all populations of reindeer provides a fixed geographical location within the annual pattern of movement. Foraging conditions and insect harassment may encourage nomadic movement across a wide geographical range.
but the traditional use of calving grounds will always bring reindeer back to the calving area at the time of parturition.

### 3.3.4 Factors affecting overall range size

The annual range of modern reindeer populations varies in size from little more than 1000 km² for populations of woodland caribou to several hundred thousand km² amongst the barren ground populations of northern Canada and Alaska (Fuller and Keith 1981, LeResche 1975). The overall extent of the annual range appears to be dependent on two variables, population size and the maximum distance between preferred seasonal habitats.

Long-term studies of reindeer population dynamics have shown that population size is not static but fluctuates over a period of several decades. The growth curve of the Nelchina population of south central Alaska, for example, has been shown to have a periodicity approaching 100 years (Skoog 1968, Hemming 1975). Arguments abound as to the mechanisms involved in these fluctuations. Most discussions centre on the role of wolves (eg Van Ballenberghe 1985, Bergerud and Ballard 1988), although a recent study has suggested that unpredictable short-term fluctuations in weather conditions may be the principal cause of periodic changes in population size (Caughley and Gunn 1993).

Fluctuations in population size are reflected in the annual range. In the case of the Nelchina population, an increase from 10,000 animals in 1950 to a maximum of 70,000 animals in 1961 was mirrored by a threefold expansion in the annual range. The annual distance travelled by the Nelchina herd also increased from 600 km in 1955 to 1,580 km in 1964 (Hemming 1975).

Similar fluctuations in population size and annual range have been recorded for many of the barren-ground populations of northern Canada and Alaska (Parker 1972, LeResche 1975). Despite these fluctuations in annual range the areas of summer use remain substantially unchanged. As population size increases reindeer respond to grazing pressure by increasing their winter range or by emigrating to new areas. As population size declines the winter range contracts again towards the traditional summer calving grounds. Skoog (1968) identified this contracted range as the centre of habitation, around which reindeer will tend to concentrate over time.

While population dynamics affect the overall size of the annual range, the distance between preferred seasonal habitats determines the minimum area of the centre of habitation. In forest environments ideal habitats include a combination of mature forests with rich arboreal lichen growth for winter range, densely forested areas for secluded calving and open bogs, clearings and alpine tundra areas for summer pasture. In open environments the centre of habitation includes well drained open areas for summer pasture,
high exposed and broken terrain for calving, hill-tops, lakes or coastal waters for relief from insect harassment and wind-swept hills and ridges for winter foraging.

Along the ecotone between continental tundra plains and the northern timberline of boreal forests an ideal combination of forested and open habitats permits the growth of large reindeer populations and encourages the development of long distance movement between winter and summer range. This is the environment exploited by the populations of barren-ground caribou of North America and the tundra reindeer of northern Eurasia. Boreal forests provide a rich and plentiful supply of winter forage in the form of arboreal lichens, while the adjacent tundra plains offer open areas of seasonally luxuriant green plant growth. Under these circumstances the distance between preferred seasonal habitats is often great, involving a movement of several hundred kilometres. Such long distance movements are superimposed upon the nomadic movements associated with localised forage availability and may be regarded as genuine migrations.

The long distance migrations of barren-ground caribou have definite directional goals. The aim of the spring migrations is clearly to reach the traditional calving grounds. The movement is led by pregnant cows, with barren females and males bringing up the rear. Once the spring migration has begun little can change the direction of the movement or slow it down. Adverse weather conditions or early thaws cause little more than temporary diversions (Kelsall 1968). The principal goal of the autumn migration is to reach the shelter of the boreal forest and its supply of winter forage. Some bands of reindeer do not make the return journey to the forests, however, but winter on the arctic plains (Banfield 1954, Kelsall 1968).

Long distance migrations often make use of traditional routes and river crossings. Occasionally routes will change, however, and new areas of winter range will be exploited. Traditional migrations may also cease altogether as a result of a population crash. The deaths of most of the population of the Novosibirsk Island in the 1930s, for example, resulted in the cessation of migration to the mainland (Baskin 1986). Although the island population was restored to its former levels by the 1970s the reindeer have not resumed their former migrations.

While the nomadic behaviour of reindeer in woodland, alpine and open environments has often being described as migratory, these movements seldom involve the whole population in a single directional relocation. Nomadic movements are not as random as they might at first appear and may be predictable under certain environmental conditions. Such nomadic movements are not comparable, however, with the highly predictable migrations undertaken by barren-ground populations. The use of the term "migration" should therefore be reserved for situations where a broad ecological zonation results in the long distance separation of seasonally preferred habitats.
3.4 Summary

The social organisation and movement patterns of reindeer are clearly influenced by a number of environmental factors. The mean annual size of reindeer groups is governed by two primary factors, latitude and predation. The former determines forage availability and resource patchiness, resulting in a decrease in group size as one moves northwards along the latitudinal gradient. Predation affects reindeer group size differently according to habitat type. Reindeer respond to predation in open environments by forming large aggregations. In the closed habitats of wooded environments reindeer have developed a dispersed anti-predator strategy and group size is generally small. Several secondary factors also affect mean group size on a seasonal basis. Biting flies, breeding strategies and migration all influence the seasonal pattern of reindeer aggregation and dispersal.

The primary factor influencing reindeer movement patterns is the differential availability of forage. In response to the highly seasonal environments of northern latitudes, reindeer have developed an extreme form of nomadism and they are constantly on the move in search of good quality forage. In closed forest habitats small group sizes result in seemingly random movements of animals throughout their annual range. In open environments, where aggregation sizes are generally larger, it is possible to observe patterns within the annual cycle of movements.

Movement patterns are most predictable in environments which offer a high degree of floral diversity, such as the small scale topographic variation offered by alpine environments and the unique combination of habitat types offered by the ecotone between tundra and boreal forest. Movements patterns within homogeneous environments such as rolling open tundra plains are relatively opportunistic and are generally less predictable than those in alpine environments. One aspect of the annual cycle which offers a degree of predictability, however, in all reindeer populations is the time of parturition. Traditional calving grounds are re-used over a period of years and decades and provide a fixed point within the annual cycle of movement in all habitat types.

In attempting to reconstruct the behaviour patterns of Devensian reindeer in Britain, it is necessary, therefore, to begin with an analysis of environmental conditions. Factors such as climate, habitat type and predation may be assessed through an analysis of the fossil floral and faunal record (Chapter 7 to 9). While a reconstruction of Devensian environmental conditions will facilitate the modelling of reindeer behaviour patterns, the seasonal distribution of Devensian reindeer must also be assessed through the zoo-archaeological analysis of Devensian faunal remains.
4.1 Introduction
In order to reconstruct the behavioural ecology of Devensian reindeer, it is first necessary to determine the seasonal distribution of reindeer from an analysis of the faunal remains. Seasonality in faunal remains is of considerable interest to zoo-archaeologists concerned with the study of human settlement and subsistence patterns. A number of methods have therefore been devised by which seasonality may be determined (Chaplin 1971, Davis 1987). These methods are mostly derived from zoological and veterinarian studies and are adapted for use with archaeofaunal material. The basic premise of these methods is that seasonal aspects of an animal's life history will be reflected in the growth and development of the skeleton.

Reindeer life history has been extensively studied by zoologists working in both Eurasia and North America and is well documented in the zoological literature (Banfield 1954, Egorov 1967, Kelsall 1968, Skoog 1968, Leader-Williams 1988). These studies have revealed two seasonal aspects of reindeer life history, the breeding season and the antler cycle, which have a significant effect on patterns of skeletal growth. The highly seasonal nature of the reproductive cycle in reindeer affects the development of the entire skeleton but is particularly visible in the growth patterns of mandibles, maxillae and long bones. As seasonality in teeth and bones is visible only where growth is incomplete, adult bones have not been considered in this study. In contrast with bones, the growth and shedding of antlers occurs on an annual basis and continues throughout life. This cycle of growth is also highly seasonal in nature and offers a valuable source of information in the determination of seasonality.

4.2 The breeding season
As with all northern ungulates, reindeer have adapted to the highly seasonal nature of their environment by developing a short and synchronous breeding season (Baker 1938). Reindeer mate in autumn when animals come together for the rut, a period of intense sexual activity which lasts for little more than two weeks. Studies of both reindeer and caribou have shown that 80-95% of conceptions occur within a period of 10 days (Dauphiné and McClure 1974, Leader-Williams 1988). This short rut produces an equally short and synchronous calving season. While calving may be spread over a total of 4-5 weeks, 80-90% of all calves are born within a peak 10 day period (Lent 1966, Kelsall 1968, Skoog 1968, Holthe 1975, Bergerud 1975, Leader-Williams, 1988).
This marked synchronicity in calving ensures that all animals in a single year-class are of roughly equal age and will pass through the same developmental stages at approximately the same time. An ability to determine age at death may therefore be used to determine seasonality in faunal remains.

The exact timing of calving in modern populations ranges from mid-April to mid-June. Such variation in timing is thought to be an evolutionary adaptation to latitude, ensuring that parturition coincides with the peak of plant productivity. Leader-Williams (1988) has established a correlation between latitude and the timing of calving which suggests that calving in British populations between latitudes 49 and 57° N would have occurred around the middle of May. While this might be appropriate for modern day conditions, other factors, such as climate, may also influence the timing of calving and may have resulted in earlier or later calving times during the last glaciation. Nonetheless, an assumed calving date of mid-May provides a reasonable basis for the timetabling of development and growth in calf and yearling animals and will be used throughout this work.

4.2.1 Mandibles and maxillae
Three zoo-archaeological methods have been established for determining age and season of death from mandibles and maxillae. These methods involve the analysis of tooth eruption sequences, wear patterns and crown heights. Each of these methods draws upon the assumption that synchronicity in the timing of births will be reflected in the eruption and wear of the teeth.

The study of tooth eruption sequences makes use of the sequential eruption and wear of deciduous and permanent teeth. At birth reindeer calves have a full set of milk incisors and canines but their deciduous premolars are either absent or in the process of erupting. In the course of the following 29 months these deciduous premolars come into occlusion and are worn down, permanent molars begin to erupt, and the deciduous premolars are eventually replaced by their permanent successors (Fig. 4.1). These events occur in a well documented sequence (Miller 1974) and three occur within a sufficiently short period that they may be used to determine age and season of death (Table 4.1).

The discovery of juvenile mandibles with deciduous premolars which are not yet fully erupted provides clear evidence of neonatal death within the first week of life. Similarly a mandible or maxillary fragment with the first molar in the process of erupting above the bone can also be used to determine season of death within a three month period from mid-August to mid-October. While the second molar does not begin to appear above the gum until the early spring, the formation of the tooth is already well under way by the end of the first summer. During the winter months, from October to March, the second molar
Fig. 4.1 Deciduous (a) and permanent (b) dentition of reindeer.
Table 4.1 Age and season of eruption of deciduous and permanent teeth in reindeer.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Age</th>
<th>Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous premolars</td>
<td>Birth - 1 week</td>
<td>Late May</td>
</tr>
<tr>
<td>Molar 1</td>
<td>3 - 5 months</td>
<td>Mid-August - mid-October</td>
</tr>
<tr>
<td>Molar 1 erupted, Molar 2 in crypt</td>
<td>5 - 10 months</td>
<td>Mid-October - mid-March</td>
</tr>
<tr>
<td>Molar 2</td>
<td>10 - 15 months</td>
<td>Mid-March - mid-October</td>
</tr>
</tbody>
</table>

will be visible in the crypt and a perforation may already have formed in the surface of the bone. The tooth may begin to erupt above the gum-line at any time between months 10 - 15, suggesting a season of death between March and August.

While patterns of eruption and replacement may be used to determine season of death for complete tooth rows, two additional methods are often used to determine seasonality from incomplete tooth rows and isolated teeth. These methods estimate age at death by measuring the degree of wear which is visible in high-crowned cheek teeth (Hillson 1986).

Reindeer belong to the order Artiodactyla (even-toed ungulates) and the suborder Ruminantia (Banfield 1961). All ruminants have high-crowned (hypodont) teeth with many deep infoldings on the enamel surface (Hillson 1986). The herbivorous diet of ruminants results in rapid attrition of the teeth which continues throughout life. This wear is usually recorded as a series of changing patterns on the occlusal surface as complex loops and pleats of enamel, dentine and cementum are gradually exposed.

Bouchud (1966) attempted to determine age (and hence season of death) from a study of these wear patterns in reindeer teeth. He devised 11 categories, ranging in age from 3 weeks to 48 months. Subsequent research (Miller 1974, Spiess 1979) has shown that the range of individual variation, both in the timing of eruption and the progress of wear on the teeth, is far greater than Bouchud had expected and that wear patterns in permanent teeth can only be used to determine broad age classes. The progress of wear is faster, however, in the deciduous teeth of calves and the wear patterns produced can be used to determine approximate age and season of death.

The deciduous premolars of reindeer come into occlusion during the first few weeks of life and are subject to immediate and rapid wear. Calves begin to forage within days of their birth but their initial attempts are experimental and include many unlikely items such as dirt and rocks (Bergerud 1972). Unworn teeth are therefore clear indicators of neonatal death. Subsequent wear on the teeth has been classified by Spiess (1979) into three categories, high relief, moderate wear and heavy wear (Table 4.2). High relief teeth are characterised by cusps which are higher on the lingual side of the tooth and which feel sharp to the touch. This category corresponds with an age class of 1-7 months and a
Table 4.2 Wear stages in reindeer deciduous teeth.

<table>
<thead>
<tr>
<th>Wear pattern</th>
<th>Age</th>
<th>Season of death</th>
</tr>
</thead>
<tbody>
<tr>
<td>High Relief</td>
<td>1-7 months</td>
<td>June to December</td>
</tr>
<tr>
<td>Moderate wear</td>
<td>8-15 months</td>
<td>January to August</td>
</tr>
<tr>
<td>Heavy wear</td>
<td>16-29 months</td>
<td>No evidence of seasonality</td>
</tr>
</tbody>
</table>

seasonality of June to December. The cusps of moderately worn teeth are more rounded and the buccal and lingual sides are approximately the same height. These teeth can be assigned to an 8-15 month age category and a broad season of death of January to August. The third wear class of heavily worn teeth covers the period of 16-29 months but is too imprecise for use in determining seasonality.

A more precise measure of wear which does not rely on a subjective interpretation of wear stages is the measurement of crown height. This measurement is taken on the most mesial cusp of the tooth and is measured from the neck of the tooth to the surface using Vernier calipers (Fig. 4.2).

Crown heights are widely used to determine age at death in both zoological and archaeological samples. Several archaeological studies have also attempted to determine seasonality from an analysis of crown heights and have been particularly successful for species such as roe deer and gazelle whose deciduous dentition is replaced within little more than a year (Legge and Rowley-Conwy 1987, Legge and Rowley-Conwy 1988). Any discontinuity in the distribution of crown heights may be used to determine the degree of seasonality in the sample and the season concerned may be estimated by comparison with attrition rates in modern populations.

Crown heights have been recorded for the permanent molariform teeth of reindeer (Miller 1974) but unfortunately no comparable information is available for the deciduous teeth. As with the analysis of wear patterns, the faster rate of attrition in the deciduous premolars makes them the preferred choice for an analysis of seasonality. In the absence of comparative modern data, crown heights may only be used to determine the degree of seasonality within a sample and can not give any precise indication as to the season of death. In conjunction with wear patterns and eruption sequences, however, crown heights may provide valuable additional information on the seasonal distribution of deer.

4.2.2 Epiphysial fusion and bone growth

As with mandibles and maxillae, the determination of seasonality from bones rests on the assumption that synchronous birth in reindeer will produce discrete size classes visible in
Fig. 4.2 Crown height measurements.
the archaeological material. While adult reindeer exhibit a marked sexual dimorphism, this
does not begin to appear until the second year of life (Leader-Williams and Ricketts 1982).
There is thus no size variation between male and female calves, and size at birth is largely
dependent on maternal health and nutrition (Skogland 1983, Skogland 1984). As 80-90% of
calves are born within a two week period in early summer, the mean size of a sample is
therefore indicative of both age and season of death.

In the analysis of an archaeofaunal assemblage, discontinuity in the size distribution of
juvenile bones may be used to determine the seasonality of death. Bone dimensions are
recorded in millimetres using Vernier calipers and a range of standard measures established
by von den Driesch (1976). Continuity in the size distribution indicates year round
presence, while gaps in the spread of measures may be interpreted as seasonal absence

In order to eliminate size variation as a result of sexual dimorphism it is essential to
distinguish between size groupings which reflect age classes and those which reflect sex.
This is possible only for bones whose age can be identified on the basis of epiphysial fusion.

Most long bones of the body consist of two parts, the diaphysis (shaft) and the
epiphyses (articular ends). At birth these two portions of the bone are unfused allowing
continued growth to take place at the epiphysial end. Once the bone reaches its maximum
length the epiphysis fuses with the diaphysis and no further growth occurs. The age at
which fusion takes place varies from one skeletal element to another and the sequence and
approximate age at which these events occur in reindeer is given in Table 4.3.

The timing of epiphysial fusion is not precise enough to determine the exact season of
death but does enable the identification of discrete year groups. When used in conjunction
with a measure of size, it is therefore possible to determine the degree of seasonality in the
age and size distribution of an archaeofaunal assemblage.

4.2.3 Size distribution of juvenile bones

By comparing archaeofaunal collections with data obtained from modern populations, it
may be possible to calibrate the size distribution of a prehistoric sample. Reindeer biology
has been extensively studied and data are available for many skeletal elements, including the
hindfoot, mandible and femur (Kelsall 1968, Reimers 1972, Miller 1974, Dauphiné 1976,
Leader-Williams and Ricketts 1982).

Spiess (1979) used modern records of foetal hindfoot length to calibrate season of death
in reindeer at the Palaeolithic site of Abri Pataud in western France. The hindfoot measure
recorded by zoologists is not directly comparable, however, with any single bone. In order
to overcome this problem, Spiess analysed the size relationship between the hindfoot and
other skeletal elements in modern museum specimens. The resulting proportions were
<table>
<thead>
<tr>
<th>Epiphysis</th>
<th>&lt;1</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
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<tr>
<td>Proximal first phalanx</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal second phalanx</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal third phalanx</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Calcaneum</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal metacarpus</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal metacarpus</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal metatarsus</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
</tr>
<tr>
<td>Distal metatarsus</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal ulna</td>
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<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal ulna</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal radius</td>
<td>++</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal radius</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal tibia</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal tibia</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal humerus</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal humerus</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Proximal femur</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Distal femur</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ilium tuberosity</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Ischium tuberosity</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Fusion of ilium &amp; ischium</td>
<td>+</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
<td>++</td>
</tr>
</tbody>
</table>

Table 4: Epiphyseal fusion of the postcranial skeleton in reindeer. (- = unfused, + = fused but suture visible, ++ = completely fused, blank = no data available (from Egorov 1967)
used to determine age and season of death in the archaeological material. The validity of this technique rests on the assumption that the bones of growing animals are in the same proportions as those of the adult skeleton. The pattern of growth varies greatly however, from one skeletal element to another. Some bones, such as the distal humerus, fuse at a very early age, while others, such as the mandible, may continue to increase in size up to 6 years in age (Reimers 1972). Recent research has also shown that rates of growth vary considerably from one element to another (Leader-Williams and Ricketts 1982). The calibration of seasonality in the size distribution of juvenile bones should therefore be restricted to those bones for which good modern data are available.

Two bones, the mandible and femur, have been studied in detail by zoologists. A sample of 943 caribou mandibles was obtained from the Kaminuriak population in northern Canada (Dauphine 1976) and a smaller sample of 300 mandibles and femurs was studied from a population of introduced reindeer on South Georgia (Leader-Williams and Ricketts 1982). The measures used correspond with the measures of greatest length (GL) established by von den Driesch (1976).

Leader-Williams and Ricketts (1982) have established two growth curves which describe growth in reindeer from conception through to adulthood. Reindeer exhibit very rapid growth during the first year of life increasing their body weight by 800% and achieving approximately 80-90% of total adult size (Dauphine 1976, Leader-Williams 1988). Growth rates are not fixed, however, and drop markedly during the first winter in response to a reduction in food intake and a decline in fasting/resting metabolic rate (Reimers 1983). This pattern of growth from conception to 12 months can be described by a logistical curve which has been defined as:

\[ t = t_i - \frac{1}{k} \ln(A-Y/Y) \]

where \( t \) = age (in months), \( t_i = 0 \), \( Y \) = length, \( k \) = growth rate and \( A \) = asymptotic length (Leader-Williams and Ricketts 1982).

Growth from 12 months onwards is at a greatly reduced rate and is described by a standard growth curve with the equation:

\[ Y = A - Be^{-kt} \]

where \( Y \) = mean length at age "\( t \)" months, \( A \) = asymptotic length, \( B \) = integration constant and \( k \) = growth rate.

Growth rates and asymptotic lengths have been established for both mandibles and femurs from the population of introduced reindeer on South Georgia (Table 4.4). The growth rate from 12 months onwards is too slow to allow the accurate determination of age from a measure of bone length. The curve from -6 to 12 months is sufficiently steep, however, to be used on foetal and calf bones to establish both age and season of death.
<table>
<thead>
<tr>
<th>Measurement and sex</th>
<th>Growth from -6 to 12 months</th>
<th>Growth after 12 months in age</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Growth rate (k)</td>
<td>Asymptotic length (A)</td>
</tr>
<tr>
<td>Jaw</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>0.30</td>
<td>208</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>0.42</td>
<td>225</td>
</tr>
<tr>
<td>Female</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 4.4 Growth rates and asymptotic lengths (mm) for reindeer mandibles and femurs (from Leader-Williams and Ricketts 1982).
In applying this method to archaeological material it must be remembered, however, that the mean size of adult animals may vary considerably from one population to another (Banfield 1961, Skogland 1983). The asymptotic lengths established by Leader-Williams and Ricketts (1982) relate to a modern population of reindeer derived from Norwegian stock. The asymptotic lengths of prehistoric populations are unknown and may have varied considerably from those of the South Georgian sample. The calibration of seasonality in the size distribution of juvenile bones should therefore be used with care and, where possible, with the support of alternative lines of evidence.

4.3 The antler cycle

Antlers of deer are a dermal bone formation attached to the frontal bones of the skull. They consist of living tissue which resembles bone in its physiology, chemical composition and cellular structure (Modell 1969). In contrast to the true bones of the body, however, antlers are grown and shed annually. This annual cycle of growth has three distinct stages which may be used to determine season of death from archaeological samples.

The first stage in antler development is the period of growth when antlers are covered with velvet. This layer of skin protects the numerous nerves and blood vessels which supply the antlers with the nutrients necessary for rapid growth. Once growth is complete, antlers become ossified, the velvet is shed and the hardened antler is exposed. Clean, hardened antlers are carried for varying lengths of time according to species, until resorption of bone at the base of the antler results in shedding. New skin grows over the antler scar and thus regeneration begins.

In most species of deer antler growth is a male secondary sexual characteristic which is related to testosterone levels in the blood (Goss 1983). Females and castrated males of these species do not usually carry antlers. Reindeer are unique amongst cervids in this respect, however, and antler growth occurs in all animals regardless of age and sex.

The timetabling of antler growth in reindeer has been widely studied by zoologists and a generalised pattern of events has been established (Fig. 4.3) (Banfield 1954, Skoog 1968, Leader-Williams 1979, Bergerud 1976). Variation in the exact timing of events occurs from one population to another and is illustrated in Fig. 4.3 by the overlapping stages of growth.

Reindeer calves are born without antlers but growth begins at two months of age and continues throughout the first summer. A prolonged period of velvet cleaning begins in September or October and the antlers are not shed until late spring or early summer. Male calves may shed their antlers a few weeks earlier than females, a pattern of events which becomes more pronounced with each successive year of life. By the time they reach adulthood, the antler cycles of male and female reindeer are approximately six months out of phase. Adult males shed their antlers shortly after the rut, between October and
Fig. 4.3 Generalised timetable of annual antler cycle in reindeer (data from Bantfield 1954, Skoog, 1968, Bergerud 1976, Leader-Williams 1979)
December, while females shed their antlers on the calving ground within a few days of parturition.

This sexual variation in the timing of the antler cycle has a significant effect on the usefulness of reindeer antler in zoo-archaeological studies. Antlers may only be assigned to the correct season of death/shedding if both age and sex are known. The pattern of reindeer antler growth varies with both these parameters and several methods have been devised which enable the determination of age and sex from shed and unshed antler.

4.3.1 Unshed antler

The age and sex of unshed antlers which are still attached to the skull may be determined by analysing the shape of the suture between the frontal and parietal bones (Wollebaek 1926, Bouchud 1966). Antlers are attached to the skull through a bony outgrowth of the frontal bone known as a pedicle. The pedicles of male antlers increase in size on an annual basis (Banfield 1960). This increase occurs at the expense of the parietal bone and results in a change in the shape of the frontal-parietal suture. In females and juvenile males the angle formed by this suture is obtuse while that of adult males is close to 90° (Figs. 4.4 - 4.6). Adult females can also be separated from juvenile animals of either sex on the basis of the complexity of the suture. Suture patterns in young animals are very simple allowing for the continued growth and expansion of the bones (Fig. 4.6). In adult skulls the two bones are thoroughly interwoven creating a complicated pattern which will remain throughout life (Fig. 4.4).

Given the fragile nature of cranial bones, skulls are rarely found in the archaeological record with the frontal-parietal suture intact. In order to compensate for this, Bouchud (1966) suggested a method for determining the sex of skulls where only a fragment of the suture survives. This method is based on the observation that the distance between the pedicle and the frontal-parietal suture is greater in females than in males. No statistical analyses have been carried out to confirm this observation and the method relies on a subjective classification of distance. This method has therefore not been used in this study. An alternative method uses antler size to identify adult males from juvenile males and females. This method is particularly useful for shed antlers, where the sex of the animal is known, but may also be used with unshed antlers to aid in the identification of mature adult males (see further discussion below).

In the case of skulls where the frontal-parietal sutures are complete, age and sex may be determined with some measure of accuracy. Season of death may also be established for such antlers through an analysis of their stage of development in the annual cycle of growth (Bouchud 1966, Sturdy 1975). Three changes may be observed in fossil antler which correspond with the stages of active growth, ossification and incipient shedding.
Fig. 4.4 Frontal-parietal suture pattern in adult males.
Fig. 4.5  Frontal-parietal suture pattern in adult females.
Fig. 4.6  Frontal-parietal suture pattern in juveniles.
During the stage of active growth (March-July in males, July-September in females) arteries and veins carry blood to and from the developing antler. These arteries are visible in fossil antler in the form of perforations near the base of the pedicle. The perforations disappear once the growing antler has reached its maximum development and ossification begins.

The process of ossification results in the transformation of the spongy bone in the base and lower half of the antler into compact, calcified bone. Compact bone begins to appear in July in males and in September in females. The presence of compact bone in fossil antlers can therefore be used to determine a crude season of death of July to December in males and September to May in females. As calves and yearlings do not form compact bone, this method may only be applied to clearly adult skulls.

Resorption of bone occurs at the base of the antler shortly before casting in response to hormonal change. This is visible in the form of a clear shed line which appears around the pedicle (Fig. 4.7). As casting takes place within two weeks of the appearance of a shed line, these lines may also be used with some accuracy to determine season of death.

After casting, a new layer of velvet forms over the surface of the pedicle scar and regrowth of the antler begins. Female and juvenile males begin antler regrowth almost immediately after casting. In adult males the period between casting and regrowth becomes increasingly longer with age and fully mature males may remain antlerless for periods of up to six months. The discovery of skulls with pedicle scars and no antler regrowth may therefore also provide some indication of season of death. Female skulls with pedicle scars indicate death in May or early June, those of juvenile males indicate death between February and May, and those of adult males indicate death at some time between October and March.

4.3.2 Shed antler
Two methods have been developed which enable the determination of age and sex from shed antlers. These methods make use of morphological distinctions in the shape of the antler base and of size variations in the girth of the antler beam.

4.3.2.1 Morphology of the antler base
A clear distinction may be observed in the shape of the antler base in males and castrated deer (Hatt 1918, Jacobi 1931). The antlers of castrated deer are shed immediately below the burr and the basal surface of the antler is generally concave or flat. Male antlers, on the other hand, retain a small portion of the pedicle which forms a collar below the burr. The shedding surface is usually convex but may also be concave or flat.
Fig. 4.7 Shed line on female pedicle indicative of imminent casting.
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| N      | 33    | 32    | 32    | 33    | 26    | 26    |
| x      | 21.9  | 18.6  | 27.8  | 23.7  | 22.0  | 15.2  |
| SD     | 4.7   | 4.3   | 6.3   | 5.5   | 5.4   | 3.6   |

Table 4.5 Morphology and size of 34 female antlers from Glenmore, Cairngorm. Measurements (in mm) correspond to those illustrated in Fig. 4.11 (Bws = Broken while shedding).

Bouchud (1966) suggested that a similar distinction might exist between the shedding surface of females and males, the female surface corresponding to that of castrated deer. This method was adopted by Sturdy (1975) in his study of Late Glacial reindeer in Germany but was dismissed by Spiess (1979) in his major study of reindeer zoo-archaeology on the grounds that it was too inaccurate. Spiess based his criticisms on the results of a
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Table 4.6 Morphology and size of 26 male antlers from Glenmore, Cairngorm. Measurements (in mm) correspond to those illustrated in Fig. 4.11.

study of 11 male antlers from museum collections which showed the curvature of the antler base to be an unreliable indicator of sex. In order to test this method more fully, a sample of modern antlers has been collected for analysis and the data obtained are listed in Tables 4.5 and 4.6.

The modern sample was obtained from a herd of domestic reindeer which was introduced to Scotland between 1951 and 1954 (Reindeer Council of the United Kingdom 1952, 1953, 1954, 1955). The reindeer, which are of Norwegian stock, graze freely on the hills and feed predominantly on the natural vegetation of the Cairngorms. For periods of the year, however, the animals are enclosed and their diet is supplemented with a grain feed. The antlers of these deer are usually collected and sold to tourists. Females and calves shed their antlers as normal but male antlers are sawn shortly before the rut because of the danger that they represent to themselves. No naturally shed adult males were therefore available for study.
The Cairngorm reindeer herd is small, numbering no more than 80 animals at any one time. Each of these animals is known to the keeper by name and the age and sex of the collected antlers is recorded. Thirty three female antlers were studied, all of which were shed immediately below the burr in the manner described by Hatt and Bouchud (Fig. 4.8). While the majority had a concave basal surface, the shedding surface in 4 cases was more or less flat. Five shed juvenile male antlers were also available for study and each of these exhibited the collar below the burr, described by Hatt and Bouchud as being characteristic of males (Fig. 4.9). This feature was absent from all the female antlers studied.

The Cairngorm antlers appear to confirm Spiess' criticism of the use of the curvature of the antler base as an indicator of sex. The variation in the position of the shedding surface is a clear sexual characteristic, however, and may be used to determine the sex of shed antlers and hence their season of casting.

In the case of females, most antlers are shed on the calving ground within 7 days after parturition (Lent 1965b, Epsmark 1971, Bergerud 1976) As calving is a highly synchronous activity, the discovery of shed female antlers will usually indicate a clear season of presence during middle to late May. Barren cows may shed their antlers up to two months earlier than pregnant cows, however, and this may affect the determination of season of presence. Pregnancy rates obviously vary according to the health and nutritional status of a population but a study of introduced reindeer on South Georgia indicated pregnancy rates of more than 90% in all animals aged one year and over (Leader-Williams 1980). The antlers of barren females may therefore occur in small numbers and this possibility must be borne in mind, particularly when assessing season of herd presence from small collections of female antlers.

The season of antler shedding in males is less precise than that of females and is dependent upon the age of the animal concerned. This may be determined through an analysis of antler size, as the length, girth and complexity of male antlers increase on an annual basis.

4.3.2.2 Size as an indicator of age
The antlers of male calves are little more than spikes. By the time they have reached adulthood, however, they have increased in size and complexity to form massive and elaborate racks (Banfield 1954, Kelsall 1968). This increase in size may be measured in terms of length, girth and weight (Banfield 1960, Bergerud 1974b). As antler growth is discontinuous, Rackham (1982) suggested that a measure of antler girth might be used to identify discrete age classes. Antler growth is not only affected by age, however, but is also strongly correlated with weight and general health (Bergerud 1974b). In the case of elderly senile males antlers also become progressively simpler in form, a process known as "going-
Fig. 4.8 Morphology of antler shedding surface in female reindeer.
Fig. 4.9  Morphology of antler shedding surface in male reindeer.
Table 4.7 Diameter of antler beam in adult caribou (from Banfield 1954)

<table>
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<tr>
<th>Sex</th>
<th>N</th>
<th>Mean (mm)</th>
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<tr>
<td>Females</td>
<td>23</td>
<td>24.7</td>
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back". This overlap in age/size classes may be seen in the diameter of antlers of known age, collected as part of this study (Table 4.6) (Fig. 4.10).

While individual size classes may not be recognised from a measure of antler girth, it is nonetheless possible to distinguish between the antlers of juveniles and adults on the basis of antler size (Banfield 1954, Sturdy 1975). Banfield (1954) found a complete overlap in the size of female antlers with those of yearling and two year old males. The antlers of three year old males and above, however, showed no overlap with those of females (Table 4.7).

Banfield used a measure of beam width immediately above the burr. This measure was not illustrated and is therefore not replicated in this study. Six measures have been established, however, which record the diameter of the beam at various points along its length (Fig. 4.11). These measures were used in the analysis of modern antlers from the reindeer herd at Glenmore (Tables 4.5 and 4.6).

The adult male antlers in the Glenmore sample were sawn off immediately above the burr. Consequently, only two measures, M5 and M6, were recorded during this study. These two measures are not ideal indicators of antler size as they are often affected by the exaggerated development of the beam between the anterior tines. A scattergram of measures 5 and 6 (Fig. 4.12), however, produces a result similar to that obtained by Banfield with no overlap between the size range of females and fully adult males.

In the analysis of archaeofaunal material, measure 2 is the preferred measure as it is unaffected by the growth of the burr or by the development of the anterior tines. In the sample of female antlers from Glenmore, measure 2 ranges in size from 11-29mm. Fossil antlers which exceed this size range are therefore considered to be fully adult males and, in the case of shed antler, indicative of seasonal presence between October and December. Male antlers which overlap with the size range of females are considered to be juveniles, indicative of seasonal presence between February and May. While a few large two year old males may exceed the size range of females and be incorrectly identified as adult, no fully adult males will fall within the juvenile and female size range.
Fig. 4.11 Measurements of antler beam girth.
Fig. 4.12 Size distribution of male and female antlers from Glenmore, Cairngorm.
4.4 Cementum increment analysis

Aside from the breeding season and the antler cycle, a third method of determining seasonality in reindeer remains makes use of a seasonal phenomenon in the growth and development of teeth. The roots of mammalian teeth are coated with a deposit of cementum, a bone-like substance which anchors the tooth in the jaw. When analysed under a microscope the cementum of many mammals can be seen to have a layered structure consisting of paired bands of varying thickness. Each pair represents one year's growth. Thin layers are formed during the winter rest period and thicker layers are laid down during the period of maximum growth in the summer months (Hillson 1986).

This phenomenon has been exploited by zoologists in order to determine an animal's age at death. Archaeologists have also made use of this technique to determine age of death in archaeofaunal samples (Stallibrass 1982), and have recently adapted it further to determine site seasonality (Gordon 1988, Pike-Tay 1991).

In order to observe cementum increments under a microscope the tooth must first be prepared for analysis. This can be done in two ways. The first method involves the preparation of a polished surface which is studied under a microscope using reflected light. With this technique the increments show up as contrasting dark summer bands and lighter winter bands. The second method requires the analysis of a ground and polished thin-section. Under a polarised light microscope the increments on the thin-section are visible as opaque and translucent layers.

Determining age at death from a polished surface or thin-section is a relatively simple matter which involves the counting of the paired rings of cementum. Determining seasonality is equally straightforward and involves the observation of the nature of the outermost increment. This outer ring should provide an indication of the season in which the animal died. The period represented by each increment is very broad, however, and may represent a time-span of up to six months.

The timing of cemental incrementation in reindeer has been assessed through two studies of modern populations (Reimers and Nordby 1968, Miller 1974). These studies suggest that the summer band is formed during the annual growth periods of July-September in males and July-December in females. The timing of the formation of the winter rest line is less precisely known but is thought to occur at some point after December and before April of the following year. This technique can therefore be used with reindeer teeth to determine two broad seasons of death, December to April and July to December.

As these periods are very broad, Gordon (1988) has attempted to refine the technique by measuring the width of the outermost increment and comparing it with previous increments of the same seasonality. By estimating the degree of completeness of the
outermost ring, Gordon claims to be able to obtain a more precise seasonal determination. Gordon’s technique was tested on modern Canadian samples of known age, sex and season of death. These samples had already been studied previously by Miller (1974).

Using Miller’s data for the timing of rest line formation and assuming continuous deposition, Gordon suggests that it is possible to discriminate the timing of death within the period between December to March down to the level of individual months. He also suggests that it is possible to distinguish three stages within the summer growth band which can be assigned to the seasons of summer (June-August, half-width), autumn (September-November, 3/4 width) and winter (December-March, full width).

While Gordon claims over 80% accuracy for his blind tests on the modern Canadian sample, his methods can be criticised on several grounds. Firstly, his claims for the degree of precision in determining seasonality from the winter rest line are unfounded as no individuals with this seasonality were included within his test sample. Despite this he assumes that winter rest line formation is continuous and uniform, occurring between the months of December and March. As has already been shown, however, the exact timing of the onset of deposition of the winter rest line is currently unknown.

The problems with the interpretation of winter seasonality are compounded by the fact that Gordon claims to be able to determine winter seasonality (December to March) from specimens exhibiting no winter rest line at all but a complete summer growth band. This appears to be in direct contradiction to his assertion that winter rest line formation is continuous and takes place between the months of December and March.

Finally, Gordon makes no mention of the possibility of sexual differences in the season of summer band formation, although these differences were previously inferred from the same sample by Miller (1974). Such differences would clearly affect the rate of summer band formation and the ability to obtain accurate determinations of seasonality from specimens with an outermost summer band.

The problems outlined above suggest that cementum increment analysis may currently be used to provide a rough guide to season of death but that further research into the timing of increment formation will be required before Gordon’s refined techniques can be used with confidence.

While a very broad indication of seasonality may be obtained through this method of research, there are considerable costs to be borne, not only in terms of time and labour, but also in terms of the necessary destruction of museum specimens. In the light of the limited degree of information which this method can currently provide, it was decided not to proceed with cementum increment analysis for the purposes of this study.
4.5 Summary of methods used in this study

Several different methods have been employed in this study in an attempt to determine season of reindeer presence in the vicinity of archaeological and geological sites. These methods have involved the analysis of antlers, skulls, juvenile bones and juvenile mandibles and maxillae.

Where possible, all shed antlers and most unshed antlers have been recorded using the morphological and metrical methods outlined above. Sex has been determined on the basis of the morphology of the antler base and the age of male antlers has been determined from an analysis of antler size. In a few cases, where sex has been difficult to determine, this is noted in the appendices by a question mark after the determination. In the case of unshed antlers the appropriate measurements (measures 1 and 2) have been taken on the pedicle immediately below the burr. The information obtained from these analyses has been summarised in Chapter 5 in the form of tables and graphs. Detailed measurements and descriptions are listed in Appendix 1. Complete or partial skulls with the frontal-parietal sutures intact have been listed separately in Appendix 2. In the case of skulls with unshed antlers, measures 1 and 2 relate to the size of the pedicle immediately below the burr. In the case of those skulls with shed antlers, measurements have been taken across the pedicle scar. Left and right antlers have been recorded separately but only one set of measures per skull appears in the summary graphs illustrated in Chapter 5.

The stage of eruption and wear of deciduous and permanent teeth has been recorded for all juvenile mandibles and maxillae (Appendices 3 and 4). The crown heights of deciduous premolars have also been recorded for two sizeable faunal collections from the sites of Sandford Hill, Mendip and Reindeer Cave, Inchnadamph (Appendix 5). Unfused juvenile bones from these two sites have also recorded in detail using standard measurements described by von den Driesch (1976) (Appendix 6).
Material studied

5.1 Introduction
Faunal material has been studied from a series of 28 Devensian sites in Britain. In the following descriptions a brief account is given of the history of excavation at each site and the contexts from which the reindeer remains were derived. As many of the sites were excavated during the 19th century, however, contextual information is often poor or lacking.

The faunal collections from the earliest excavations were rarely kept together, and material from these excavations may be found in museums throughout Britain. While extensive museum searches have been conducted as part of this study, it is inevitable that some faunal material from the sites analysed will have been missed. Unless specifically stated otherwise, therefore, it must be assumed that many of the samples described here are incomplete.

As the primary aim of this study has been to investigate reindeer behavioural ecology, it was not thought to be necessary, or even desirable, to restrict the study to archaeological collections. Human exploitation of reindeer during the last glaciation may have been organised seasonally and the limitation of the study to archaeofaunal collections might have resulted in built-in biases in the seasonality of reindeer presence.

Faunal remains may be incorporated into deposits through a variety of alternative means. Natural forces such as rivers and pit fall traps may be responsible for the accumulation of antlers and bones in river terraces and on cave floors. Similarly, the denning behaviour of predators such as hyaena (Crocuta crocuta) and wolf may also result in the formation of faunal assemblages in caves. These mechanisms of accumulation may also be seasonally biased. Predator denning behaviour, for example, may be restricted to the breeding season. Wherever possible, the taphonomic processes involved in the accumulation of the assemblage have been assessed and potential biases in the determination of seasonality have been taken into consideration.

The seasonality of reindeer presence is described for each site and/or recognisable context and the age of the collection is discussed. Where radiocarbon dates are available these are quoted as uncalibrated dates BP. Direct radiocarbon dates on reindeer bone and antler provide the most reliable guide to age. A series of ten new radiocarbon dates has therefore been obtained through the Oxford AMS system. Where no radiocarbon dates are available, however, relative dating methods are considered.
5.2 Badger Hole, Wookey Hole, Somerset

Badger Hole lies on the eastern face of the Wookey Hole ravine, not far from the source of the River Axe. The cave consists of a broad entrance area which leads through a narrow passage into an inner chamber with several side passages. Three excavations have been undertaken within the cave entrance but little work has been carried out in the inner chamber.

The first excavations were undertaken by a local amateur archaeologist, H.E. Balch, between 1938 and 1953 (McBurney 1961). Balch excavated by yard squares (ca 0.9m²) at vertical intervals of one foot (ca 30cm). He excavated down to bed-rock and removed approximately 1.5 metres of deposits. While much of the cave had been heavily disturbed by badgers, Balch discovered a Late Pleistocene fauna together with a series of characteristic Early Upper Palaeolithic artefacts. The vertical and horizontal position of these finds was recorded but no note was made of their location relative to the cave stratigraphy.

Two soundings were later made in the entrance area by McBurney in 1958. These revealed that, while most of the entrance area had been excavated previously, some Late Pleistocene deposits still survived. The latter were carefully excavated by Campbell (1970, 1977), who exposed a heavily disturbed stratigraphic sequence.

An upper topsoil covered a layer of disturbed red sand, apparently the result of previous excavations. This was underlain by a stratum of redeposited dark red sand with thermoclastic scree and boulders (Layer III). The underlying deposit (Layer II) consisted of a red sandy thermoclastic scree, and resting on bed-rock was Layer I, a red silty sand with thermoclastic scree.

Campbell’s excavations indicated that the Devensian fauna was derived from the lowest layers within the cave (Layer I and the interface between Layers I and II). The faunal collections from these layers include woolly rhinoceros (*Coelodonta antiquitatis*), horse, reindeer, giant Irish deer (*Megaceros giganteus*), hyaena, otter (*Lutra lutra*) and fox (arctic fox - *Alopex lagopus* or red fox - *Vulpes vulpes*). Some of the remains had been gnawed by a large carnivore and were clearly the result of denning activity within the cave. The discovery of charcoal and burnt bone from the same deposit indicates that some of the faunal remains may also have been the result of human occupation. Campbell estimated that the Early Upper Palaeolithic unifacial leafpoints discovered by Balch were also derived from the lowermost deposit (Layer I).

5.2.1 Seasonality

The material studied here consists of a single shed female antler from Balch’s excavations in 1938. While female reindeer normally shed their antlers at the time of parturition in May, barren females may shed their antlers slightly earlier in March or April. A single antler
Ref. | Specimen | Date
--- | --- | ---
BM-497 | Burnt bone | > 18,000 BP
OxA-679 | Juvenile human mandible | 9,060 ± 130
OxA-680 | Human cranial fragments | 1,380 ± 70
OxA-1459 | Human mandible | 9,360 ± 100


does not necessarily indicate a reindeer calving ground but does indicate reindeer presence in early spring.

5.2.2 Dating
The antler described above was found at a depth of two feet below the surface within deposits which were heavily disturbed by badgers. The relative age of this specimen is therefore uncertain. A sample of burnt bone from Layer I has produced an infinite radiocarbon date of > 18,000 BP (BM-497). Reindeer bones have been identified from this level and it is possible that the antler was originally derived from this deposit.

Pollen analyses indicate a post-glacial age for the deposition of Layer III, however, and radiocarbon dates on three human specimens indicate that human occupation of the cave extended into the early Holocene (Table 5.1). As several early Holocene dates have been obtained on reindeer remains it is not impossible that this specimen was derived from later deposits within the cave.

5.3 Banwell Bone Cave, Banwell, Somerset
Banwell Bone Cave is situated above the village of Banwell on the western edge of the Mendips. The cave consists of a main central chamber with three side branches running to the east, west and south. The southern and western branches are roughly level with the floor of the main chamber but the eastern branch falls steeply to a depth of about 13 metres below the cave floor (Rutter 1829, Hunt n.d.).

At the time of its discovery the cave was filled to a depth of approximately three metres. An early account describes the deposits as a mixture of "sand, mud, loose stones, and fragments of mountain limestone fallen from the roof, intermingled with an immense quantity of bones of various animals" (Rutter 1829, 149).
5.3.1. History of excavations

The site was first discovered in 1824 by William Beard, a local farmer who gave up farming to dedicate his life to the exploration of the cave. The local landowner, the Bishop of Bath and Wells, also took an early interest in the findings within the cave and encouraged its exploration by eminent geologists of the time. These early excavations were carried out by workmen, and no record was kept of the context of the finds. The bones were sorted by Beard, however, and most were returned to the cave and arranged in decorative stacks. The site was subsequently opened to the public as a show-cave and quickly became a local attraction for Victorian holiday-makers at Weston-super-Mare.

Banwell’s popularity as a local tourist attraction declined after the opening of the show caves in Cheddar Gorge and no further exploration work was undertaken until the early 1950s. Interest in the cave and its deposits was revived when a group of local cavers and amateur archaeologists, the Axbridge Caving Group and Archaeological Society (ACGAS), began a re-investigation of the site in 1951.

The ACGAS excavated several areas within the cave, including parts of the main chamber and the western branch. Most of their work was concentrated in the eastern branch, however, where a considerable quantity of undisturbed deposits had survived (Hunt n.d., Tucker 1964). While the excavators received some professional advice from archaeologists at the University of London, the excavations were organised and undertaken on an entirely amateur basis.

The excavations in the eastern branch were divided into two areas. Material was removed in arbitrary one foot layers and a record was kept of the stratigraphic context of major finds. Some soil samples were also washed and sieved in order to aid the recovery of microfauna (Tucker 1964).

Unfortunately, the published accounts do not provide a complete list of the animal bones discovered within each area and stratum. The species identified from the 20th century excavations include reindeer, red deer, bison, horse, hyaena, wolf, fox and bear. The 19th century faunal list is more extensive and, in addition to the species mentioned above, includes mammoth (*Mammuthus primigenius*), woolly rhinoceros, lion (*Panthera leo*) and lynx (Jackson 1962).

5.3.2. Taphonomy

There is little evidence to suggest that any of the faunal material at Banwell was the product of human occupation. Some 20 flints which are supposed to have been found at the site are held in Woodspring Museum in Weston-super-Mare. There is no record of their discovery, however, and there is some doubt about their provenance (Campbell 1977). Some of the bones have clearly been gnawed by carnivores and may have been the product of denning.
within the cave. Many of the bones are unmarked, however, and it has been suggested that a natural pit-fall trap in the roof of the cave may have been responsible for the accumulation of at least part of the bone assemblage (Hunt 1954). This suggestion appears to be supported by a marked dip in the deposits in the eastern branch of the cave. The bones and limestone slabs in this area were found to slope eastwards at an angle of ca 15°.

5.3.3 Material Studied
Faunal material from the 19th century excavations at Banwell has been dispersed throughout the country and much has apparently been lost. Many of the bones from the original excavations were stacked in the cave but these stacks have been depleted over the years through a combination of weathering and the collecting activities of sightseers. Some of Beard's material also found its way into museums, however, and several of these collections have been analysed for the purposes of this study. Beard's own personal collection of bones is housed in Taunton Castle Museum. A few specimens were gifted to the Geological Museum in Bath by the Bishop of Bath and Wells and a sizeable sample of bones was collected by Dean William Buckland and is housed in Oxford University Museum.

Most of the finds from the ACGAS excavations were also returned to the cave in order to reconstruct Beard's decorative stacks. These were not available for study. A sizeable collection of material from Banwell is held in the Museum of the University of Bristol Speleological Society, however, and it seems probable that these were also derived from the 1950s excavations. In addition to the latter assemblage, a few clearly marked specimens from the later excavations are also on display in Axbridge Museum.

5.3.4 Seasonality
A total of 26 shed antlers has been analysed as part of this study. Of these, 15 were juvenile males, two were adult males and nine were females. In addition to the shed antlers, seven unshed antlers have been studied, of which five are clearly adult males (Fig. 5.1). Nine partial skulls have also been studied. On the basis of size and suture shape, all but one of these skulls may be identified as adult males. Three of these animals carried their antlers intact, while five showed pedicle scars.

Nine of the shed antlers discussed above were found during the course of the 20th century excavations. These specimens were all small and have been identified as females or juvenile males. This small group of antlers may have formed part of a larger collection which was studied by Sutcliffe (1955). He analysed a sample of 100 antlers, of which 91 were shed and only 9 were unshed. The diameter of the base of the shed antlers (Measure 2)
ranged in size from 15-29 mm, with an average measurement of 19-22 mm. These figures are well within the size range of modern females and juvenile males.

The shed and unshed antlers from Banwell Bone Cave represent almost every possible season of reindeer presence. The shed females and juvenile males are indicative of spring and early summer presence. The shed male antlers provide evidence of late autumn and early winter presence and the animals whose skulls show pedicle scars with no new growth could have been killed at any time between October and March.

In addition to the antler evidence, two juvenile mandibles and a fragment of a juvenile maxilla have also been preserved. The eruption and wear patterns of these three specimens indicate reindeer presence during two different seasons, between the months of August and October and at some time between October and March.

5.3.5 Dating
No radiocarbon dates have yet been obtained on any material from Banwell Bone Cave. It was hoped that reindeer remains from the site would be submitted for radiocarbon dating as an integral part of this study. Unfortunately much of the existing material from Banwell appears to have been treated with glue (Tucker 1964, Currant pers. comm!). Such preservatives introduce a potential source of error into radiocarbon dates, reducing their reliability. Fresh material must therefore be sought from the surviving sections before reliable radiocarbon dates can be obtained from the site.

In the absence of any direct dates, it is only possible to assess the relative age of the deposits on the basis of faunal associations. The occurrence of two extinct species, woolly rhinoceros and bison, is particularly noteworthy in this regard. While both species have been found in Lateglacial contexts in Europe, neither species has yet been found in British deposits which postdate the height of the last glaciation (Stuart 1991). This may indicate that at least some of the deposits date from a period before ca 18,000 BP.

5.4 Barnwell Station, Cambridgeshire
The Barnwell Station beds consist of a series of sands and gravels ca 1.5m thick overlying Gault clay. They form part of the second terrace of the River Cam and were exposed near Barnwell Station, Cambridge in the early years of this century. Lenses of peat within the sands contained plant macro-fossils and beetles, while the gravels produced a number of large mammal remains.

The deposits were initially described by Marr and Gardner (1916) but were re-assessed by Coope (1968) and Bell and Dickson (1971). From his analysis of the beetle fauna, Coope

1. Andrew Currant, Dept. of Palaeontology, Natural History Museum, Cromwell Road, London.
concluded that the environment was open and devoid of trees. The limited number of species and the combination of arctic and arctic/alpine beetles is suggestive of an arctic climatic regime. The plant macro-fossils also indicate open habitat with a rich herbaceous vegetation including shrub species such as dwarf birch (*Betula nana*) and willows (Bell and Dickson 1971)

5.4.1 Material studied
Large mammal remains were not found *in situ* in the peat deposits but were recovered by workmen from the sand and gravel layers. The species represented include mammoth, horse, woolly rhinoceros and reindeer. A few specimens are preserved in the Sedgwick Museum, Cambridge, including a single antler of reindeer. This specimen is a shed male antler which falls within the size range of juvenile males. It probably belonged to a yearling or two year old animal and represents reindeer presence in the area between February and May.

5.4.2 Dating
Coope suggested a late Middle Devensian age for the formation of the peats on the basis of his analyses of the beetle fauna. A radiocarbon date of 19,500 ± 650 years BP (Q-590) was obtained on plant detritus (Godwin and Willis 1964), however, dating the formation of the peats to the height of the last glaciation. It has been suggested, however, that this date may be too young, having been obtained on a peat sample which had been stored for many years (Stuart 1982).

While the large mammal remains were found in the gravels rather than the peats, it seems likely that the fauna represented in the Barnwell Station beds may be dated either to the Late Middle Devensian or Early Late Devensian periods.

5.5 Black Rock Quarries, Tenby, Pembrokeshire
A small collection of reindeer remains from the site of Black Rock Quarries, near Tenby, is preserved in Sedgwick Museum, Cambridge, and includes several pieces which are indicative of reindeer seasonality. Despite an extensive search through the relevant literature, however, no details of this site have yet been uncovered.

The collection consists of several antlers, mandibles, maxillae and juvenile long bones. The latter were not recorded, but the stages of eruption and wear of the juvenile mandibles and maxillae can give some indication as to age and season of death. Four juvenile mandibles and 3 juvenile maxillae can be assigned to the age class of 3 - 5 months. A further three maxillae and one mandible have been assigned to the age class of 5 - 10 months. The
former indicate reindeer presence between the months of August and October, while the latter indicate reindeer presence during the winter, between the months of October and March.

Antlers have provided additional evidence of seasonality, although most of the specimens are unshed and of uncertain sex. Two shed pedicle scars of a female and juvenile male, indicate reindeer presence during the spring or early summer, between February and May.

In the absence of any further information, little can be said at present about the age of this collection. The nature of the seasonal evidence, which appears to indicate several seasons of reindeer presence, is of interest, however, and would merit radiocarbon dating.

5.6 Bone Cave, Inchnadamph, Sutherland

Bone Cave lies at a height of 330 m OD overlooking the dry valley of the Allt nan Uamh (Burn of the Caves), near Inchnadamph, Sutherland. It is one of several caves and rock-shelters in the steep limestone cliffs of the Creag nan Uamh (See also Reindeer Cave, Inchnadamph). The cave consists of a single chamber with a passage running westwards to connect with Reindeer Cave (Outer Chamber). A passage at the back of cave descends in a southeasterly direction but has not been fully explored.

Bone Cave was first excavated in 1889 by B.N. Peach and J. Horne of the Geological Survey (Peach and Horne 1917). It was re-excavated in 1927 under the direction of J.E. Cree in association with J.G. Callander of the National Museum of Antiquities of Scotland and J. Ritchie of the Royal Scottish Museum (Callander et al. 1927, Cree 1927). While no final report of the latter excavation has ever been published, many letters and manuscripts relating to the excavations are preserved in the Royal Museum of Scotland. A recent summary of the excavations has also been published by Lawson (1981).

5.6.1 Excavation and stratigraphy

Peach and Horne reported the discovery of six distinct layers. The lowermost deposit consisted of a well-rounded gravel which was overlain by a thermoclastic scree, the latter deposit containing an arctic fauna. Layer 4 consisted of a grey clay which was thought to have been derived from glacial debris. This was overlain by a red cave earth containing many faunal remains and limestone splinters. The presence of man was reported on the basis of the discovery of hearths within this layer. The uppermost deposits consisted of a whitish marl (Layer 2) and a peaty layer (Layer 1).

The exact location of Peach and Horne's excavations within the cave are unknown but Cree et al. discovered that large sections of deposits remained in situ. Their own excavations
began on the terrace outside the cave and worked inwards along a median trench. Both the
cave and its connecting passage with Reindeer Cave (Outer Chamber) were almost fully
excavated to bed-rock.

The stratigraphy described by Cree et al is rather different from that of Peach and
Horne (Lawson 1981). The basal deposits consisted of a dark grey clay overlain by a thick
layer of clay (up to 0.6 m thick) containing quartzite stones. Above this, on the west side of
the cave only, was a clean grey gravel which was restricted to a discrete channel. This ran
into the western passage and through into Reindeer Cave (Outer Chamber) where it is
thought to have formed the lower barren gravel. Overlying the gravel in the western
passage and the clay layer elsewhere in Bone Cave was a red cave earth.

5.6.2 Seasonality

The faunal collection from Cree's excavations in 1927 is housed in the Royal Museum of
Scotland and has been available for intensive study. In addition to reindeer, the finds from
Bone Cave included bones of bear, fox and fish.

Five shed antlers have been recorded from Bone Cave, of which four are from female
reindeer and one is from a juvenile male. Only two specimens are from known contexts.
Both are female antlers which are said to have been found in the second layer (gravel above
clay). These antlers, indicative of reindeer presence in the Assynt area during May, are
particularly noteworthy as the gravel in the connecting tunnel was reported to have been
barren (Lawson 1981) and is thought to have formed the lower barren gravel in the Outer
Chamber of Reindeer Cave. Given the crude methods of excavation, however, it is possible
that the antlers were in fact recovered from the overlying red cave earth.

Juvenile reindeer bones were also recovered in some numbers from Bone Cave. These
are all labelled as having been found above the western passage connecting with Reindeer
Cave (Outer Chamber) (ie red cave earth). A total of 39 bones and teeth has been recorded,
representing a minimum of four individuals (Table 5.2). This collection includes two
deciduous lower premolars with no wear and no roots. As these teeth normally come into
occlusion and wear by the end of the first week of life, these teeth are indicative of neonatal
death in May.

The small size of all the post-cranial bones found in Bone Cave suggests that animals
represented by this collection were all very young calves. Most of the bones are highly
fragmented but two radii are sufficiently complete to enable comparison with a sample of
radii from Sandford Hill, Mendip (Fig. 5.2). The latter animals are thought to range in age
from 3 - 10 months (for discussion see section on Sandford Hill). A sample of radii from
the neighbouring Reindeer Cave is also included for comparison. The distinct gap in size
distributions between the samples from Bone Cave and Sandford Hill suggest that the
<table>
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<th>MNI</th>
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</tr>
<tr>
<td>Teeth</td>
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</tr>
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</tr>
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</tr>
<tr>
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</tr>
<tr>
<td>Metatarsal</td>
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</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>44</strong></td>
<td><strong>4</strong></td>
</tr>
</tbody>
</table>

Table 5.2 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of reindeer from Bone Cave, Inchnadamph, Sutherland.

animals represented by the Assynt collection are significantly younger. This appears to confirm the suggestion that the Assynt area was used as a calving ground at some time in the past.

5.6.3 Dating
No radiocarbon dates have been obtained on samples from Bone Cave. Most of the reindeer remains were found within the red cave earth although at least two of the shed antlers may have been found within the gravel in the connecting passage with Reindeer Cave (Outer Chamber). A similar red cave earth was found in the outer chamber of Reindeer Cave and is thought to date to the Late Devensian and post-glacial period (Murray et al 1993). As the red cave earth was found throughout both caves and was also found in the connecting passage, it is perhaps reasonable to suppose that the two deposits are of broadly similar age.

5.7 Bosco's Den, Gower, Glamorgan
This cave, also known as Bacon's Eye, is located in an area of limestone cliffs on the coast of the Gower peninsula, South Wales (Allen and Rutter 1944). Access to the cave is difficult and is only possible at low tide. The cave system is on two levels with a lower chamber at
Fig. 5.2. Size distribution of juvenile radii from Bone Cave, Reindeer Cave (Inner Chamber) and Sandford Hill. (Measurements as described in Appendix 6).
approximately 8 metres above the present beach and an upper chamber at a height of ca 33 metres above sea-level.

The cave was investigated by a local antiquarian, Colonel Wood, in the middle of the last century (Falconer 1868). The lower chamber was found to contain marine sands and gravels with no fossiliferous deposits. The upper chamber, which penetrates the cliff face to a depth of ca 34 metres, was found to contain abundant animal remains, including those of bear, fox, wolf, and reindeer. A chimney in the roof of the upper cave is now choked with sediments but would originally have communicated with the cliff surface above. The two chambers are separated by a limestone floor, some 2 to 4 metres thick, consisting of huge limestone blocks interspersed with smaller angular fragments and cemented together by stalagmite.

5.7.1 Stratigraphy of the upper cave
Wood supervised the excavation of the outer 8 metres of the cave to the level of the limestone floor. This involved the removal of approximately 5 m of deposits. Towards the back of the cave the excavations were less extensive and were restricted to the upper 75 cm of deposits.

Six distinct layers were recognised in the outer section of the cave. The uppermost layer consisted of a sandy peat, 30-40 cm deep, containing the remains of wolf, reindeer and a bovid. This was underlain by a regular and uniform bed of stalagmite with a thickness of ca 15 cm. Underlying the stalagmite were 40 cm of sandy loam containing dispersed angular fragments of rock. The fourth and fifth strata consisted of a barren sand (0.75 m thick) and a loose angular breccia (1.2 m thick). The lowermost deposit consisted of a yellow cave earth, 1.8 - 2.1 m thick, containing abundant faunal remains and dispersed angular fragments of limestone.

5.7.2 Reindeer remains
Reindeer were found in two layers within the upper cave, from the sandy peat and the yellow cave earth. More than 30 shed bases are reported to have been recovered from the peat. This is a tiny fraction of the number which were found within the yellow cave earth, however. Only bases were counted and these amounted to nearly 1100 specimens, 95% of which were shed. They were generally of small size and Falconer concluded that the great majority belonged to young animals.

5.7.3 Material studied
The faunal remains from the cave were donated to the Royal Institute of South Wales in Swansea. Despite a thorough search of the collections in the museum, only two fragments
of reindeer antler were located. Both of these antlers are tiny and clearly belonged to calves. Only one antler was measurable. The beam width of this specimen, which appears to have been broken from the pedicle during shedding, was 9.8mm. This falls at the lower end of the size range for juvenile and female animals and may be compared with a modern calf specimen from Glenmore, Cairngorm with a beam width of 11mm.

Shed calf antler is indicative of reindeer presence in the Gower peninsula between February and late May. While most of the existing collection from the site has apparently been lost, it seems likely that Falconer was correct in his assessment that many of the specimens belonged to young animals. As female antlers overlap in size with the antlers of juvenile males, however, it is probable that this collection consisted of a mixture of females and juvenile animals and that the Gower peninsula formed part of a former calving ground.

5.7.4 Taphonomy
Falconer reported that most of the reindeer antlers were broken and that some of them had been rolled. He also suggested that a chimney in the roof of the cave would have been open at the time of the accumulation of the cave earth. If the Gower peninsula was the focus of reindeer calving activity during the last glaciation, large numbers of shed antlers would have accumulated on the limestone plateau and could easily have been washed into the cave by surface streams. This would account for the large numbers recovered and the reported patterns of breakage and wear. Wolves are also reported to have been abundant amongst the faunal remains from this site, however, and it is possible that some of the antlers represent the result of wolf denning activity within the cave.

5.7.5 Dating
As yet, no radiocarbon dates have been obtained on material from Bosco’s Den. As with many 19th century collections, it is likely that the faunal remains were treated to aid their preservation, thus reducing the accuracy of radiocarbon dates. As considerable quantities of deposit survive intact in the cave, however, future excavation of this site may produce valuable information on the context of this assemblage.

5.8 Bridged Pot Shelter, Ebbor Gorge, Somerset
This small shelter is one of many rock shelters in the Ebbor Gorge, Mendip. It was discovered and excavated by Balch (1928) and was subsequently re-excavated by McBurney in 1958 (McBurney 1959).

The shelter consists of a funnel-shaped dissolution hole ca one metre in diameter which was filled with a cone of deposits. Balch’s excavations removed the interior slope of the
cone leaving the outer talus slope intact. The early excavations were somewhat rudimentary and involved the removal of material in one foot spits (ca 30cm). From a depth of ca one metre Balch began to encounter Pleistocene deposits containing the remains of reindeer, red deer, arctic fox, wolf, lemmings, voles, steppe pika (*Ochotona pusilla*), ptarmigan (*Lagopus mutus*) and red grouse (*Lagopus lagopus*) (Jackson 1962).

McBurney’s excavations of the outer talus slope revealed a more complex stratigraphy with six principal layers (A-F). While the upper layers appear to cover several periods of the Holocene, a fossiliferous Late Pleistocene thermoclastic scree (Layer B) was found overlying largely sterile basal deposits (Layer A). The faunal remains from McBurney’s Layer B include reindeer, arctic lemming (*Dicrostonyx torquatus*) and pika.

5.8.1 Material studied
A single unshed antler provides evidence for reindeer seasonality. The specimen is female and has a clear shed line which indicates incipient shedding and a season of death in May.

5.8.2 Dating
The antler described above was derived from Balch’s excavations at a depth of about 2 metres. Its condition is very similar to that of other reindeer remains from McBurney’s Layer B, however, and it is possible that this specimen was derived from the same deposit.

A single radiocarbon date has been obtained on a fragmentary mammal bone from the thermoclastic scree (Layer B). This date of 8,890 ± 340 BP (BM-2102) is rather later than expected on the basis of faunal associations (Burleigh, Ambers and Matthews 1984). Given the combination of cold climate conditions, indicated by the formation of the scree, and a cold stage fauna it seems likely that this deposit was formed during the Lateglacial stadial.

5.9 Chelm’s Combe, Cheddar, Somerset
Chelm’s Combe rock shelter was situated at the edge of an infilled ravine near Cheddar Gorge. The site has now been destroyed by quarrying, but substantial excavations were undertaken in 1925 under the direction of H.E. Balch (Balch et al 1927). These excavations revealed a series of archaeological horizons dating from the postglacial period overlying Late Pleistocene limestone screees. A total depth of about 7 metres of deposits was explored and material was removed in arbitrary one foot spits. Unfortunately, no record was kept of internal stratigraphy and, given the steeply sloping nature of the site, it seems unlikely that the horizontal spits coincided with natural formations.
5.9.1 Formation of the Pleistocene deposits

The Late Pleistocene deposits appear to have been formed by the gradual build-up of thermoclastic screes (Currant 1991). Numerous faunal remains were found within the deposits, including those of mammals, birds and molluscs. The mammalian remains were studied by Jackson (Balch et al 1927, Jackson 1962) and include reindeer, red deer, horse, mountain hare (Lepus timidus), pika, lemmings, extinct voles, red and arctic fox. Notable amongst the avifauna were the abundant remains of ptarmigan and red grouse.

While two bone artefacts, a notched mammal bone and a drilled bird bone, have been assigned tentatively to the Late Upper Palaeolithic (Campbell 1977), there is no evidence to suggest that man was the agent responsible for the collection of animal bones listed above. Rather, it has been proposed that the faunal collection from this site represents the remains of animals which died by falling over the precipitous cliffs above (Currant 1991).

5.9.2 Seasonality

Amongst the reindeer remains from the site were three fragmentary juvenile dentitions which give some indication as to season of death. The first of these, a maxillary fragment, has lightly worn deciduous premolars and the first permanent molar is in the process of erupting. This indicates an age of death of 3 - 5 months and a seasonality of mid-August to mid-October. A fragmentary mandible with light wear on the deciduous premolars supports this seasonality. A second mandible with deciduous premolars showing moderate wear, molar 1 with light wear and molar 2 piercing the jaw bone, indicates an age at death of 5 - 10 months and a seasonality of mid-October to mid-March.

Two partially shed female antlers are indicative of reindeer presence at the time of calving in May or June, while a single example of a shed adult male pedicle scar is indicative of reindeer presence at some point between October and March.

The evidence from teeth and antlers suggests a minimum season of presence from June through to October. The evidence presented may cover a much wider period, however, which, at its maximum, extends from May through to March.

5.9.3 Dating

Several radiocarbon dates have been obtained on faunal remains from the site. These are listed in Table 5.3. Dates on reindeer material range from 10,140 ± 100 BP to 10,600 ± 200 BP. This places reindeer presence at Chelm's Combe within the Lateglacial stadial.
Table 5.3 Radiocarbon dates from Chelm's Combe, Cheddar, Somerset (Currant 1991).

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5.10 Church Hole, Holbeck, Nottinghamshire

Church Hole lies on the southwestern cliff face of Creswell Crags gorge on the boundary between Derbyshire and Nottinghamshire. The cave consists of two parts, an outer entrance chamber and a narrow inner passage which penetrates the limestone bed-rock for a distance of ca 34 metres.

Explorations within the cave began ca 1872 when the supervisor of the Creswell Quarry noticed the existence of animal bones in the cave deposits. Major excavations were undertaken in the summers of 1875 and 1876 under the auspices of an Exploration Committee (Mello 1877, Dawkins 1877). The results of these excavations have been summarised by Jenkinson (1984).

The excavations revealed a complex stratigraphy which was not continuous throughout the cave. Five stratigraphic levels were recognised. The surface levels consisted of organic silts and humic material which were underlain by a layer of breccia. The latter deposit was discontinuous towards the rear of the cave but, where it existed, it formed a seal over the earlier Devensian deposits. Beneath the breccia were a series of three "cave earths", an upper reddish cave earth, a middle layer of lighter-coloured material and a lower cave earth, known as the Mottled Bed. The two upper cave earths contained flint artefacts associated with animal bones and charcoal. The lower Mottled Bed produced numerous quartzite implements and a few bone tools. The cave earths were underlain by a layer of red sand which occurred throughout the whole cave. This layer produced abundant faunal remains and a few quartzite implements. The lowest stratigraphic level was a barren white sand which rested directly on the limestone bed-rock.
5.10.1 Faunal remains
Large numbers of faunal remains were discovered in the course of the excavations. Eleven species have been identified from Devensian levels. These include hyaena, lion, wolf, fox, hare, mammoth, woolly rhinoceros, horse, reindeer, giant Irish deer and bison.

5.10.2 Material studied
Twenty shed antlers from Church Hole have been analysed as part of this study (Fig. 5.3). Labels indicate that at least eighteen of these were found during the 1876 excavations. The stratigraphic location is known for only one specimen (A62), however, a juvenile male antler which was found in the red sand. The remainder of the antlers are from unknown contexts. Ten are female, three are adult males and six are from juvenile males.

5.10.3 Seasonality
The female antlers lend support to evidence from the neighbouring cave of Pin Hole which suggests that the Creswell area was used as a reindeer calving ground on several occasions during the last glaciation. As at Pin Hole, the occurrence of shed male antlers indicates that the area was also grazed by reindeer during the winter and early spring months.

5.10.4 Dating
Jenkinson (1984) has drawn comparisons between the quartzite artefacts from the red sand and those from the lower levels of the neighbouring cave of Pin Hole. On the basis of radiocarbon dates from the latter site, he has suggested an Early or Middle Devensian age for the formation of the white and red sands. He has also suggested a Middle Devensian age for the formation of the Mottled Bed. The occurrence of a Late Upper Palaeolithic industry in the overlying cave earths indicates that at least part of this deposit was laid down during the Late Devensian Lateglacial. A single radiocarbon date of 12,240 ± 150 BP (OxA-735), obtained on a humerus of mountain hare from the breccia, confirms the Lateglacial age of the upper deposits (Gowlett, Hedges, Law and Perry 1986).

In the absence of contextual information for the antlers studied here, it is impossible to assign a relative age for this collection. The material from Church Hole may be compared with that from the neighbouring cave of Pin Hole, however, where a series of radiocarbon dates on reindeer antler indicate several periods of reindeer presence ranging from the Middle Devensian period to the Late Devensian Lateglacial.
Fig. 5.3 Size distribution of antlers from Church Hole, Holbeck, Nottinghamshire.
5.11 Coygan Cave, Laugharne, Carmarthen

Coygan Cave was set in an outcrop of carboniferous limestone overlooking Carmarthen Bay at a height of ca 80m above sea level. Before its destruction by quarrying in the 1960s the cave was the focus of several investigations. The earliest explorations were undertaken by a geologist, Henry Hicks, in the 1860s. These were followed by further excavations by Edward Laws and Ernest Lloyd Jones in the 1880s (Jones 1882) and by Herbert Eccles in the early years of this century (Grimes and Cowley 1935). The most substantial excavations were those of Grimes and Cowley which were carried out in 1933. A final season of exploration was undertaken in 1963-4 in advance of the cave's destruction by quarrying (Clegg 1970).

5.11.1 Stratigraphy

Grimes' and Cowley's excavations revealed a sequence of five deposits. A basal deposit of clean yellow sand (Layer 1) was overlain by a fossiliferous stony clay. A thin layer of stalagmite (Layer 3) separated the clay from the overlying cave earth (Layer 4). The latter deposit reached a thickness of one metre in some places and was rich in mammalian remains. It was overlain by a thick layer of stalagmite (Layer 5).

The stratigraphic sequence reported by Clegg (1970) was more complex and appeared to lack the stony clay layer which Grimes and Cowley referred to as Layer 2. Clegg's sequence consisted of a basal maroon clay overlain by a clean yellow sand. A thin layer of stalagmite (stalagmite C) separated the sand from an overlying brown sandy earth (Layer 4). A second layer of stalagmite (stalagmite B) separated the latter deposit from Layer 5, a buff sandy earth. The whole sequence was sealed by an upper stalagmite (stalagmite A).

Clegg correlated his stalagmite C with the lower stalagmite (Layer 3) of Grimes' and Cowley's excavations. This would suggest that the cave earth identified as Layer 4 by Grimes and Cowley was the equivalent deposit to Layers 4 and 5 as described by Clegg. Jones (1882) described a similar fossiliferous cave earth sealed by a layer of stalagmite from the early excavations of the 1880s. It seems likely that this cave earth was the equivalent deposit to Clegg's Layers 4 and 5.

5.11.2 Cave earth fauna

Clegg reported some difficulty in distinguishing between the sediments of Layers 4 and 5. The faunal remains from these two layers have been treated as a single unit by Scott (1986a). The large mammal fauna from the cave earths included the remains of woolly rhinoceros, mammoth, horse, red deer, reindeer, giant deer, bison, hyaena, wolf, brown bear and arctic fox. The presence of man was also indicated by the discovery of two bout coupé handaxes and a small chert flake.
The abundant remains of hyaena, coupled with the high proportion of gnawed and fractured bones, led Jones (1882) to suggest that the cave earth fauna was largely a product of hyaena denning activity. This conclusion was supported by Scott (1986a) whose analysis of bone breakage patterns and body part representation indicated that hyaena was the primary factor involved in the accumulation of this collection.

5.11.3 Material studied
The antlers studied here form part of two early faunal collections from the site and probably represent only a fraction of the total number which have been uncovered over the years. The collections studied are housed in Tenby Museum and in Sedgwick Museum, Cambridge. The latter collection was gifted to Sedgwick Museum by Ernest Lloyd Jones and was probably derived from the cave earth excavations of the 1880s. The former collection was gifted to Tenby Museum by Rev. G.N. Smith and was discussed by Dawkins (1874). This collection was clearly made at an early stage in the exploration of the cave and, while it is now impossible to reconstruct the context from which they were derived, the heavily gnawed condition of the antlers suggests that they were also derived from the cave earth deposits.

5.11.4 Seasonality
A total of 13 shed antlers has been studied from this site, all of which are male. Eight of these antlers have suffered severe damage from gnawing and the width of the antler beam must be regarded as a minimum estimate of size (Fig. 5.4). In an undamaged state it is likely that all the antlers would have fallen within the range of fully adult males, indicative of reindeer presence during the winter months from October to January.

5.11.5 Dating
No radiocarbon dates have been obtained on the faunal remains from the cave earth deposits. A single radiocarbon date has been obtained on charcoal from Layer 5 (Green 1986a). This date of $38,684 \pm 2137/2024$ BP (BM-499) is thought to date human presence within the cave to the Middle Devensian period. A similar Middle Devensian date for the accumulation of the faunal remains would not be unexpected.

5.12 Eel Point, Caldey Island, Pembrokeshire
The discovery of a cave at Eel Point, Caldey Island was reported by Rev. Gilbert Smith (1861). This cave was situated in a sea-cliff at the western end of Priory Bay. At the time of writing, the cave had already been destroyed by quarrying, but a large collection of animal
Fig. 5.4 Size distribution of antlers from Coygan Cave, Laugharne, Carmarthen.
remains had been recovered from a layer of reddish loam. These included the remains of mammoth, rhinoceros, pig (*Sus scrofa*), horse, deer, cattle (*Bos* sp), bear, hyaena, lion, wolf and fox.

5.12.1 Material studied
The material studied here consists of a single shed antler from a large adult male. This specimen indicates that the area formed part of the winter range of reindeer populations at some stage during the Devensian. No radiocarbon dates are available for the collection from this site, however, and it is therefore impossible to assign the specimen to any specific period within the last glaciation.

5.13 Ffynnon Beuno, Tremerchion, Flintshire
Ffynnon Beuno is one of two caves which lie in a small ravine near Tremerchion in the Vale of Clwyd. Both caves were excavated by Hicks and Luxmore in the 1880s (Hicks 1886). Ffynnon Beuno is the lower of the two caves, lying at a height of approximately 13 metres above the valley floor. The cave consists of several narrow tunnels which meet in a central chamber. The latter is thought to have been artificially enlarged in the course of mining operations.

Excavations were undertaken throughout the cave and revealed that many of the deposits had been disturbed, possibly by water action. An undisturbed section within the principal tunnel revealed a sequence of four stratigraphic layers. The uppermost deposit consisted of surface soil containing a few bones of sheep (*Ovis* sp) and domestic fowl. This was underlain by a stalagmitic breccia which produced large quantities of charcoal. An undisturbed red cave earth was found beneath the breccia and produced abundant faunal remains and a few flint artefacts. The lowermost deposit consisted of a barren gravel layer.

5.13.1 Faunal remains
Numerous faunal remains were recovered from Ffynnon Beuno and these were reported jointly with the remains from the neighbouring cave of Cae Gwyn (Davies in Hicks 1886). Sixteen species were recorded including lion, wild cat (*Felis sylvestris*), hyaena, wolf, fox, bear, mammoth, woolly rhinoceros, horse, cattle and reindeer. The remains of horse, rhinoceros, hyaena and reindeer were reported to have been particularly numerous.

5.13.2 Material studied
The faunal remains from the site were donated to numerous museums by the excavators. Part of their collection survives in the Sedgwick Museum in Cambridge and the Natural
History Museum in London. A total of nine shed antlers has been studied, of which four were adult males, four were juvenile males and one was female (Fig. 5.5). Two unshed antlers were also recovered, one being an adult male and the other of unknown sex. A skull of an adult male animal with shed antlers was also recorded.

The combination of antlers reflects reindeer presence during several seasons of the year. The male shed antlers indicate reindeer presence between October and May, while the unshed male antler could indicate presence at some time between July and December. The single female antler is insufficient evidence for reindeer calving but confirms the presence of reindeer during the months of April or May.

5.13.3 Dating

The deposits within the two caves of Cae Gwyn and Ffynnon Beuno are said to have been sealed by undisturbed northern boulder clay. A single radiocarbon date of 18,000 ± 1400/1200 BP (Birm-146) on mammoth bone from the red cave earth layer in Cae Gwyn provides a minimum age for the formation of this deposit (Rowlands 1971). The discovery of Early Upper Palaeolithic artefacts within the red cave earth of Ffynnon Beuno also suggests that this deposit was formed at some point during the Middle Devensian period (Jacobi 1980).

5.14 Gough’s Cave, Cheddar, Somerset

Gough’s (New) Cave is the lower part of an extensive cave system which opens at the base of limestone cliffs on the southern side of Cheddar Gorge. The cave has been open to the public as a show-cave since the 1890s and several excavations have been undertaken in the main entrance passage in order to remove the Lateglacial deposits.

The earliest excavations were undertaken in the late 19th century by the proprietor of the cave, R.C. Gough, who cut a path through the deposits to a depth of ca 1.35 metres. The section left by Gough’s excavations was described by Davies (1904). In 1903 the burial of a young adult male was found during the course of drainage work in a small fissure in the north side of the cave. Radiocarbon dates have shown this burial to be of early Holocene date (Barker, Burleigh and Meeks 1971).

The most systematic excavations were undertaken by R.F. Parry from 1927 to 1931 and involved the removal of undisturbed banks of material on either side of the path (Parry 1929, 1931). The deposits were removed in arbitrary six inch spits (ca 15cm) and all the material was sieved. A daily record was kept of all the finds and their stratigraphic position was recorded.
Fig. 5.5 Size distribution of antlers from Ffynnon Beuno, Tremerchion, Flintshire.
Parry's excavations ceased at approximately 25 metres from the cave entrance. Most of the remaining fossiliferous deposits were removed by Victor Painter between 1948 and 1953. These excavations were less controlled than those of Parry and were reported by Donovan (1955). The most recent excavations within the cave were undertaken in 1986 and 1987 (Currant et al 1989). The latter excavations were not extensive but produced valuable additional information on the Lateglacial fauna.

5.14.1 Lateglacial deposits

Parry's excavations produced evidence for extensive human activity within the cave during the Late Upper Palaeolithic. Hearths, faunal remains and numerous flint and bone tools were uncovered during the course of excavation. Parry's six inch spits did not invariably coincide with the bedding of the cave deposits, however, and, as a result, the upper layers produced a considerable mixture of Lateglacial and more recent faunas and artefacts.

The uppermost layers (Spits 1-5) contained only modern mammal species and produced artefacts of Iron Age and Romano-British date. Layers 6 to 14 produced a mixture of Lateglacial and recent faunas, the latter decreasing in number with depth. The lowest layers (15 to 24) contained only Lateglacial remains.

The faunal remains from Parry's excavations have been re-analysed recently in conjunction with the latest excavations (Currant 1986, 1991). The species represented include wolf, fox, arctic fox, bear, lynx, mammoth, horse, red deer, reindeer, aurochs (Bos primigenius), saiga antelope and mountain hare. Many of the bones bear butchery marks and appear to have been the product of human activity in the cave.

5.14.2 Material studied

Very few reindeer remains were found in Gough's Cave and only two fragmentary skulls provide evidence of seasonality. The first skull, which was found in Spit 8, is a large adult male with shed antlers. This specimen indicates reindeer presence in the Mendips at some time between October and March. The second skull, from an unknown context, is that of a calf with one antler intact. The left antler is missing and may have been naturally shed or broken prior to shedding. Shed calf antler would indicate reindeer presence between February and May.

5.14.3 Dating

A large series of radiocarbon dates has been obtained on humanly modified and unworked bone from Gough's Cave (Table 5.4). Most of the dates fall between ca 12,800 and 12,000 BP and indicate human use of the cave during the Lateglacial interstadial. Two dates on reindeer remains suggest that this species did not form part of the interstadial fauna but

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rather belongs to a younger phase of accumulation during the Late glacial stadial and early Holocene.

Despite the apparent absence of reindeer from the Mendip area during the Late glacial interstadial, several artefacts from Gough’s Cave were manufactured from reindeer antler. While the latter may have been carried to the site from some distance away, they are nonetheless significant in that they indicate the relative importance of this species during the Late Upper Palaeolithic.

5.15 Hyaena Den, Wookey Hole, Somerset

Hyaena Den lies on the left bank of the Wookey Hole ravine about 50 metres downstream from the source of the River Axe. The cave was first discovered in the 1850s and was explored over the course of several years from 1859 onwards. The principal excavator was William Boyd Dawkins but he was assisted by local amateurs during several seasons (Dawkins 1862, 1863a, 1863b, 1874). Later explorations were also undertaken by Balch from 1877 onwards (Balch 1914). Relatively recent excavations, by Trauma, Donovan and
Campbell (1971), have revealed that Dawkins et al removed most of the deposits down to bed-rock.

The cave consists of a main chamber (called the Antrum by Dawkins) with two branches leading from it to the northeast and southwest. At the back of the Antrum a vertical shaft leads to an opening in the roof.

5.15.1 Stratigraphy of the site
The excavations during the 1860s were undertaken by workmen under the supervision of Dawkins and his associates. Excavation techniques were extremely crude. The cave was excavated from front to back and the stratigraphy was recorded from sections. Artefacts and faunal remains were collected but no record was kept of their stratigraphic position.

Dawkins recorded the presence of three principal layers within the cave. A basal layer of red earth and stones was overlain by a fossiliferous deposit known as the "Bone Layer". This deposit was not continuous throughout the cave but, where it occurred, was said to consist of three black bands of manganese peroxide containing many bone splinters. Overlying the fossiliferous Bone Layer was an upper red earth. Both the lower and upper red earths contained mammalian remains but not in the quantities discovered from the Bone Layer.

Human artefacts were found at four locations within the cave. An analysis of these artefacts suggests that human occupation occurred during three discrete periods, the Late Middle Palaeolithic, the Early Upper Palaeolithic and a subsequent occupation of unknown date represented by the discovery of a single artefact (Trauma et al 1971). Owing to the methods of excavation, the relationship between artefacts and stratigraphic layers is uncertain.

Further stratigraphic detail for the uppermost deposits was obtained by Trauma et al (1971). In the course of their excavations a section of in situ deposits covering the uppermost layers was cleared and recorded. The lowest deposit (layer 3) was composed of red earth and stones and contained a few bones and teeth. This layer may be correlated with Dawkins' Upper Red Earth. Pollen analyses suggest that this layer dates from the Early or Middle Devensian. Layer 3 was overlain by a yellow silty clay (Layer 2) and a layer of humus and dark earth (Layer 1). The latter deposits are thought to date to the Lateglacial and Holocene periods.

5.15.2 Material studied
The material studied was derived from Dawkins' early excavations during the 1860s. The fauna listed by Dawkins in his publications represent a mixture of both temperate and arctic species. Mammoth, woolly rhinoceros and reindeer are listed alongside more
temperate elements such as aurochs, giant Irish deer and slender-nosed rhinoceros (*Dicerorhinus hemitoechus*). This association is probably the result of the mixing of interglacial and glacial deposits.

The collection of reindeer remains from the site includes 30 antlers. The location of some of these antlers has been determined from a notebook held in Oxford University Museum. This notebook was kept by one of Dawkins' colleagues, James Parker, and consists of a catalogue of finds from two seasons of excavation in 1862 and 1865. Of the 30 antlers studied, 21 were recorded in Parker's catalogue. Three antlers were found in the Antrum, 1 was found in an unspecified passage, 16 were found in the vertical shaft at the back of the cave and the location of the remaining specimen was not recorded.

5.15.3 Seasonality

Of the 16 antlers which were found in the vertical shaft at the back of the cave, 13 are shed males (Fig. 5.6). Six may be classified as adult males on the basis of size, representing a season of reindeer presence between October and January. The remaining seven juvenile males represent a season of presence between February and May. Two unshed antlers were also found in the shaft. One of these is a juvenile male while the other is female bearing a shed line. The former may not be used to give any indication of season but the latter indicates probable reindeer presence in April or May. A single shed female antler also supports this seasonality.

The three antlers from the Antrum include two shed adult males and a juvenile male with an incipient shed line. This indicates a season of reindeer presence between October and May.

Additional seasonal information may also be obtained from a further 11 antlers, a mandible and a fragmentary skull. Owing to the lack of contextual information, however, these specimens have not been considered here.

5.15.4 Dating

While the horizontal stratigraphy of many of the antlers has been recorded, no details of vertical stratigraphic context have been preserved. Antlers discovered in the Antrum may have been derived from any of the three contexts recognised by Dawkins. The antlers from this area may not therefore be considered to be a unitary sample. As the Bone Layer did not reach the back of the cave it can be assumed that the antlers from the vertical shaft were derived from either the Upper or Lower Red Earth. The occurrence of *Dicerorhinus* within

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Fig. 5.6 Size distribution of antlers from Hyaena Den, Wookey Hole, Somerset.
basal deposits suggests that the Lower Red Earth was formed during the Ipswichian interglacial, while pollen analysis suggests that the Upper Red Earth was formed during the Early or Middle Devensian. Reindeer has not been recorded previously from any deposit of known Ipswichian age and it is likely, therefore, that the antlers derive from the later deposit dating from the Early or Middle Devensian.

5.16 Kent's Cavern, Torquay, Devon

Kent's Cavern lies within the eastern limits of the town of Torquay, on the small peninsula which forms the northern side of Tor Bay, south Devon. The cavern is not a single chamber but a series of large solution cavities linked together by narrow fissures.

The earliest excavations within the cave system were begun by Thomas Northmore in 1824. Since then more than 15 excavation campaigns have been carried out within the cave system (Campbell and Sampson 1971). Many of these were small-scale investigations which were inadequately recorded. The most significant explorations were undertaken by Rev. J. MacEnery between 1825 and 1829 and by William Pengelly between 1865 and 1880. MacEnery left detailed notes of his work which were subsequently published by Vivian (1859) and Pengelly (1869).

In contrast to most excavations which were undertaken in the 19th century, Pengelly's excavations paid careful attention to stratigraphy and context. A grid system was laid out, consisting of one foot wide parallels intersected at right angles at intervals of one yard. Material was removed in spits of one foot and the vertical and horizontal position of each find was recorded. Pengelly published summary reports of his findings within the cave (Pengelly 1868, 1871, 1878) but most of the detail of his excavations was never published. This is preserved in his diary covering the period 1865-1880.3

5.16.1 Pengelly's excavations

Campbell and Sampson (1971) used Pengelly's diary to reconstruct the stratigraphy and extent of his excavations within the eastern part of the cave system. Within this area they list a total of nine stratigraphic layers, of which two are of particular interest here. These are the cave earths, Layers B2 and A2.

Layer B2, the Stony Cave Earth, consisted of sharp angular limestone fragments in a light red sand/silt matrix. This deposit contained Late Upper Palaeolithic artefacts and faunas and, in the Vestibule, produced a palimpsest of Late Upper Palaeolithic hearths known as the Black Band.

3. Kent's Cavern Exploration Journal held in Torquay Natural History Museum
Layer A2, the Loamy Cave Earth, was a light red silty sand. Early Upper Palaeolithic artefacts occurred at the top of this layer but were replaced by Middle Palaeolithic artefacts at lower depths within the deposit.

5.16.2 Material studied
Faunal remains from Kent's Cavern were sent to numerous museums throughout the country. Many of the specimens analysed in the course of this study are from unknown contexts. A substantial number, however, were derived from the cave earth deposits excavated by Pengelly. Only these specimens are considered in detail here.

5.16.3 Seasonality
A total of 28 antlers has been studied from the cave earth deposits. Of these, 26 are from shed males and two are unshed. The two unshed antlers both fall within the size range of females and juvenile males and give no indication as to season of death (Fig. 5.7). The size of many of the shed males is greatly affected by gnawing. The measures plotted in Fig. 5.7 should therefore be considered as minimum figures rather than absolute measures of size. The overall size range for Measure 2 is 24-44 mm. Eight specimens fall below the size range of adult males, but, of these, 6 are heavily worn or gnawed. It is likely, therefore, that most of the antlers represented by this collection were derived from adult or sub-adult (2 year old) males. This indicates a season of reindeer presence at some time between October and January.

In addition to the evidence provided by the antlers, three juvenile mandibles were also preserved in the cave earths. The stage of eruption of the second permanent molar in each of these specimens indicates a season of death between mid-October and mid-March. This compliments the evidence from the antlers and indicates reindeer presence during the winter months.

5.16.4 Accumulation of the faunal remains
The reindeer remains described above form part of a larger collection of faunal remains from the Loamy Cave Earth (A2) which includes woolly rhinoceros, mammoth, horse, giant Irish deer, a bovid, hyaena, lion, wolf, fox and bear. Human presence is also attested by both artefacts and bones. The heavily gnawed state of most of the antlers and the presence of many post-cranial elements suggests that this accumulation of remains was not the product of natural processes, but rather the result of hyaena denning activity within the cave.
Fig. 5.7 Size distribution of antlers from Kent's Cavern, Torquay, Devon.
5.15.5 Dating
Despite Pengelly's careful excavations, contextual information is still lacking for many of
the finds from this site. While some of the material from his excavations has been labelled
"Cave Earth", this labelling does not distinguish between the Stony Cave Earth (B2) and the
Loamy Cave Earth (A2). The long time range represented by these two deposits can be
seen from the cultural material preserved within them. The former deposit (B2) has
produced Late Upper Palaeolithic artefacts, while the latter deposit has produced artefacts
of both Early Upper Palaeolithic and Middle Palaeolithic date.

No direct radiocarbon dates exist on reindeer remains from Kent's Cavern. In the
absence of such dates it is impossible to assign the reindeer specimens from the cave to a
given period with any certainty. Two dates are available for other species from the Loamy
Cave Earth, however (Campbell 1977). These dates of 28,160 ± 435 BP (GrN-6201 -
Coelodonta antiquitatis) and 27,720 ± 450 BP (GrN-6202 - Ursus arctos), confirm the Middle
Devensian age of this deposit and suggest a possible age for the reindeer remains described
above. Four dates on later material from the layer known as the Black Band range from
14,275 ± 120 BP (GrN-6203 - Ursus arctos) to 11,570 ± 410 BP (BM-2168 - bovid) and
confirm the Lateglacial date of that deposit (Ambers, Matthews and Bowman 1987,

5.17 Ossom's Cave, Manifold Valley, Staffordshire
Ossom's Cave lies on the western slope of the Manifold valley in the Staffordshire Peak
District. It was excavated in the 1950s by members of the Peakland Archaeological Society
(Bramwell et al 1987). These excavations revealed a detailed stratigraphic sequence with five
distinct layers, labelled A to E. Of particular interest to this study is Layer C, a Lateglacial
breccia deposit containing large quantities of animal bones in association with
archaeological remains.

5.17.1 Lateglacial Fauna
The Lateglacial fauna from Layer C has been the subject of a detailed taphonomic study
(Scott 1986a, 1986b). Almost 1000 large mammal bones were recovered from this deposit
and, of those which can be accurately assigned to species, over 99% are identifiable as
reindeer. The minimum number of deer represented by the assemblage has been estimated
at six individuals. Only four bones were recovered from species other than reindeer. These
consist of two horse incisors, a fragment of a bovine distal tibia and the proximal end of a
human ulna. Radiocarbon dates on the latter bones have revealed that they are significantly
later in date and represent a Holocene intrusion into the Lateglacial deposit.
5.17.2 Accumulation of the faunal assemblage
The factors involved in the formation of this assemblage have been the subject of a debate which has yet to be resolved (Scott 1986a and 1986b, Bramwell et al 1987, Jacobi 1987). Detailed analyses of bone breakage patterns and body part representation have led Scott (1986a, 1986b) to suggest that man was the principal agent responsible for the formation of this collection. While a few of the bones have been gnawed by small rodents there are no toothmarks to indicate the activity of large predators. No direct evidence of cutmarks has been found but the differential representation of reindeer body parts is thought to be indicative of human activity and suggests that the cave may have been used as a butchery site to which selected parts of the carcass were brought for processing. In addition to the taphonomic indicators of human activity outlined above it has also been argued that Lateglacial artefacts were found in association with the reindeer bones (Bramwell et al 1987).

Jacobi (1987) has questioned this association between the artefacts and reindeer bones and has suggested that the faunal assemblage may be interpreted as a natural accumulation of carcasses at the base of a precipitous cliff. The differential representation of body parts which was illustrated by Scott may also be interpreted as the result of loss of deposit through erosion at the cliff edge.

5.17.3 Seasonality
The reindeer material from this site has not been studied at first hand. Scott (1986a, 1986b, Bramwell et al 1987) has published detailed analyses of reindeer seasonality, however, which are re-assessed here. Scott's interpretations of reindeer seasonality at Ossom's Cave draw upon analyses of juvenile dentition and antler. In the case of dentitions, juvenile animals are represented by five mandibles and three maxillae. These represent a minimum of three individuals.

Each of the juvenile jaws is at an early growth stage where a quarter, or just under a quarter, of the second molar has erupted above the bone. Scott followed the growth timetable outlined by Spiess (1979) and concluded that these juvenile animals were 10 - 11 months old at death, having been killed during March or April.

As has been demonstrated earlier, the eruption of the second molar may not be used to determine season of death with such precision. Molar 2 may begin to perforate the jaw bone at any time between the ages of five and 12 months, although eruption above the gum line will only begin between the ages of 10 - 12 months. At least one mandible from the sample at Ossom's Cave has not yet reached the latter stage of eruption (Scott 1986b, Plate 4). The second molar of this specimen has perforated the bone but has not yet erupted above the gum line.
In order to determine the ages of these individuals with greater precision, a measure of the crown height of the deciduous fourth premolar may be used. The crown heights of five deciduous premolars have been plotted in Fig. 5.8. When compared with a sample of crown heights from Sandford Hill (Fig. 5.23), where the second molar is just beginning to break through the bone, the crown heights of three of the five teeth at Ossom’s Cave illustrate heavier wear. This suggests that they are indeed older than the Sandford Hill sample, perhaps falling within the time range of late winter/early spring. The remaining teeth in this sample are less heavily worn, however. One of these teeth forms part of the mandible described above in which the second molar has yet to erupt above the gum line. The combination of eruption stages and wear patterns for this tooth suggests that this animal was rather younger than the others and that it died in the autumn months.

In addition to juvenile dentition, Scott also used supplementary evidence from unshed antlers to strengthen her argument in favour of a spring kill. Five unshed antlers were recovered from the site, of which four clearly belonged to calves. As the calf antlers were already fully formed Scott suggested that they were indicative of a spring season of death. Calf antlers are fully formed by the end of September, however, and may be carried through until the end of May. The presence of unshed calf antlers cannot therefore be used to assign a more precise season of death for the Ossom’s Cave assemblage.

5.17.4 Dating

Two radiocarbon dates have been obtained on reindeer remains from Ossom’s Cave (Table 5.5). Both dates indicate reindeer presence in the Staffordshire Peak District during the Lateglacial stadial. A third date, BM-2127, was obtained on a limb bone fragment which was thought to be reindeer. This date of 11,930 ± 310 BP is somewhat earlier and would date reindeer presence in the area to the Lateglacial interstadial.

<table>
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<th>Element</th>
<th>Date</th>
</tr>
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<tbody>
<tr>
<td>BM-2127</td>
<td>Large mammal/reindeer?</td>
<td>Limb bone</td>
<td>11,930 ± 310</td>
</tr>
<tr>
<td>OxA-631</td>
<td>Reindeer</td>
<td>Left mandible</td>
<td>10,780 ± 160</td>
</tr>
<tr>
<td>OxA-632</td>
<td>Reindeer</td>
<td>Unshed antler</td>
<td>10,600 ± 160</td>
</tr>
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<td>OxA-630</td>
<td>Man</td>
<td>Right ulna</td>
<td>4,860 ± 80</td>
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<td>OxA-629</td>
<td>Bovini</td>
<td>Right tibia</td>
<td>2,030 ± 80</td>
</tr>
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Table 5.5 Radiocarbon dates from Layer C, Ossom’s Cave, Manifold Valley, Staffordshire (Burleigh, Ambers and Matthews 1984, Gowlett, Hall, Hedges and Perry 1986)
Fig. 5.8 Crown heights of deciduous premolar 4 from Ossom's Cave, Manifold Valley, Staffordshire (data from Bramwell et al 1987).
5.18 Paviland Cave, Rhossili, Glamorgan

Paviland Cave, also known as Goat's Hole, is situated in a steep sea-cliff on the Gower coast, at a height of about 9 m above the present day sea level. The cave consists of a single chamber approximately 21 m in length. A narrow chimney in the roof communicates with the cliff face above.

The cave was first explored in 1822, initially by the curate and surgeon from Port Eynon, and subsequently by Mr L.W. Dillwyn and Miss Talbot of Penrice. The latter excavations unearthed a large number of faunal remains and brought the existence of the cave to the attention of William Buckland. Buckland visited the cave in 1823 and undertook extensive excavations (Buckland 1823). He unearthed large quantities of animal bones and teeth and a partial human skeleton adorned with red ochre, ivory artefacts and numerous sea shells. Buckland believed this to be the skeleton of a young Romano-British woman (The Red Lady) but more recent research has indicated that the skeleton was that of a young man. An early radiocarbon date suggested that this individual died ca 18,000 BP but a more recent assay has produced a date of 26,350 ± 550 BP (OxA-1815).

Buckland's excavations revealed no clear stratigraphy and produced a mixed faunal assemblage consisting of both Devensian and Holocene species. Buckland suggested that this mixture was the product of repeated diggings in the cave. Sollas (1913) found similarly disturbed deposits during the course of his excavations in 1912. The latter excavations produced large numbers of artefacts and bones, none of which were found within any recognisable stratum. Over 3,600 flint and chert artefacts were recovered, of which some 700 were retouched tools. Analyses of these tool types suggest that human occupation within the cave may have occurred on four separate occasions during the last glaciation (Jacobi 1980).

5.18.1 Material studied

The material studied here formed part of the original collection made by L.W. Dillwyn and Miss Talbot in 1823. At the time of Buckland's visit to the cave this collection was housed in Penrice Castle. In 1836, however, Miss Talbot donated the collection to the Royal Institution of South Wales where it is still held.

5.18.2 Seasonality

Twelve shed antlers have been studied, all of which are male. The measure of antler beam width (Measure 2) for these specimens ranges from 14-43 mm (Fig. 5.9). Despite this wide range, only two antlers fall within the size range of juvenile males and females. One of these specimens, with a measure of 28 mm, was heavily gnawed and should be regarded as
Fig. 5.9 Size distribution of antlers from Paviland Cave, Rhossili, Glamorgan.
fully adult. The adult males represent reindeer presence between October and January. The single juvenile male antler represents reindeer presence between February and May.

A single juvenile maxilla has also been recorded from the 1823 collections. The state of eruption of the first permanent molar of this specimen indicates that the animal died between the ages of three to five months, at some time between mid-August and mid-October.

5.18.3 Taphonomy of the collection
Sollas reported that many of the animal bones were broken and he suggested that this breakage was the result of human activity in order to extract marrow. Many of the bones were also burnt and blackened, indicating that at least part of the faunal assemblage was the product of human occupation.

In addition to the clear evidence for human activity, the remains of several predators have also been found within the cave. These include wolf, fox, hyaena, and cave bear (*Ursus spelaeus*). Buckland and Sollas both reported an absence of gnawed bones and Sollas concluded that the hyaena remains represented human food refuse. This observation does not match with those made in the course of this study. Of the 12 shed antlers studied here, seven have been gnawed around the base, beam and tines. It seems likely, therefore that the antlers were not collected by man but were the product of denning activity within the cave.

5.18.4 Dating
Several radiocarbon dates have been obtained on faunal remains from Paviland Cave (Table 5.6). Two of these dates (OxA-365 and OxA-366), were obtained on charred bone and indicate human activity within the cave around 27,000 - 31,000 BP. This is in reasonable agreement with the most recent date on the Palaeolithic interment (The Red Lady). Two samples of uncharred animal bone have also been dated. These have produced dates of ca 27,000 and 39,000 BP.

As has already been noted, at least four phases of human occupation have been recognised at Paviland Cave. These range in age from the Middle Devensian to the Late Devensian Lateglacial. Holocene use of the cave has also been documented through the occurrence a post-glacial fauna and artefacts of Neolithic date and younger. A radiocarbon date on a second human skeleton has produced a date of ca 7,000 BP.

Given the mixed nature of the assemblages from Paviland Cave, it is impossible to determine the age of the reindeer remains described here with any certainty. The two radiocarbon dates on uncharred bone suggest that the reindeer antlers may have been accumulated by hyaenas during the Middle Devensian period. In the absence of direct dates on reindeer antlers, however, a Late Devensian age can not be ruled out.
Ref. Specimen Context Date

BM-374 Homo sapiens (Red Lady) Buckland's excavations 18,460 ± 140
BM-1367 Bos primigenius Sollas' excavations 27,600 ± 1300
OxA-1815 Homo sapiens (Red Lady) Buckland's excavations 26,350 ± 350
OxA-140 Uncharred bone Buckland's or Sollas' excavations 38,800 ± 8000/4000
OxA-365 Charred bone Buckland's or Sollas' excavations 29,600 ± 1900
OxA-366 Humic acids from OxA-365 28,000 ± 1700
OxA-681 Homo sapiens (Paviland 2) Sollas' excavations 7,190 ± 80


5.19 Picken's Hole, Compton Bishop, Somerset

Picken's Hole lies on the south side of the Mendip Hills approximately six kilometres west of Cheddar. It was excavated in the 1960s by Professor E.K. Trauma and the results have been described in two preliminary notes (Trauma 1964, ApSimon 1986).

A sequence of seven stratigraphic units has been recognised. The lowest deposit consisted of water lain sands. These were overlain by a series of frost shattered angular limestone breccias between which were sandwiched two distinct cave earths (Units 5 and 3). The latter units both contained numerous animal remains (Stuart 1982). The species represented in Unit 5 include reindeer, red deer, wolf, red fox, brown bear and a large bovid. Small mammal remains from this unit include mountain hare, northern vole (Microtus oeconomus) and tundra vole (Microtus gregalis). The upper cave earth (Unit 3) produced a very different fauna, including mammoth, woolly rhinoceros, horse, hyaena, lion, reindeer and red deer. Human remains were also present in the upper cave earth, represented by both artefacts and teeth.

5.19.1 Accumulation of the faunal assemblages

The factors involved in the accumulation of the faunal assemblages from the two cave earths have been considered by Scott (1986a). Patterns of skeletal representation were compared with bone breakage patterns in order to determine the mechanisms involved in the formation of each assemblage. Scott concluded that the earlier assemblage from Unit 5 was the product of wolf denning within the cave. Despite the presence of human artefacts within the upper cave earth, a similar analysis of the faunal collection from this deposit led Scott to conclude that most of the faunal remains from Unit 3 were the product of hyaena denning activity.

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5.19.2 Material studied
The faunal remains from Picken's Hole are held in the University of Bristol Speleological Society Museum. Reindeer remains were preserved within both cave earths and evidence for seasonality was available from each unit.

5.19.3 Seasonality - Unit 5
Seven shed antlers were recovered from this unit. Five of these were female and two were juvenile males. Four unshed antlers were also recovered, all within the size range of females or juvenile males (Fig. 5.10). One of these unshed antlers bore a clear shed line, indicative of incipient shedding. The shed female antlers indicate reindeer presence in the vicinity of the cave during the time of calving in May. The presence of shed juvenile males may be evidence for a longer season of presence from February through to May. Two isolated teeth from Unit 5 support this interpretation of reindeer presence during the time of calving. The two upper deciduous premolars had not yet developed roots. One showed no wear at all, while the other showed only light wear on the anterior cusp. Unworn deciduous teeth such as these are a clear indication of death within the first week of life.

Reindeer presence in the vicinity of Picken's Hole may have covered a longer period, however, than that represented by the antlers and teeth. Evidence for this may be found in the form of a juvenile mandible and a fragmentary skull. The stage of eruption of the second permanent molar of the juvenile mandible indicates a season of death between mid-October and mid-March. This seasonality is matched by the fragmentary skull of an adult male reindeer with shed antlers which clearly died at some time between October and March.

5.19.4 Unit 3
Evidence for reindeer seasonality from the upper cave earth is derived from a single antler. This specimen is an unshed female with a clear shed line indicating incipient shedding. A single female antler may have been derived from either a barren or a gravid cow and would reflect reindeer presence at some time between March and May.

5.19.5 Dating
Radiocarbon dates exist for material from both the upper and lower cave earths (Burleigh and Hewson 1979, Burleigh, Ambers and Matthews 1984). Two dates from Unit 3, (34,265 ± 2600/1950 BP (BM-654); 27,540 ± 2,440 BP (BM-2117)), place the formation of this deposit within the Middle Devensian period. Three dates on material from the earlier deposit, Unit 5, (26,650 ± 1,700/1,400 BP (BM-655A); 27,000 ± 1,850/1,500 BP (BM-655B); 12,400 ± 1,500 BP (BM-2118)) are considerably younger than those from the
Fig. 5.10 Size distribution of antlers from Picken's Hole (Unit 5), Compton Bishop, Somerset.
overlying Unit 3. It has been suggested that the specimen used to obtain BM-655A and B was chemically weathered and may have been contaminated (Burleigh and Hewson 1979). The Lateglacial age suggested by sample BM-2118 may indicate some mixing with overlying deposits (Burleigh, Ambers and Matthews 1984).

The faunal elements from Unit 5 may all be found within present day boreal environments (ApSimon 1986). The absence of cryoclastic weathering activity during the formation of this deposit suggests that winters were generally mild. In the absence of temperate faunal elements typical of interglacial conditions, it has been suggested that the faunal assemblage from Unit 5 represents an early interstadial within the Devensian glaciation, possibly the Chelford interstadial (ApSimon 1986).

5.20 Pin Hole, Creswell, Derbyshire

Pin Hole Cave is a long narrow fissure in the northern face of the Creswell Crags gorge, on the boundary between Nottinghamshire and Derbyshire. The cave extends over a distance of ca 31 metres into the limestone bed-rock and has an average width of between one and two metres (Jenkinson 1984). A small inner chamber has been formed by the intersection of two solution cavities at a distance of 16.5 metres from the entrance. The cave has only a single entrance but the roof is high throughout most of its length and it extends almost to the surface of the limestone plateau in some places. Restricted surface openings occur above the Inner Chamber.

5.20.1 Excavation history

The first systematic explorations within the cave were undertaken by J. Magens Mello and Thomas Heath in 1875 (Mello 1875). These excavations were restricted to the outer seven metres of the cave and were discontinued at a point where large limestone rocks appeared to block the narrowing fissure.

Excavation was resumed in 1924 by the Committee for the Archaeological Exploration of Derbyshire Caves under the direction of A.L. Armstrong (Armstrong 1929a, 1929b, 1937). These excavations, which continued until 1936, involved the careful removal of the deposits in spits of one foot. A two-dimensional recording system was used and any artefacts or faunal remains which were found in situ were marked in pencil with details of the vertical spit in which they were found and their horizontal distance from the cave entrance. The vertical depth which was recorded does not refer to a depth beneath a single horizontal datum line but rather the depth beneath an undulating layer of flowstone which sealed the Devensian deposits. The excavated sediment was also sieved through a 1/4 inch mesh and finds were labelled as outlined above.
5.20.2 Stratigraphy

Four distinct depositional units were recognised by Mello and Armstrong. The uppermost stratum consisted of a series of Holocene deposits, most of which appear to have been greatly disturbed. This was underlain by a layer of flowstone and breccia which was present throughout the entire length of the cave. Beneath the flowstone were two cave earths, an upper red cave earth, ca 1.8 to 2.1 metres thick, and a lower yellow cave earth, ca 3.0 to 3.3 metres thick.

Evidence for human use of the cave has been found in both cave earths in the form of skeletal remains, hearths, and bone and lithic tools. Analyses of the artefact assemblages indicate that several phases of occupation are represented at Pin Hole ranging from the Middle Palaeolithic through to the Late Upper Palaeolithic periods (Armstrong 1937, Campbell 1977, Jacobi 1980, Jenkinson 1984).

Faunal remains were also abundant in both cave earths and over 22,000 specimens were recovered (Jackson 1967, Jenkinson 1984). The species represented by this collection include hyaena, wild cat, fox, wolf, bear, lion, mammoth, woolly rhinoceros, reindeer, giant deer, bison and horse. Smaller mammals were also common and mountain hare was particularly abundant in the upper strata.

In his re-analysis of the Pin Hole faunas, Jenkinson (1984) considered the taphonomic processes involved in their formation. He concluded that carnivore predatory behaviour was the principal factor involved in the accumulation of the faunas and that hyaena was the dominant species, particularly in the lower strata. Human activity may also have accounted for some of the faunal material, however, and Jenkinson found good agreement between the stratigraphic distribution of artefact assemblages and the occurrence of ungnawed bone. The occurrence of restricted openings in the roof of the Inner Chamber may also have been responsible for the accumulation of faunal remains, however, and, in particular, the accumulation of shed reindeer antler. Such remains may have been washed into the cave during periods of heavy rainfall.

5.20.3 Material studied

Reindeer remains were found in almost every level of Armstrong’s excavations (Spits 0 - 16 and Spit 19) (Jenkinson 1984). The material studied here forms part of two large collections of faunal remains from his excavations which are housed in Manchester Museum and the Natural History Museum in London. All shed antlers were recorded but most unshed antlers were disregarded. Skulls fragments and juvenile bones were also recorded but no juvenile mandibles were found. Wherever possible the stratigraphic details were noted but in many cases Armstrong’s original pencil notation was illegible. Several specimens also appear to have been unmarked.
5.20.4 Seasonality - Shed antlers

A total of 444 shed antlers has been studied. 312 of these have been identified as females and 132 as males. Of the latter, 92 fall within the size range of juvenile animals while the remaining 40 specimens may be classified as fully adult.

The stratigraphic distribution of the marked antlers shows no clear separation according to sex or age classes. Females, juvenile and adult males are found throughout the length of the cave and appear to be randomly scattered through the deposits. Radiocarbon dates indicate that Armstrong's stratigraphic levels are not particularly useful indicators of relative age and, given the long time span involved in the formation of the deposits, it is not possible to consider the antlers from Pin Hole in terms of discrete populations (Table 5.8). The sample studied here has clearly accumulated over the course of several thousands of years.

While this sample of shed antlers does not represent a single population, two observations can nonetheless be made about the size distributions of the antlers on the basis of a measure of beam width (Measure 2).

The female shed antlers have a unimodal distribution which approaches the normal distribution which would be expected from a random sample of a female population (Fig. 5.11). The distribution is slightly skewed, however, and exhibits a slight kurtosis (see Table 5.7 for descriptive statistics). The curve is sufficiently close to normal, however, to regard this sample as representative of the entire female population.

The size distribution of the male shed antlers is distinctly bimodal, however, with modal values of 17 and 38 mm. This suggests that calf, yearling and fully adult animals are present in this sample but that the two to three year old size class is under-represented. As the sample is not derived from a single discrete population it is not possible to test the validity of this distribution pattern statistically. One possible interpretation of this

<table>
<thead>
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<th>Mean</th>
<th>17.47</th>
<th>Std Err</th>
<th>0.18</th>
<th>Min</th>
<th>10</th>
<th>Skewness</th>
<th>0.34</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median</td>
<td>17.0</td>
<td>Variance</td>
<td>10.08</td>
<td>Max</td>
<td>28</td>
<td>Std Err of Skew</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Std Dev</td>
<td>3.17</td>
<td>Range</td>
<td>18</td>
<td>Kurtosis</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>IQR</td>
<td>5</td>
<td>Std Err of Kurtosis</td>
<td>0.28</td>
</tr>
</tbody>
</table>

Table 5.7 Descriptive statistics of antler beam width (Measure 2) in a sample of 303 shed female antlers from Pin Hole, Creswell, Derbyshire.
Fig. 5.11 Size distribution of shed antlers from Pin Hole, Creswell, Derbyshire.
bimodal distribution, however, is that it represents a seasonal absence from the Creswell Crags area. The occurrence of large adult male antlers indicate that reindeer were present in the Creswell area during the early winter months of October to December. The calf and yearling antlers indicate a somewhat different season of presence between March and May. The relative absence of the expected size class of two to three year old animals suggests that reindeer were absent from the area during the late winter months of January and February.

The large sample of shed female antlers indicates that the Creswell area formed a traditional calving ground which was frequented by large herds of female reindeer at the time of parturition in May.

5.20.5 Additional sources of evidence
Unshed antlers were also found at Pin Hole in some quantity but most were not included in this study. Nine specimens were recorded of which five are adult males and four are of unknown sex. The adult males add little further seasonal information, indicating simply that reindeer were present between the months of July and December.

Three fragments of male skulls have also been recorded, all of which display shed antler pedicles. Two of these were too fragmentary to measure but the third clearly belonged to a large adult male. This indicates reindeer presence at some time between October and March.

No juvenile mandibles or maxillae were found in the collections studied but four juvenile long bones were recorded. Two of these specimens, a metatarsal and a metacarpal, fall within the size range of a sample of juvenile animals from the site of Sandford Hill (see below). The Sandford Hill sample is thought to represent a 3-10 month age class and indicates a broad season of reindeer presence at some time between August and March. Two further juvenile long bones (a radius and a metacarpal) are significantly smaller than the specimens from Sandford Hill, however, and may be compared with a sample of neonatal calf bones from Reindeer Cave, near Inchnadamph. These very young animals probably died within the first few weeks of life and confirm that the Creswell area was used as a reindeer calving ground.

5.20.6 Dating
In recent times Pin Hole Cave has been used extensively by badgers and the deposits have been considerably disturbed. This can be illustrated by the stratigraphic distribution of a series of radiocarbon dates which range in age from ca 43,000 to 4,000 BP (Table 5.8). Reconstructions of relative age on the basis of stratigraphic level are therefore impossible.

Several radiocarbon dates have been obtained on samples of shed reindeer antler, however, all of which are of known age and sex. Four dates which were obtained on shed
female antlers indicate that the Creswell area was used as a calving ground on at least 3 occasions during the Devensian glaciation, at ca 13,000, 31,000 and 34,000 BP. Two dates on shed male antlers also indicate winter presence in the Creswell area during at least two periods, ca 34,000 BP and ca 44,000 BP or earlier. The former date (OxA-3790), which was obtained on a two or three year old male, is particularly interesting when considered in association with OxA-3407 and 3409. These broadly contemporary dates suggest that Middle Devensian reindeer were present in the Creswell area during at least two seasons of the year, in late winter and early summer.

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4. Dr R.M. Jacobi, The University of Nottingham, Department of Classical and Archaeological Studies, University Park, Nottingham NG7 2RD.
5.21 Reindeer Cave, Inchnadamph, Sutherland

Reindeer Cave lies at a height of 330 metres OD on the south side of the Allt nan Uarnh valley, near Inchnadamph, Sutherland. The site is one of several caves and rockshelters in the steep limestone cliffs of the Creag nan Uamh (See also Bone Cave, Inchnadamph). Reindeer Cave consists of two chambers which are connected by a narrow shaft. The Outer Chamber is the smaller of the two caves, measuring approximately 12 metres by five metres. The full dimensions of the Inner Chamber have yet to be established but it is extends at least 27 metres back into the cliff-face.

The two chambers were excavated in 1926-27 by James Cree, an amateur archaeologist, in association with Graham Callander, an archaeologist from the National Museum of Antiquities of Scotland, and James Ritchie, a zoologist from the Royal Scottish Museum (Callander et al 1927, Cree 1927). While no final report of the excavation has ever been published, many letters and manuscripts relating to the excavations are preserved in the Royal Museum of Scotland. A recent summary of the excavations has also been published by Lawson (1981).

5.21.1 Stratigraphy - Outer Chamber

Cree's excavation methods were somewhat crude and much of the work was undertaken by local workmen. In the Outer Chamber, material was removed in vertical sections working backwards from the mouth of the cave. The stratigraphy of the site was recorded from these sections. Sediment samples were also collected and the lithology of these samples has been described by Lawson (1983).

The lowest sediments from the Outer Chamber consisted of grey and yellow clays which occurred in pockets in the cave floor. Towards the rear of the Outer Chamber these clays were overlain by a bed of barren gravel. This deposit contained frequent sub-rounded to rounded clasts of lithologies which were derived from outwith the cave system. Overlying this barren deposit was a distinct fossiliferous gravel (Cree's Layer 3) which occurred throughout the outer chamber and also filled the shaft at the rear of the cave. This gravel, which reached a thickness of 0.9 metres in places, contained abundant reindeer antlers and a few postcranial bones. The uppermost layer of the Outer Chamber consisted of a red cave earth. This sandy-silt deposit produced evidence of human activity within the cave in the form of both artefacts and bones.

5.21.2 Stratigraphy - Inner Chamber

Access to the Inner Chamber was only possible once the Outer Chamber had been fully excavated and the deposits filling the connecting shaft had been removed. The cave was discovered in 1926 and excavations were attempted in 1927. This proved to be rather
difficult, however, owing to the problems associated with removing sediment via the shaft. As a result, the Inner Cave has been only partially explored and excavations were limited.

The cave was found to be almost filled with silts and lenses of gravels. Faunal remains were abundant but restricted to the upper 30 cm of deposits. In contrast to the Outer Chamber, the faunal remains from the Inner Chamber included numerous postcranial bones of reindeer. Shed antlers were also numerous.

5.21.3 Material studied
The entire faunal collection from Reindeer Cave is housed in the Royal Scottish Museum and has been available for intensive study. In addition to reindeer, the remains of several other mammals are reported to have been found within the caves. These include bear, arctic fox, lynx and several species of vole. Detailed analyses of the fauna are currently being undertaken but the context of these finds has yet to be established.

5.21.4 Seasonality - Outer Chamber
Cree (1927) reported the discovery of numerous reindeer remains from the Outer Chamber. These included over 800 shed antlers and a few postcranial bones. 668 shed bases have been analysed as part of this study. Many antler bases were too fragmentary to be measured and are therefore not included in this total. The contexts in which the antlers were found are listed in Table 5.9.

A sample of 555 shed antlers has been studied from the fossiliferous gravel (Layer 3) in the Outer Chamber and the shaft at the back of the cave. No unshed antlers were recorded.

<table>
<thead>
<tr>
<th>Context</th>
<th>Females</th>
<th>Range</th>
<th>Males</th>
<th>Range</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>2</td>
<td>16-28</td>
<td>1</td>
<td>16-28</td>
<td>2</td>
</tr>
<tr>
<td>Cave earth</td>
<td>1</td>
<td>18-27</td>
<td>1</td>
<td>16-28</td>
<td>2</td>
</tr>
<tr>
<td>Layer 3</td>
<td>349</td>
<td>9-27</td>
<td>45</td>
<td>9-19</td>
<td>394</td>
</tr>
<tr>
<td>Shaft 0-3'</td>
<td>68</td>
<td>12-24</td>
<td>6</td>
<td>12-18</td>
<td>74</td>
</tr>
<tr>
<td>Shaft 3-4'</td>
<td>33</td>
<td>12-20</td>
<td>5</td>
<td>14-19</td>
<td>38</td>
</tr>
<tr>
<td>Shaft 4-5'</td>
<td>4</td>
<td>15-22</td>
<td>4</td>
<td>12-16</td>
<td>4</td>
</tr>
<tr>
<td>Shaft 5-6'</td>
<td>41</td>
<td>13-22</td>
<td>4</td>
<td>12-16</td>
<td>45</td>
</tr>
<tr>
<td>Near mouth of cave</td>
<td>3</td>
<td>17-22</td>
<td>3</td>
<td>13-18</td>
<td>106</td>
</tr>
<tr>
<td>Unlabelled</td>
<td>92</td>
<td>13-25</td>
<td>14</td>
<td>13-18</td>
<td>106</td>
</tr>
</tbody>
</table>

Table 5.9 Size range (measure 2 - mm) of shed antlers from Reindeer Cave (Outer Chamber). Inchnadamph, Sutherland.
Table 5.10 Descriptive statistics of antler beam width (Measure 2) in a sample of 486 shed female antlers from Reindeer Cave (Outer Chamber), Inchnadamph, Sutherland.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Std Err</th>
<th>Minimum</th>
<th>Kurtosis</th>
<th>Mode</th>
<th>Std Dev</th>
<th>Maximum</th>
<th>SE Kurt</th>
<th>Skewness</th>
<th>SE Skew</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>17.749</td>
<td>.124</td>
<td>9.0</td>
<td>.587</td>
<td>18.0</td>
<td>2.739</td>
<td>27.0</td>
<td>.221</td>
<td>.223</td>
<td>.111</td>
</tr>
<tr>
<td></td>
<td>18.000</td>
<td></td>
<td>18.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

495 (89%) of the antlers are from females and 85 are from males. The size range of the male antlers (9-19mm) is well within the expected range of juvenile animals (Fig. 5.12). The size distribution of the female antlers approximates the normal distribution which would be expected if a random sample of an entire population were represented by this collection (for descriptive statistics see Table 5.10).

The female antlers are clear indicators of reindeer presence during calving in May. The juvenile male antlers indicate seasonal presence between February and May. The small size range of the male antlers indicates that most of the animals were yearlings and are more likely to have shed their antlers in late spring. This combination of females and juvenile males implies that the area formed a calving ground. This interpretation is supported by the discovery of a single humerus of a neonatal reindeer calf in the same deposit. Several other calf bones which were simply recorded as having been found in “Reindeer Cave” may also have been derived from this deposit.

5.21.5 Seasonality - Inner Chamber

Postcranial remains of reindeer were more numerous in the silts of the Inner Chamber. A total of 99 bones has been recorded, representing a minimum of 10 individuals (Table 5.11).

All of these bones belonged to very young animals with unfused epiphyses. The state of fusion of the metapodials is particularly noteworthy as the proximal epiphyses are unfused in all but one metacarpal. The age of fusion of this bone in reindeer is unknown but in most ungulates fusion has already occurred at the time of birth. Several specimens have also been found in which the third and fourth metapodials are unfused. The very small size of the metacarpals may also be illustrated by comparing them with a sample of calf (aged 3-10 months) and yearling bones from Sandford Hill, Mendip (Fig. 5.13).

While the ages of the long bones may not be established precisely, a study of the mandibles and teeth indicates that most of the individuals represented by this collection were neonatal calves. Three mandibles have been recorded in which the deciduous premolars are in the process of eruption. Eight isolated deciduous premolars have also been
Fig. 5.12 Size distribution of antlers from Reindeer Cave (Outer Chamber), Inchnadamph, Sutherland.
Fig. 5.13  Size distribution of juvenile metacarpals from Reindeer Cave (Inner Chamber) and Sandford Hill.
Table 5.11 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of reindeer from Reindeer Cave (Inner Chamber), Inchnadamph, Sutherland.

<table>
<thead>
<tr>
<th>Element</th>
<th>NISP</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antlers</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>Mandible</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Teeth</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Scapula</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Humerus</td>
<td>12</td>
<td>6</td>
</tr>
<tr>
<td>Radius</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>Ulna1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Metacarpal</td>
<td>17</td>
<td>9</td>
</tr>
<tr>
<td>Innominate</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Femur</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Tibia</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Calcaneus</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Talus</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Metatarsal,</td>
<td>23</td>
<td>10</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>183</td>
<td>10</td>
</tr>
</tbody>
</table>

Table 5.12 Size range of shed antlers from Reindeer Cave (Inner Chamber), Inchnadamph, Sutherland.

<table>
<thead>
<tr>
<th>Context</th>
<th>Females</th>
<th>Range</th>
<th>Males</th>
<th>Range</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface</td>
<td>4</td>
<td>15-18</td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Scree</td>
<td>4</td>
<td>13-18</td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Top 12&quot;</td>
<td>59</td>
<td>13-26</td>
<td>13</td>
<td>13-20</td>
<td>72</td>
</tr>
<tr>
<td>Unlabelled</td>
<td>4</td>
<td>22-23</td>
<td></td>
<td></td>
<td>4</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>84</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

recorded with no roots and no wear. As the premolars come into occlusion during the first week of life, these teeth indicate death within a few days of birth.

A sample of 84 shed antlers has also been analysed from the Inner Chamber. A summary of the measurements taken is given in Table 5.12. Of the 72 shed antlers which were found in the top 12" of deposit, 59 were from females and 13 were from juvenile males (Fig. 5.14). As with the sample from the Outer Cave, the size range of juvenile males (13-20 mm) suggests that the animals represented by this collection were yearlings. The size range of the female antlers corresponds with that found in modern populations.
5.21.6 Dating

Several radiocarbon dates have been obtained from reindeer bone and antler from both the inner and outer chambers (Table 5.13). Three dates from the fossiliferous gravel (Layer 3) in the Outer Chamber range in age from 28,000 to 44,000 BP. Three samples from the gravels in the shaft connecting the Inner and Outer Chambers have produced dates which range from 22,000 to 32,000 BP. These latter dates are not in depth order but, given the crude methods of excavation and a possible fluvial origin for the gravels, this inconsistency is not unexpected. All of the above dates were obtained from single specimens.

Four dates have also been obtained on single samples of reindeer bone and antler from the Inner Chamber. Two of these dates were obtained on shed antlers and fall at the boundary between the Middle and Late Devensian. Two assays on neonatal reindeer bones have produced markedly different dates, one falling within the Middle Devensian and the other within the early Holocene.

Two dates have also been obtained on bulk samples of antler. These dates suggest that reindeer were present in the Assynt area at the height of the last glaciation and during the Lateglacial stadial. Given the wide range of ages which have now been obtained on single specimens from both the Inner and Outer Chambers both these dates must now be considered to be unreliable.

In summary, the radiocarbon dates indicate that reindeer were calving in the Inchnadamph area during three distinct periods, at around 43,000 - 48,000 BP between 22,000 and 32,000 BP and in the early Holocene.

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Species</th>
<th>Element</th>
<th>Context</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>OxA-3786</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Shaft 0-3'</td>
<td>31,580 ± 520</td>
</tr>
<tr>
<td>OxA-3792</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Shaft 4-5'</td>
<td>22,300 ± 240</td>
</tr>
<tr>
<td>OxA-3787</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Shaft 5'-6'</td>
<td>28,800 ± 450</td>
</tr>
<tr>
<td>OxA-3793</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Layer 3</td>
<td>33,800 ± 2,400</td>
</tr>
<tr>
<td>OxA-3984</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Layer 3</td>
<td>28,240 ± 390</td>
</tr>
<tr>
<td>OxA-3985</td>
<td>Reindeer</td>
<td>Shed female antler</td>
<td>Layer 3</td>
<td>31,490 ± 570</td>
</tr>
<tr>
<td>SRR-1788</td>
<td>Reindeer</td>
<td>Antlers</td>
<td>Layer 3</td>
<td>10,080 ± 70</td>
</tr>
<tr>
<td>SRR-1789</td>
<td>Reindeer</td>
<td>Antlers</td>
<td>0-12&quot;</td>
<td>18,040 ± 240</td>
</tr>
<tr>
<td>SRR-2103</td>
<td>Reindeer</td>
<td>Shed antler</td>
<td>0-12&quot;</td>
<td>25,360 ± 810/740</td>
</tr>
<tr>
<td>SRR-2104</td>
<td>Reindeer</td>
<td>Shed antler</td>
<td>0-12&quot;</td>
<td>24,590 ± 790/720</td>
</tr>
<tr>
<td>SRR-2105</td>
<td>Reindeer</td>
<td>Limb bone</td>
<td>0-12&quot;</td>
<td>8,300 ± 90</td>
</tr>
<tr>
<td>OxA-3788</td>
<td>Reindeer</td>
<td>Proximal metacarpal</td>
<td>0-12&quot;</td>
<td>47,900 ± 3600</td>
</tr>
</tbody>
</table>

Table 5.13 Radiocarbon dates from Reindeer Cave, Inchnadamph, Sutherland (Lawson 1984, Murray et al 1993).
5.21.7 Accumulation of the reindeer remains

The exceptionally large collection of reindeer antlers from the Outer Chamber has given rise to speculation about the agents involved in its accumulation. Assuming that the gravels of Layer 3 were formed during the Lateglacial stadial, Lawson and Bonsall (1986) suggested that man may have been the agent responsible for the accumulation of this collection. While there is no evidence that the antlers have been worked in any way, it was suggested that the collection may have formed a cache. Callander et al (1927) reported evidence for Palaeolithic occupation within the cave in the form of charcoal, scratched reindeer antlers and a single antler artefact from the shaft at the back of the cave. This artefact is now lost and its authenticity can not be verified.

An alternative explanation for the formation of this assemblage has been suggested by Scott (1986a). She compared the collection of antlers from Reindeer Cave with the faunal collection from Picken's Hole, Mendip and suggested that both assemblages were accumulated by wolves. The absence of any evidence of gnawing and the almost complete lack of reindeer postcranial bones from the Outer Chamber argues against this interpretation.

The recent radiocarbon dates have indicated that the accumulation of the antlers took place over thousands of years, thus arguing against their collection and storage by man. The precise mechanism by which the antlers were introduced into the cave remains uncertain however.

The mechanisms involved in the accumulation of the faunal collection from the Inner Chamber may be rather different. Unlike the Outer Chamber, where bones and antlers were dispersed throughout a gravel deposit of possible fluvial origin, the reindeer remains from the Inner Chamber were restricted to the upper 30cm of a silt deposit. Many are reported to have been found on the surface.

A considerably higher proportion of postcranial bones were found within this cave than were recovered from the gravels of the Outer Chamber. The animals represented by this collection were all very young calves. Neonatal deaths in reindeer are not uncommon and may amount to 30% in modern populations (Leader-Williams 1988). Young calves are also vulnerable to predation by many animals, however, including wolf, lynx and fox. The reindeer bones from this collection are remarkably well preserved and only 3 specimens (3%) show any signs of possible carnivore damage. None shows any signs of cut marks. In situ death from natural causes seems to be the most likely explanation for the accumulation of this assemblage. Given the wide range of radiocarbon dates which have been obtained from the Inner Chamber, however, it is quite possible that several different mechanisms were responsible for its formation.
5.22 Sandford Hill, Mendip, Somerset

Sandford Hill lies to the east of Banwell on the western edge of Mendip. The earliest reference to caves at this site is found in a published letter from David Williams, an amateur geologist and rector of Bleadon and Kingston Seymour, to William Patteson, rector of Shaftesbury (Williams 1829). This letter makes reference to two caves. The first was an enormous cavern which was explored by miners and was said to be over 240 feet deep, with no signs of sides or bottom. The second cave was an extensive cavern, lying further to the west and near to the site at which an elephant skeleton was found in 1770. No additional details of either cave were given.

No further description of the Sandford Hill caves has been found. Dawkins (1874) and Balch (1948) make reference to a fossil-bearing cave and its excavation by the local farmer, William Beard, but both authors rely on the early description of the caves made by David Williams.

The exact location of the fossil-bearing cave is unknown and no details of Beard's excavations are given in any published work. A note in the Visitors and Accounts Book for the Banwell Bone Caves³, however, details the purchase of Beard's collections of fossil bones from six different caves. These were bought by Capt. Sandford and Rev. Jones of Taunton and were "removed to the Institution" (Somerset Natural History and Archaeological Society Museum) in 1864.

5.22.1 Material studied

The material studied here is held in Taunton Castle Museum, formerly the museum of the Somerset Natural History and Archaeological Society. The entire collection is marked in ink, either with the initials

S.H.
B.

or with the words

Sandford Hill
Beard.

The faunal collection from Sandford Hill has not been fully catalogued and the full range of species represented at the site is currently unknown. The remains of two species have been studied in some detail, however. Hyaena remains have been investigated by Turner (1981), while the material studied here has been restricted to reindeer, of which a total of 478 bones has been recorded (Table 5.14).

---
<table>
<thead>
<tr>
<th>Element</th>
<th>NISP</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antlers</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>Cranium</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Maxilla</td>
<td>21</td>
<td>11</td>
</tr>
<tr>
<td>Mandible</td>
<td>65</td>
<td>34</td>
</tr>
<tr>
<td>Vertebræ</td>
<td></td>
<td></td>
</tr>
<tr>
<td>atlas</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>axis</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>cervical</td>
<td></td>
<td></td>
</tr>
<tr>
<td>thoracic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>lumbar</td>
<td></td>
<td></td>
</tr>
<tr>
<td>sacrum,</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>Ribs</td>
<td>35</td>
<td>18</td>
</tr>
<tr>
<td>Scapula</td>
<td>37</td>
<td>22</td>
</tr>
<tr>
<td>Humerus</td>
<td>36</td>
<td>20</td>
</tr>
<tr>
<td>Ulna</td>
<td>13</td>
<td>9</td>
</tr>
<tr>
<td>Metacarpal</td>
<td>55</td>
<td>23</td>
</tr>
<tr>
<td>Innominate</td>
<td>18</td>
<td>10</td>
</tr>
<tr>
<td>Femur</td>
<td>27</td>
<td>16</td>
</tr>
<tr>
<td>Tibia</td>
<td>45</td>
<td>19</td>
</tr>
<tr>
<td>Tarsals,</td>
<td></td>
<td></td>
</tr>
<tr>
<td>calcaneus</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>talus</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>centroquartal bone</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Metatarsal,</td>
<td>41</td>
<td>18</td>
</tr>
<tr>
<td>Phalanges</td>
<td></td>
<td></td>
</tr>
<tr>
<td>proximal</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>middle</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>478</td>
<td>34</td>
</tr>
</tbody>
</table>

Table 5.14 Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) for reindeer from Sandford Hill, Mendip, Somerset.

5.22.2 Formation of the deposits

While very little is known about the cave or the deposits from which this collection was derived, the bones themselves do give some indications as to the mechanisms involved in their accumulation. Of the six main limb bones (humerus, radius, femur, tibia and metapodials) 46.9% are complete or almost complete. No bone bears any signs of cut-marking or gnawing by carnivores and, in general, the bones are in remarkably fine condition. As Beard's excavation methods and sampling strategies are unknown, it is impossible to know whether this sample is representative of the original collection. The relative proportions of different elements of the body are therefore of little significance here. It is noteworthy, however, that Beard's collection includes small items as phalanges.
albeit in smaller numbers than those of the larger elements. The almost complete representation of the skeleton, when considered in conjunction with the completeness and excellent preservation of the bones, suggests that this collection represents the remains of entire animals which either died in situ, or which were brought into the cave by some natural mechanism.

5.22.3 Seasonality
The large size of this sample of reindeer bones, antlers and teeth has facilitated the use of a number of methods to identify the degree of seasonality within the collection. The survival of many intact juvenile dentitions has enabled the study of tooth eruption sequences, while the excellent preservation of the long bones has enabled a detailed analysis of bone size distributions. Additional detail on the degree of seasonality within the collection has been obtained through the study of crown heights, the calibration of juvenile femur size distributions and the analysis of a small sample of shed and unshed antler.

5.22.3.1 Tooth eruption sequences
A total of 86 reindeer dentitions has been recorded from this collection. From a detailed study of the mandibles it has been possible to establish a minimum number of 34 individuals (Table 5.15). Of these, 26 specimens may be classified as calves, whose state of tooth eruption may be used to determine age and season of death.

Seven specimens show light wear on the deciduous premolars and the first permanent molar is in the process of erupting. These may be classified as 3-5 month old animals. A further 6 specimens also have light wear on the deciduous premolars but the first molar is missing. These have also been assigned tentatively to the 3-5 month age class.

Seven mandibles show the second molar in the process of piercing the mandibular bone. These specimens exhibit light wear on a fully erupted molar 1 and moderate wear on the deciduous premolars. Given their stage of eruption, these individuals may be assigned

<table>
<thead>
<tr>
<th>Age</th>
<th>Left</th>
<th>Right</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-5 months</td>
<td>8</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>5-10 months</td>
<td>7</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Calf 1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>15 months plus</td>
<td>23</td>
<td>16</td>
<td>18</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>34</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5.15 Age classes of reindeer mandibles from Sandford Hill, Mendip, Somerset.
to a 5 - 10 month age class. A further 4 specimens lack both the first and second molar but the deciduous premolars may be described as moderately worn. These have also been assigned to the older age group of 5 - 10 months.

The two remaining mandibles have not been classified under either of these two groups. The first of these has deciduous premolars which may be described as showing light to moderate wear. The second only preserves one premolar in the jaw (dp2) which exhibits moderate wear. Neither of these specimens provides sufficient information to enable the determination of age and has therefore been assigned to an indeterminate category of "calf".

Aside from the positive seasonalities indicated by the mandibles described above, there is also negative evidence in the form of a total absence of mandibles indicating a spring or early summer seasonality. No neonatal specimens have been found, nor any with molar 2 in the process of erupting.

5.22.3.2 Bone size distributions

The evidence from the mandibles suggests reindeer presence from mid-August to mid-March. This interpretation of limited seasonal presence is supported by evidence from the size distribution of juvenile long bones. As reindeer begin to exhibit sexual dimorphism during the second year of life, size distribution patterns may only provide evidence of the degree of seasonality in bones which are of known age. Six bones (radius, humerus, metapodials, tibia and innominate) fuse sufficiently early to enable the determination of age and to distinguish between patterns which reflect seasonality and those which reflect sexual dimorphism. The pattern of size distribution of each of these elements is discussed in detail below.

Radius

According to Egorov (1967) (Table 4.3), the proximal radius in reindeer fuses during the first year of life and is fully fused at 1 year of age. As the distal epiphysis remains unfused until the fourth year of life, it is possible to distinguish two classes of juvenile animals from the state of fusion of radii. Where neither epiphysis is fused the animal may be classed as a calf aged less than one year. Where the proximal epiphysis is fused but the distal epiphysis is unfused the animal may be classed as a one-three year old. Where both epiphyses are fused the animal may be considered to be fully adult.

A total of 36 radii has been found at Sandford Hill. As the assessment of age requires complete specimens the sample size is reduced to 17. These are classified in Table 5.16.
Table 5.16 Age classes of reindeer radii from Sandford Hill, Mendip, Somerset.

<table>
<thead>
<tr>
<th>Age</th>
<th>Left</th>
<th>Right</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf</td>
<td>2</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>1-3 year old</td>
<td>5</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Adult</td>
<td>3</td>
<td>1</td>
<td>3</td>
</tr>
</tbody>
</table>

In Figure 5.15 two measures of radius size, the greatest length of the bone (GL) and the smallest breadth of the diaphysis (Sd), have been plotted against one another in a scattergram. Adults have been included in this plot in order to illustrate the full size range but it is the distribution of the juvenile bones which is of particular interest to this study. While the sample size is very small, it is clear that the distribution pattern is not continuous. It should be noted, however, that the distinction between calf and juvenile animals on the basis of the measure of greatest length (GL) is exaggerated by the fusion of the proximal epiphysis. There is also a partial separation of the two groups on the basis of breadth of the diaphysis but this is not complete and there is thus some overlap between the two juvenile age groups.

Humerus
As with the proximal radius, the distal humeri of reindeer fuse early in life. Fusion has already occurred by the age of one but is not completed until the animal is three years old. The trochlea fuses first, followed by the distal condyles. While the latter fuse during the second year of life, the suture remains visible until the age of three. Four age classes may therefore be determined on the basis of the state of fusion of the distal humeri (Table 5.17).

Table 5.17 Criteria for the identification of age classes in the distal humerus of reindeer

<table>
<thead>
<tr>
<th>Distal epiphyses</th>
<th>Age.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfused</td>
<td>Calf</td>
</tr>
<tr>
<td>Trochlea fused, condyles unfused</td>
<td>Yearling</td>
</tr>
<tr>
<td>Fully fused with suture visible</td>
<td>2-3 years</td>
</tr>
<tr>
<td>Fully fused, no suture visible</td>
<td>3 years plus</td>
</tr>
</tbody>
</table>

6. The measurements used here, and their abbreviations, follow those recommended by von den Driesch in with the exception of the length of the diaphysis of the humerus. These measures are described in Appendix 6.
Fig. 5.15 Size distribution of radii from Sandford Hill, Mendip, Somerset.
At Sandford Hill a total of 37 humeri has been found and the distal end is preserved in all but three cases. These have been classified into their respective age groups and are listed in Table 5.18.

The relative sizes of these humeri have been plotted in Figure 5.16. The fractured nature of many of the bones has reduced the sample size to sixteen. As with radii, the unfused nature of the juvenile bones exaggerates the distinction between age groups on the basis of greatest length. A measure of diaphysis length has therefore been employed here (DL), which enables direct comparison between fused and unfused bones. Clear gaps are visible in the plot of diaphysis length between calves, yearlings and 2 year olds/adults. While the measure of diaphysis width does not produce such clear separation into size groups, there is no overlap in the range of this measure between the calf, yearling and 2 year old age classes.

**Metacarpal**

In the case of reindeer metacarpals, the distal epiphyses are already fused by the age of two. Suture lines do not disappear until the following year and three age groups may therefore be recognised through an analysis of the state of fusion of this element (Table 5.19).

Of the 55 metacarpal fragments found at Sandford Hill, 16 did not preserve the distal end. The remaining 39 specimens have been listed in Table 5.20 according to their age.

<table>
<thead>
<tr>
<th>Distal epiphyses</th>
<th>Age.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfused</td>
<td>0-2 years</td>
</tr>
<tr>
<td>Fused with suture visible</td>
<td>2-3 years</td>
</tr>
<tr>
<td>Fully fused, no suture visible</td>
<td>3 years plus</td>
</tr>
</tbody>
</table>

Table 5.19 Criteria for the identification of age classes in the distal metacarpal of reindeer.
Fig. 5.16 Size distribution of humeri from Sandford Hill, Mendip, Somerset.
Sixteen of the juvenile specimens (0-2 years) are complete and a measure of greatest length of the bone (GL) has been recorded. When these measures are plotted in the form of a bar chart, a clear bimodal distribution pattern is revealed with no overlap between the two groups (Figure 5.17). When this measure of bone length is compared with two measures of bone width and depth, a further sub-division becomes apparent within the larger of the two groups (Figs. 5.18, 5.19). As with the radii and humeri, the measure of bone length produces a clearer pattern of separation than either measure of bone width.

Metatarsal
As with reindeer metacarpals, the metatarsals fuse during the second year of life and suture lines disappear by the time the animal reaches the age of three. Three age classes, comparable with those for metacarpals, can therefore be discerned from an analysis of the state of fusion of distal metatarsals.

A collection of 41 metatarsal fragments has been studied from Sandford Hill. The distal end was preserved in 32 cases and these have been classified according to age in Table 5.21. Unfortunately few specimens are complete (n = 11), and the small sample size inhibits the recognition of age groups on the basis of greatest length. (Fig. 5.20) A measure of the width of the distal end does appear to indicate a degree of separation within the juvenile bones, however, when plotted against a measure of diaphysis depth (Fig. 5.21).

<table>
<thead>
<tr>
<th>Age</th>
<th>Left</th>
<th>Right</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2 years</td>
<td>9</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>2-3 years</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3 years plus</td>
<td>8</td>
<td>5</td>
<td>9</td>
</tr>
</tbody>
</table>

Table 5.21 Age classes of reindeer metatarsals from Sandford Hill, Mendip, Somerset.
Fig. 5.17 Size distribution of unfused metacarpals from Sandford Hill, Mendip, Somerset.
Fig. 5.19 Size distribution of metacarpals from Sandford Hill, Mendip, Somerset (DD/SD).
Fig. 5.20 Size distribution of metatarsals from Sandford Hill, Mendip, Somerset (SD/GL).
Fig. 5.21 Size distribution of metatarsals from Sandford Hill, Mendip, Somerset (DD/Bd).
Table 5.22 Age classes of reindeer tibiae from Sandford Hill, Mendip, Somerset.

<table>
<thead>
<tr>
<th>Age</th>
<th>Left</th>
<th>Right</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2 years</td>
<td>10</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>2-3 years</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3 years plus</td>
<td>8</td>
<td>3</td>
<td>8</td>
</tr>
</tbody>
</table>

Tibia
The pattern of fusion of the distal tibiae of reindeer mirrors that of the distal metapodials. Fusion begins in the second year of life and is completed by the age of three.

From a collection of 45 reindeer tibiae from Sandford Hill, 28 distal fragments have been analysed and classified according to age group (Table 5.22).

Few of the tibiae fragments from Sandford Hill are complete and patterns of their size distribution are therefore rather unclear. A plot of the spread of measures for length against depth is neither indicative of continuity nor discontinuity (Fig. 5.22). The presence of a single example of a 2 year old animal is notable, however, as this age group is absent from the rest of the bone samples.

Innominate
The fusion of the ilium and ischium occurs during the first year of life and the suture is fully fused by the age of two. Three age groups may therefore be recognised from an analysis of pelvis fragments (Table 5.23).

A collection of 18 pelvis fragments has been studied from Sandford Hill. As the ilium and ischium are unfused in several of these examples only ilia have been included in the classification of age groups listed in Table 5.24.

The sample size in this case is extremely small and no yearling animals appear to have been preserved. It is therefore impossible to determine the degree of seasonality in this sample from an analysis of bone size.

<table>
<thead>
<tr>
<th>Ilium and ischium</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unfused</td>
<td>Calf</td>
</tr>
<tr>
<td>Fully fused with suture visible</td>
<td>Yearling</td>
</tr>
<tr>
<td>Fully fused, no suture visible</td>
<td>2 years plus</td>
</tr>
</tbody>
</table>

Table 5.23 Criteria for the identification of age classes in the innominate bones of reindeer.
Fig. 5.22 Size distribution of tibiae from Sandford Hill, Mendip, Somerset.
Table 5.24 Age classes of reindeer ilia from Sandford Hill, Mendip, Somerset.

<table>
<thead>
<tr>
<th>Age</th>
<th>Left</th>
<th>Right</th>
<th>MNI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf</td>
<td>1</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Yearling</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2 years plus</td>
<td>4</td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>

Summary of bone size distributions
A random sample of bone sizes from a biological population, representing all stages of growth, would be expected to produce a continuous size distribution pattern. In the case of reindeer, where births are synchronous, gaps in the distribution pattern may therefore be interpreted as seasonal absences. While the patterns of bone size distribution from Sandford Hill do not illustrate a complete separation into discrete size classes in each case, they do suggest that the size range of juvenile animals represented at Sandford Hill is not continuous. This is most clearly visible in the radii, humeri and metacarpals.

The standard measure of greatest length exaggerates the distinction between fused and unfused bones, however. The discontinuity in the size distribution of calf and yearling groups in the radii from Sandford Hill is lessened if the longitudinal growth of the bones is disregarded. Finding alternative measures which are recordable for both juvenile and adult bones is rather difficult and is limited to measures of diaphysis width and depth (with the exception of humeri, where a measure of diaphysis length may be estimated). Increase in bone length occurs as a result of growth at the epiphysial ends of the bone. Increase in bone girth is the result of bone re-modelling and is a secondary growth process (Davis 1987). In the juvenile animals at Sandford Hill, these measures of bone girth do not appear to distinguish groups within the size distribution as readily as the measure of bone length.

The humeri from Sandford Hill exhibit a clear separation into size groups. As the state of fusion of the distal humeri allows the identification of age classes, it can be seen that there is considerable discontinuity in size between calf, yearling and two year old animals.

In the case of the metacarpals, measures of diaphysis length, width and depth distinguish three discrete size groups within the 0 - 2 year age class. The first distinction, which is made on the basis of diaphysis length, may be compared with those observed for juvenile radii and humeri and may be interpreted as the distinction between calf and yearling age groups. The second grouping, which is apparent in plots of diaphysis width and depth (Figs 5.18, 5.19), splits the yearling group into two marked sub-groups. While the sample size is small, this latter distinction is mirrored within the adult metacarpals where it may be interpreted as the product of sexual dimorphism. As this phenomenon
begins to appear during the second year of life, it is likely that the divisions within the yearling sample are also a product of emerging dimorphism between yearling males and females.

In sum, the evidence from at least three of the reindeer skeletal elements at Sandford Hill, *ie* radii, humeri and metacarpals, appears to indicate discontinuity in the size distribution of juvenile animals. In the case of the metatarsals, tibiae and ilia, the sample sizes were too small to enable a satisfactory analysis of distribution patterns. This discontinuity in size distribution may be interpreted as the result of seasonal absence.

5.22.3.3 Calibrating the size distribution of the juvenile bones

Growth curves are only available for two skeletal elements, mandibles and femurs. While a fairly large sample of juvenile mandibles has been studied from Sandford Hill, many of these specimens are fragmentary and a measure of greatest length cannot be obtained. It is not possible, therefore, to calibrate the size distribution of the juvenile mandibles against the known growth curve. Six complete juvenile femurs have been recorded from Sandford Hill, however, and the ages of these animals have been estimated using the equation

\[ t = t_i - \frac{1}{k \ln(A - y/y)} \]

when \( t = \) age (in months), \( y = \) length, \( A = 225, t_i = 0 \) and \( k = 0.42 \). (Leader-Williams and Ricketts 1982)

The lengths and estimated ages of these specimens are given in Table 5.25.

<table>
<thead>
<tr>
<th>Ref. No.</th>
<th>Greatest length (GL-mm)</th>
<th>Estimated age</th>
</tr>
</thead>
<tbody>
<tr>
<td>161</td>
<td>198</td>
<td>4.7 months</td>
</tr>
<tr>
<td>164</td>
<td>176</td>
<td>3.0 months</td>
</tr>
<tr>
<td>201</td>
<td>205</td>
<td>5.5 months</td>
</tr>
<tr>
<td>203</td>
<td>187</td>
<td>3.8 months</td>
</tr>
<tr>
<td>210</td>
<td>203</td>
<td>5.2 months</td>
</tr>
<tr>
<td>208</td>
<td>208</td>
<td>5.9 months</td>
</tr>
</tbody>
</table>

Table 5.25 Ages of six juvenile reindeer from Sandford Hill, Mendip, Somerset, estimated on the basis of the greatest length of the femur.

---

7. In using this formula it must be noted that Leader-Williams and Ricketts (1982) did not describe their measure of femur length (y). It is therefore impossible to guarantee that the measure used here is similar to that used by Leader-Williams and Ricketts in the calculation of this formula.
These results place the juvenile femurs within a three to six month age group. This supports the evidence of seasonality derived from an analysis of tooth eruption sequences which places the juvenile mandibles within two age groups of 3 - 5 months and 5 - 10 months.

5.22.3.4 Crown heights
Crown heights have been recorded for the fourth deciduous premolar of the lower jaw. Measurements were taken on the buccal side of the posterior cusp (see Fig. 4.2) and a total of 20 teeth has been studied. The crown heights of these teeth range from 8.1 to 10.45mm. When the sample is plotted on a histogram it is clear that there is a very considerable overlap between the size range of the two age groups, 3 - 5 months and 5 - 10 months (Fig. 5.23).

While no modern data on deciduous crown heights are available for comparison, this histogram may be contrasted with that produced for reindeer teeth from the site of Ossom's Cave (Fig. 5.8). The Ossom's Cave sample includes teeth which can be placed within a 10 - 15 month age class on the basis of tooth eruption sequences. The crown heights of these teeth fall within the range of 4.8 - 5.4 mm. Clearly several factors may influence crown heights, including individual and inter-population size variation and vegetational differences, resulting in differential wear rates. It seems probable, however, that the marked distinction in crown heights which is visible between the two samples is the product of distinct age differences. This finding provides support for the determination of age in juvenile mandibles from an analysis of the wear patterns of the deciduous premolars alone. It also suggests that reindeer presence in the area of Sandford Hill during the winter was restricted to the early winter months. If the animals had been present towards the end of the winter period, one might expect a degree of overlap between the range of crown heights of the 5 - 10 month old animals from Sandford Hill and those of the 10 - 15 month old animals from Ossom's Cave. No such overlap exists.

5.22.3.5 Antlers
While the evidence from the reindeer bones and teeth appears to indicate seasonal presence in the vicinity of the Sandford Hill during late summer, autumn and early winter, the evidence from the antlers is less clear (Fig. 5.24). Only three shed antlers have been preserved in the collection. One of these is an adult male, which indicates reindeer presence between October and January. This supports the picture of seasonality generated from an analysis of the bones and teeth. The other two specimens are shed females, however, which would indicate reindeer presence in May or June. Three shed pedicle scars are of uncertain sex and may indicate reindeer presence between February and May. Three
Fig. 5.23 Crown heights of deciduous premolar 4 from Sandford Hill, Mendip, Somerset.
Fig. 5.24 Size distribution of antlers from Sandford Hill, Mendip, Somerset.
unshed adult males confuse the picture further by indicating reindeer presence between July
and December.

5.22.4 Summary of seasonality at Sandford Hill
Three lines of evidence, tooth eruption sequences, bone size distributions and tooth crown
heights, all indicate the limited seasonal presence of reindeer in the vicinity of Sandford
Hill during late summer, autumn and early winter. A fourth line of evidence from the
study of antlers has produced a markedly different picture indicating reindeer presence in
the spring and early summer.

While it is difficult to reconcile these conflicting lines of evidence into a single
interpretation of reindeer behavioural ecology, two possible explanations for this apparent
inconsistency may be proposed. Firstly, the accumulation of reindeer bones may represent
a long term and sustained use of the western Mendips by reindeer during the late summer,
autumn and early winter with only periodic use of the area during the spring and early
summer accounting for the small sample of shed female and juvenile male antlers.
Alternatively, the large sample of reindeer bones may have accumulated during a single
catastrophic event, the remaining shed antlers being the product of more sustained presence
of reindeer in the area. Unfortunately, in the absence of more detailed information on the
nature of the deposits in which this material was found, this matter may not be resolved.

5.22.5 Dating
An existing radiocarbon date on a hyaena skull from Sandford Hill (BM-1526 36,000 +/-
1900) indicated that at least part of the faunal collection from the site fell within the Middle
Devensian period (Burleigh, Matthews and Ambers 1982). A further accelerator
radiocarbon date obtained on a juvenile reindeer mandible for the purposes of this study
has confirmed a Middle Devensian age for at least some of the reindeer material. This date,
OxA-3789 40,600 +/-1500, overlaps with that obtained from the hyaena skull at two
standard deviations. The date for the reindeer material was obtained from a mandible with
the first permanent molar in the process of eruption, indicating a season of death between
mid-August and mid-October (Ref. M30). This date may therefore be used to confirm
reindeer presence in the vicinity of Sandford Hill during the Middle Devensian period in
late summer and early autumn.

5.23 Shropham JC Pit, Norfolk
Shropham JC Pit is a gravel pit located alongside the River Thet in Norfolk. It is named
after John Claydon, a local collector who first discovered fossils in the pit in the 1980s.
The pit is several hundred metres long and ca 150 metres wide and has produced large numbers of faunal remains of Ipswichian and Devensian age. A complex stratigraphic sequence has been observed in pit sections and, while the site has yet to be published, a provisional interpretation of these strata is outlined here (Stuart pers. comm\textsuperscript{8}).

The uppermost layers in the pit consist of gravels interspersed with channel deposits. These are thought to have been laid down by a fluvioglacial river with a rapidly changing pattern of braided channels. The gravels, which are cut by thick ice wedge casts, have produced large numbers of faunal remains, most notably bison and reindeer. A few reindeer bones and antlers were found \textit{in situ} but most were collected from conveyor belts during gravel extraction. Organic remains, including those of conifers, have also been recovered from the channel deposits.

Beneath the gravels, and cut and eroded by them, is a detritus mud which has produced plant macrofossils, molluscs, pollen and the bones of pond turtles. Rolled \textit{Hippopotamus amphibius} bones which were found in the overlying gravels are also thought to have been derived from these muds. Preliminary analysis of the plant macrofossils indicate that they may belong to the Ipswichian interglacial. Beneath the detritus muds are further lacustrine deposits and organic strata. The latter contain evidence for the presence of birch (\textit{Betula}) and pine (\textit{Pinus}) and are thought to date to an early stage of the Ipswichian.

5.23.1 Seasonality

Twenty-two reindeer antlers were recovered from the site between 1989 and 1990 (Fig. 5.25). Of these, 15 are shed and 7 are unshed. All the shed antlers are from males, eight of which were adult animals and seven of which were juveniles. The former are indicative of reindeer presence between October and January, while juvenile antlers may be shed at any time between February and May. The juvenile specimens from this site are all at the upper end of the size range for juvenile males (Measure 2 - 18-29 mm), however, suggesting that they were probably shed during the late winter months of February and March.

Analysis of the seven unshed antlers indicates that four were adult males, one was a female and two are of unknown sex. Only the unshed males provide any indication of seasonality, having died at some time between July and December.

5.23.3 Dating

No radiocarbon dates have been obtained on fossils from this site. Preliminary analysis of organic remains from the Devensian channel deposits suggests that the surrounding landscape may have been wooded during the formation of those channels. This has led

\textsuperscript{8} Dr A. I. Stuart, Norwich Castle Museum, Norwich.
Fig. 5.25 Size distribution of antlers from Shropham JC Pit, Norfolk.
Stuart (pers. comm.) to compare the site with that at Wretton in Norfolk where evidence for a possible Early Devensian wooded interstadial event has been found. Geomorphological evidence seems to contradict this interpretation, however. The presence of ice wedge casts in the gravels is indicative of periglacial activity, which suggests that the gravels were laid down during a period of intense cold. Braided rivers are also a common feature of periglacial environments. These features would suggest that the gravels were a rather later formation, related to the glacial phases of the Late Devensian. The resolution of this contradiction between the different lines evidence must await final publication.

5.24 Soldier's Hole, Cheddar, Somerset
Soldier's Hole is a large cave set in the cliffs of Cheddar Gorge. It was first explored by the Somerset Archaeological and Natural History Society in 1925-6 (Balch 1928), and was later excavated by R. F. Parry between 1928 and 1929 (Parry 1931). The former excavations uncovered material from several periods ranging from the Neolithic through into Roman times. The latter excavations were more extensive and removed over three metres of deposits, the lower layers dating to the Middle Devensian period.

5.24.1 Stratigraphy
Parry's excavations involved the removal of material in six inch spits but a sequence of four distinct layers was also recognised within the deposits. Layers 1 and 2 were laid down during the post-glacial period while layers 3 and 4 were formed during the last glaciation. Layer 3 (Spits 4-9) was composed of a red marl deposit which was mixed with a considerable quantity of limestone scree. Thirteen flint artefacts of Late Upper Palaeolithic type were found within this layer. Layer 4 (Spits 10-17) also consisted of a dark red marl with many limestone fragments but produced seven flint tools of Early Upper Palaeolithic age. Spits 18-21 were removed from a fissure in the floor of the cave. These deposits were similar to those of Layer 4 but produced no artefacts.

5.24.2 Devensian Faunas
The faunal remains recorded for Layer 3 include reindeer, bison, fox and saiga antelope (Parry 1931, Hedges, Housley, Law and Bronk 1989). The fauna recorded for Layer 4 is more diverse and includes mammoth, horse, reindeer, red deer, bison, cave lion, hyaena, wolf and bear.
5.24.3 Seasonality
While reindeer remains were found in both Layers 3 and 4, the material studied here is all derived from spits 10-19 of Layer 4. A total of 12 antlers has been studied of which nine are shed bases. These consist of seven adult males, one juvenile male and one female. Three unshed antlers were also studied. The age and sex of two of these is unknown but the third has been identified as female on the basis of an incipient shed line.

Several seasons are represented by this group of antlers. The shed and shedding females indicate reindeer presence in May, while the shed adult males are evidence of reindeer presence between October and January. The single juvenile male antler could have been shed at any time between February and May.

5.24.4 Dating
Several radiocarbon dates have been obtained on material from Parry's Layers 3 and 4 (Table 5.26). These dates illustrate the long time scale involved in the accumulation of Devensian deposits at Soldier's Hole and the considerable overlap in ages between material from Layers 3 and 4.

While Layer 3 appears to involve a mixture of Lateglacial and Middle Devensian faunas, all the dates obtained from Layer 4 may be placed within the broad time range of the Middle Devensian period.

Only two finite dates have been obtained on reindeer bones from Layer 4. These dates indicate at least two periods of reindeer presence in the Mendip region at ca 30,000 BP and

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Species</th>
<th>Element</th>
<th>Context</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>BM-2249R</td>
<td>Reindeer</td>
<td>Metacarpal</td>
<td>Layer 3, Spit 8</td>
<td>10,090 ± 210</td>
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<tr>
<td>OxA-1464</td>
<td>Saiga antelope</td>
<td>Metacarpal</td>
<td>Layer 3, Spit 8</td>
<td>12,120 ± 140</td>
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<td>OxA-2063</td>
<td>Bovini</td>
<td>Right femur</td>
<td>Layer 3, Spit 8</td>
<td>26,600 ± 550</td>
</tr>
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<td>OxA-1956</td>
<td>Bovini</td>
<td>Left ulna</td>
<td>Layer 3, Spit 9</td>
<td>27,500 ± 600</td>
</tr>
<tr>
<td>OxA-691</td>
<td>Reindeer</td>
<td>Calcaneus</td>
<td>Layer 4, Spit 12</td>
<td>&gt;34,500</td>
</tr>
<tr>
<td>OxA-692</td>
<td>Reindeer</td>
<td>Proximal phalanx</td>
<td>Layer 4, Spit 13</td>
<td>29,300 ± 1100</td>
</tr>
<tr>
<td>OxA-2471</td>
<td>Reindeer</td>
<td>Repeat of OxA-692</td>
<td>Layer 4, Spit 14</td>
<td>29,900 ± 450</td>
</tr>
<tr>
<td>OxA-693</td>
<td>Reindeer</td>
<td>Talus</td>
<td>Layer 4, Spit 14</td>
<td>&gt;35,200</td>
</tr>
<tr>
<td>OxA-694</td>
<td>Bovini</td>
<td>Tibia</td>
<td>Layer 4, Spit 16</td>
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<td>OxA-1465</td>
<td>Bovini</td>
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<td>Layer 4, Spit 16</td>
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<td>OxA-1777</td>
<td>Bovini</td>
<td>Repeat of OxA-694</td>
<td>Layer 4, Spit 16</td>
<td>&gt;42,900</td>
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<tr>
<td>OxA-1957</td>
<td>Reindeer</td>
<td>Left humerus</td>
<td>Layer 4, Spit 20</td>
<td>41,700 ± 3500</td>
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Table 5.26 Radiocarbon dates from Soldier's Hole, Cheddar, Somerset (Gowlett, Hedges, Law and Perry 1986, Hedges, Housley, Law and Bronk 1989, Hedges, Housley, Bronk and van Klinken 1991)
ca 42,000 BP. A third date on a reindeer metacarpal has been obtained from Layer 3. This specimen (BM-2249R) dates the presence of reindeer populations in the Mendips to the very end of the last glaciation.

5.25 Tornewton Cave, Torbryan, Devon
Tornewton Cave is one of a series of limestone caves in the Torbryan valley, an ancient course of the River Ambrook. It was first excavated by James Lyon Widger ca 1870. The results of these excavations were never fully published by Widger but were described by Lowe (1918). Subsequent excavations were undertaken by A.H. Ogilvie between 1936-39 but no account of his work was published. The most recent large scale excavations were undertaken by A.J. Sutcliffe and F.E. Zeuner between 1953 and 1960 (Sutcliffe and Zeuner 1962).

5.25.1 Stratigraphy
In addition to the shaft-like main chamber, the latter excavations also involved the investigation of the talus slope which formed outside the cave. A detailed stratigraphy has been produced as a result of these excavations which covers some 10 m of deposits, including those which had already been removed by Widger and Ogilvie. Of particular interest to this study is the "Reindeer Stratum" which consists of Layers 4 and 5 of the talus slope and Layer F of the main cave.

The Reindeer Stratum consisted of a stoneless red earthy deposit ca 60cm thick. Within the main cave, this stratum was underlain by a dark earth (Layer G) and was sealed by a few centimetres of stalagmite (Layer E). All of these deposits were completely removed by Widger. Within the talus slope the Reindeer Stratum was sandwiched between an interglacial deposit (Layer 6 - the Elk Stratum) and a loosely packed deposit of angular blocks of limestone (Layer 3 - Eboulis).

In addition to large numbers of reindeer remains, the Reindeer Stratum also produced evidence for the occurrence of wolf, fox, hyaena, stoat (Mustela erminea), bear, horse, rhinoceros and a bovid. The presence of man was also indicated by the discovery of four flint artefacts, two objects made of bone and a single human incisor. Despite the evidence for human occupation of the cave, Scott (1986a) suggests that the patterns of bone breakage and damage indicate that most of the faunal remains were the product of wolf denning.

5.25.2 Seasonality
The faunal collection from Sutcliffe and Zeuner's excavations is housed in the Natural History Museum in London. 45 antlers have been studied from the Reindeer Stratum, the
majority (93%) of which are shed bases. Only three specimens are unshed. 22 of the shed bases are from females while 22 have been identified as juvenile males (Fig 5.26). The former indicate that the area was used as a calving ground by parturient cows during May. The latter indicate reindeer presence at some time during the late winter and spring (February to May). While the overall size range of beam width (Measure 2) for the male antlers is relatively large (13-26 mm), only three specimens have a beam width greater than 20 mm. The average beam width of 17.5 mm suggests that the animals were no older than yearlings. It is likely therefore that they shed their antlers rather later in the spring, perhaps during April or May.

The three unshed antlers are of unknown sex and can therefore give no indication as to season of death.

In addition to the antlers, several reindeer bones were recovered from the Reindeer Stratum. These included a single maxillary fragment from a juvenile animal. The first permanent molar of this specimen is almost fully erupted and light wear is visible on the anterior cusps only. This stage of eruption and wear is indicative of death between the age of 3-5 months and provides evidence for reindeer presence between mid-August and Mid-October.

5.25.3 Dating
In the talus slope the Reindeer Stratum is overlain by a deposit of angular limestone blocks (Eboulis) which are thought to have fallen from the cliff above. Sutcliffe and Zeuner consider that this deposit was the product of a period of accelerated cliff destruction brought about by frost-shattering. Extensive frost-shattering is generally associated with periglacial environments. This suggests that the Reindeer Stratum was formed prior to the glacial stages of the Late Devensian.

Confirmation of a late Middle Devensian age for this deposit has been obtained from radiocarbon dates on material from the Reindeer Stratum. These dates, which have not yet been published, fall within the period between 20 to 30,000 BP (Currant pers. comm.)

5.26 Upton Warren, Worcestershire
Upton Warren was a large gravel pit in the terrace deposits of the River Salwarpe, a tributary of the Severn. The pit was worked until 1958 and a section of the deposits was described by Coope, Shotton and Strachan (1961).

The principal component of the terrace deposits was a coarse gravel which was interbedded with bands of brown sand. A number of thin fossiliferous bands were

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9. A. Currant, Department of Palaeontology, Natural History Museum, London.
Fig. 5.26 Size distribution of antlers from Tornewton Cave, Torbryan, Devon.
recognisable within the lower half of the deposit. These bands proved to be rich in pond-
dwelling plants, molluscs, ostracods, fish and water beetles. The bands have been
interpreted as large shallow pools which formed on the floodplain of the river. They
existed long enough to enable colonisation by plants and animals but were subsequently
silted up fairly rapidly by the arrival of fresh alluvial deposits.

Preserved within the fossiliferous bands were a rich flora and fauna. The coleopteran
assemblage is mixed, including three distinct elements which are normally associated with
quite different climatic regimes. The combination of northern, southern and continental
species within a single horizon has been interpreted by Coope et al as an indication of
rapidly ameliorating climate. Both the pollen and macrobotanical remains suggest a
relatively temperate climatic regime and a treeless landscape dominated by herbaceous
vegetation.

Few large vertebrate remains were found in situ but sizeable collections were made by
the quarry workmen. Where remains were found in situ, they were rarely located within
the organic silts and were more generally found within the soft sand below. The species
represented in this collection include mammoth, woolly rhinoceros, bison, horse and
reindeer.

5.26.1 Seasonality
A single shed antler from this site provides evidence for season of reindeer presence. This
antler, which was broken in the process of shedding, is that of a large adult male and is
indicative of reindeer presence in the Worcestershire area during the winter months
between October and January.

5.26.2 Dating
Two radiocarbon dates were obtained on plant material from the organic bands. These
dates of 41,500 ± 1200 BP (GRO-595) and 41,900 ± 800 BP (GRO-1063) place the
formation of the pools within the relatively warm phase of the Middle Devensian which is
now known as the Upton Warren interstadial. While the large vertebrate remains were not
directly associated with the organic material from which the dates were obtained they do
confirm a Middle Devensian age for the formation of this faunal collection.

5.27 Victoria Cave, Settle, Yorkshire
Victoria Cave lies at a height of 440m O.D. in the Settle area of the Yorkshire Pennines.
The site was excavated during the nineteenth century by William Boyd Dawkins (1874),
who revealed a sequence of Pleistocene deposits. The lowest level produced an Ipswichian-
type interstadial fauna including hippopotamus, straight-tusked elephant (*Palaeoloxodon antiquus*) and slender-nosed rhinoceros (Jackson 1962, Stuart 1982). This deposit was overlain by a laminated clay and an upper cave earth. The latter deposit produced a rich mammalian fauna, including reindeer, bear, lynx, fox, horse, badger (*Meles meles*) and red deer (Jackson 1962). This odd combination of warm and cold elements is almost certainly the result of excavation techniques resulting in the mixing of Devensian and Holocene faunas.

Several artefacts have been found in the Upper Cave Earth, including four items made from worked reindeer antler (Campbell 1977). Three of these artefacts have been radiocarbon dated and indicate human use of the cave on several occasions between c.11,720 and 10,200 BP (Table 5.27) (Hedges *et al* 1992).

5.27.1 Seasonality

The material studied consists of a single mandible which was found close to the cave mouth, in the lower part of the breccia resting directly upon glacial deposits (Jacobi, R. in Hedges *et al* 1992). This specimen preserves part of the cheek tooth row from the fourth deciduous premolar through to the second permanent molar. From an analysis of the wear patterns and the state of eruption of the second molar, the age at death of this animal may be determined as 5-10 months, giving a season of reindeer presence from mid-October to mid-March.

5.27.2 Dates

A series of five radiocarbon dates has recently been obtained on material from Victoria Cave (Table 5.27). One of these dates, OxA-2454, was obtained on the juvenile mandible described above. This date of 10,970 +/- 120 BP confirms reindeer presence in the vicinity of Victoria Cave during the Lateglacial stadial. A second assay, obtained on a left radius of reindeer, has produced a somewhat earlier date of ca 11,600 BP. This date indicates that reindeer were already present in the Yorkshire area during the latter half of the Lateglacial interstadial.

<table>
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<th>Ref.</th>
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</tr>
</thead>
<tbody>
<tr>
<td>OxA-2453</td>
<td>Grooved double-bevelled point</td>
<td>10,220 ± 110 BP</td>
</tr>
<tr>
<td>OxA-2454</td>
<td>Right mandible of reindeer</td>
<td>10,970 ± 120 BP</td>
</tr>
<tr>
<td>OxA-2455</td>
<td>Broken double-bevelled artefact</td>
<td>11,750 ± 120 BP</td>
</tr>
<tr>
<td>OxA-2457</td>
<td>Left radius of reindeer</td>
<td>11,590 ± 130 BP</td>
</tr>
<tr>
<td>OxA-2607</td>
<td>Biserially barbed harpoon</td>
<td>10,810 ± 100 BP</td>
</tr>
</tbody>
</table>

Table 5.27 Radiocarbon dates from Victoria Cave, Settle, Yorkshire (Hedges *et al* 1992).
5.28 Willment's Pit, Isleworth, Middlesex

Willment's Pit, Isleworth is a gravel pit in the Upper Floodplain terrace of the Thames which was worked during the 1950s and 1960s. A sequence of Devensian sands and gravels was uncovered overlying a fossiliferous, organic silty clay, the latter deposit dated by radiocarbon to ca 43,000 BP.

The organic silty clay bed near to the base of the sequence has produced a rich coleopteran assemblage studied by Coope and Angus (1975). This bed of evenly laminated silts was laid down under quiet water conditions in a moderately sized pool which may have been an abandoned meander of the river Thames. The beetle fauna incorporated in these deposits consists of temperate species, 91% of which are still found in Britain today. An additional 22 named species are today found in central and southern Europe. Coope and Angus considered that this collection was representative of a climatic regime similar to that of the North German plain, with average July temperatures of ca 18°C and average winter temperatures of ca 0°C. The absence of any beetles which are associated with arboreal habitats indicates an open treeless environment. This has been confirmed by pollen analyses which indicate an environment dominated by grasses and sedges (Stuart 1982).

Overlying the silty clay layer are a series of sands and gravels. In contrast to the quiet water conditions responsible for the formation of the silty clay, the overlying sands and gravels are the product of high energy conditions. The presence of ice wedge casts in the upper layers of gravel also attest to the occurrence of periglacial conditions.

5.28.1 Materials studied

In addition to the rich coleopteran assemblage a large collection of mammalian remains has also been recovered from the pit. These were collected by J.W. Simons and are held in the Natural History Museum in London. Of the ten mammalian species recovered only five were recorded in situ in the silty clay bed. These include three large mammals, reindeer, bison and bear, and two voles, northern vole and tundra vole. Most of the mammalian remains were recovered from the overlying sands and gravels, however, and their precise age is therefore uncertain.

5.28.2 Seasonality

Of the reindeer remains a total of 74 shed antlers has been studied. All were male. The overall size range of Measure 2 was 18-47 mm (Fig. 5.27). Only 14 antlers fell within the juvenile size band, the remaining sixty antlers being adult specimens. This collection provides clear evidence of reindeer presence in Middlesex between the months of October
Fig. 5.27 Size distribution of antlers from Willment's Pit, Isleworth, Middlesex.
and January and additional evidence for reindeer presence at some time between February and May.

5.28.3 Dating
Coarse plant debris from the silty clay layer has produced a radiocarbon date of $43,140 \pm 1520/1280$ BP (Birm-319). While such old dates must be treated with caution, it is generally thought that this date places the formation of the silty clay within the Upton Warren interstadial of the Middle Devensian period (Lowe and Walker 1984). It must be remembered, however, that most of the mammalian collection was derived from the overlying sands and gravels which are of an uncertain, but more recent, age.

5.29 Wretton, Norfolk
The low terrace of the River Wissey at Wretton in Norfolk consists of up to 6m of fluviatile sands and gravels which were laid down during the Devensian glaciation. These deposits were exposed in the 1960s during the course of excavations for a flood-water channel and were described in detail by West et al (1974).

Pollen analyses revealed a sequence of eight local vegetational stages (A-H) representing three phases of herbaceous vegetation and two phases of woodland formation.

The pollen spectra for the later woodland substage (F/G) included arboreal species of birch, pine and spruce (Picea). On the basis of this combination of arboreal taxa, West et al correlated this woodland substage with the Early Devensian interstadial which has been recognised at Chelford in Cheshire. They concluded that the earlier woodland substage (C/D), which was represented by birch-pine woodland, must date from a previously unrecognised interstadial event (the Wretton interstadial) in the Early Devensian period.

Large quantities of faunal remains were uncovered during the course of the excavations, and, while most of the bones were found in mounds of excavated material, some specimens were found in situ in beds with pollen spectra of substage type A/B (Stuart 1982). The fauna is dominated by bison but reindeer is also common. Other species include horse, wolf, arctic fox, bear, mammoth and woolly rhinoceros. On the basis of the uniformity of the fauna, it has been suggested that all or most of the collection was derived from the beds of sub-stage A/B (Stuart 1982).

5.29.1 Seasonality
The evidence for seasonality of reindeer presence is derived from a series of reindeer antlers and skulls. A total of 31 antlers has been studied. Of the 24 shed antlers, three can be identified as female, 12 as juvenile males and nine as adult males (Fig. 5.28). Of the seven
unshed antlers, six can be identified as adult males on the basis of size. The seventh specimen is of unknown age and sex.

Three adult male skulls have also been recorded. One skull has shed antlers. The other two animals were in the process of shedding and the skulls retain only one antler each.

The presence of cast antlers from both female and juvenile male animals indicates reindeer presence in the spring months between February and May. The occurrence of cast antlers of adult males indicates reindeer presence between October and January. Adult male skulls with cast antlers are less precise indicators of seasonality as the animals may have died at any time between October and March.

5.29.2 Dating
While the pollen evidence from Wretton suggests an early Devensian date for this fauna, contradictory evidence from the coleopteran assemblage casts some doubt on this interpretation. In an appendix to West et al (1974), Coope questions the identification of the second wooded interstadial event and its correlation with the Chelford interstadial. Coleopteran faunas from the deposits of substages F and G indicate a severe, arctic climate. This is in marked contrast to the pine and spruce forest environment suggested by the pollen evidence. Coope suggests that the arboreal pollen may have been wind-transported over long distances and that the percentages of arboreal pollen which were recorded were artificially high, reflecting a relatively barren and sparsely vegetated landscape.

This discrepancy between the two sources of evidence has yet to be resolved. Both the botanical and coleopteran evidence from deposits of substage A are in general agreement, however, and suggest that the large mammal fauna which was associated with these deposits accumulated during a period of relatively cool climatic conditions and in an open treeless environment dominated by herbaceous vegetation. Geomorphological evidence indicates that this period predates at least two phases of periglacial activity. In the absence of any absolute dates it is impossible to assign an age to these phases with any certainty but it seems likely that they predate the height of the last glaciation, and date from one of the interstadial phases of the Early or Middle Devensian.
The Devensian stage

6.1 Introduction
The timing of the onset of the last glaciation has been determined from oxygen isotope (18O) stratigraphies in deep-sea cores. Through the application of the technique of orbital tuning, a continuous chronostratigraphy has recently been established which spans the last 300,000 years (Martinson et al. 1987). Using this technique the peak of the last interglacial event (18O sub-stage 5e) has been dated to ca 122,560 - 125,190 BP. This date is in broad agreement with several uranium series dates which have been obtained on raised coral terraces. The end of the last interglacial and the onset of the last glacial period has been dated to ca 110,000 BP.

While the end of the last glaciation has been placed conventionally at 10,000 BP (Shotton 1977), recent studies of coleopteran assemblages have indicated that the climatic amelioration which marked the onset of the Holocene was already underway by 10,500 BP (Atkinson et al. 1987).

The Devensian glaciation therefore covers a time span of approximately 100,000 years. The latter part of that time span, from ca 40,000 years BP onwards, falls within the practical limits of radiocarbon dating techniques. Beyond that time range radiocarbon dates may only be regarded as minima. The dating of events within the earlier part of the Devensian glaciation is therefore problematic and relies upon other radiometric techniques such as thermoluminescence and uranium series dating, or on correlation with recognisable lithostratigraphic or biostratigraphic horizons.

6.2 Stratigraphic framework
A stratigraphic framework for the Devensian stage in Britain was first outlined by Mitchell et al. (1973) and a three-fold division of the stage was recognised. The limits of the Middle and Late Devensian periods were determined on the basis of radiocarbon dates, the boundaries of the Middle Devensian period being placed at 50,000 and 26,000 BP. As a result of improvements in dating techniques the position of the lower boundary of this period may now be revised.

In a recent survey of the biostratigraphy of the last glacial period in Europe, Behre (1989) suggested that the boundary between the Early and Middle Weichselian1 periods may be identified by the rapid decline in temperatures that marks the onset of 18O stage 4. The chronostratigraphy which has been produced from the deep-sea oxygen isotopic

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1. The term Weichselian is the name given to the last cold stage in northwest Europe. It is considered to be the correlate of the Devensian period in Great Britain (Mitchell et al 1973) and the two names will be used interchangeably throughout this text depending upon the context.
record dates this event to ca 73,250 BP (Martinson et al 1987). An alternative chronology, which has been suggested by Guiot et al (1989), places the Middle Weichselian boundary at the beginning of the relatively warm period of \textsuperscript{18}O stage 3 (ca 59,000 BP). While it is clear that the determination of period boundaries is to some extent arbitrary, the marked stadial period of \textsuperscript{18}O stage 4 has traditionally been considered to fall within the boundaries of the Early Devensian period. It is also evident that there is a sharp distinction between the stadial conditions prior to 60,000 BP and those of the succeeding period. For the purposes of this study, therefore, Guiot’s chronology will be followed and the lower limit of the Middle Devensian will be considered to be in the region of ca 60,000 BP (Fig. 6.1).

6.3 The Early Devensian (110,000 - 60,000 BP)

Two major interstadials have long been recognised during the early Weichselian period in northwest Europe. The earlier of these was first identified at the Danish type site of Brørup (Andersen 1961). A later interstadial event overlying Brørup deposits has also been identified in pollen profiles from several sites. This event is known as the Odderade interstadial after the type site in northern Germany (Averdieck 1967). These interstadials have been correlated with \textsuperscript{18}O substages 5c and 5a and represent the occurrence of forested conditions throughout northern Europe.

A third interstadial event was recognised by Zagwijn (1961) at the site of Amersfoort in The Netherlands where a bipartite layer of peat appeared to indicate an earlier interstadial underlying Brørup deposits. It has since been shown that both layers belong to the Brørup event and that the intercalated sand layer was the product of local edaphic conditions rather than a more general climatic deterioration (Behre 1989).

The Early Devensian period in Britain is less well understood, and, until recently, only a single forested interstadial was recognised. This interstadial is known as the Chelford interstadial after its type site in Cheshire and was identified on the basis of both pollen and coleopteran evidence (Simpson and West 1958, Coope 1959). Similarities in the pollen profiles have resulted in the correlation of this event with the Brørup interstadial of northwest Europe (Shotton 1977). A series of radiocarbon dates placed the Chelford interstadial at ca 60,000 BP (Worsley 1980) but, as this is beyond the reliable limits of radiocarbon dating, the dates were only regarded as minima. More recently, thermoluminescence dates of 90 - 100,000 years BP have been obtained from the Chelford Sand (Green 1991). This is in broad agreement with the date of ca 90,000 to 107,000 BP which has been estimated for the Brørup interstadial and \textsuperscript{18}O sub-stage 5c (Martinson et al 1987).

A second Early Devensian interstadial has been recognised more recently at the site of Brimpton in Berkshire (Bryant et al 1983). The analysis of the pollen profiles from this site
<table>
<thead>
<tr>
<th>Years BP</th>
<th>British events</th>
<th>European events</th>
<th>Oxygen isotope stages</th>
</tr>
</thead>
<tbody>
<tr>
<td>10,000</td>
<td><strong>Lateglacial stadial</strong></td>
<td>Younger Dryas</td>
<td>Stage 1</td>
</tr>
<tr>
<td>11,400</td>
<td></td>
<td>Allerød</td>
<td></td>
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<tr>
<td></td>
<td>Lateglacial interstadial</td>
<td>Older Dryas, Bølling</td>
<td></td>
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<tr>
<td>13,000</td>
<td></td>
<td>Oldest Dryas, Pleni-Weichselian</td>
<td>Stage 2</td>
</tr>
<tr>
<td>25,000</td>
<td><strong>Dimlington stadial</strong></td>
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<td></td>
<td>Upton Warren interstadial</td>
<td>Denekamp interstadial, Hengelo interstadial, Moershoofd interstadial</td>
<td>Stage 3</td>
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<td>Glinde interstadial, <strong>Ebersdorf stadial</strong>, Oerel interstadial</td>
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<tr>
<td>60,000</td>
<td></td>
<td><strong>Schalkholz stadial</strong></td>
<td>Stage 4</td>
</tr>
<tr>
<td>73,000</td>
<td>Brimpton interstadial</td>
<td>Oderrade interstadial, <strong>Rederstall stadial</strong></td>
<td>Stage 5a</td>
</tr>
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<td></td>
<td>Chelford interstadial</td>
<td>Brørup interstadial, <strong>Herning stadial</strong></td>
<td>Stage 5b</td>
</tr>
<tr>
<td>110,000</td>
<td></td>
<td></td>
<td>Stage 5c, 5d</td>
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<tr>
<td>125,000</td>
<td>Ipswichian interglacial</td>
<td>Eemian interglacial</td>
<td>Stage 5e</td>
</tr>
</tbody>
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Fig. 6.1 Stratigraphic framework of the Devensian stage in Britain and northwest Europe (cold stages highlighted in bold type).
has revealed a sequence of three wooded phases separated by herb biozones. The relative age of these deposits has been established from their stratigraphic position beneath stadial deposits of Middle Devensian age. The earliest wooded stage indicates a regional environment dominated by birch-pine forest. It has been suggested that this episode may represent either an Early Devensian interstadial or the final stages of the last interglacial. The environment of the second wooded stage is dominated by birch, pine and spruce. The overall vegetation pattern is very similar to that of the Chelford interstadial with which it has been correlated. The third wooded phase represents a boreal forest environment in which species of birch and pine were the regional dominants. This previously unrecognised interstadial episode has been named the Brimpton interstadial and has been correlated with the Odderade interstadial event of mainland Europe.

6.4 The Middle Devensian (60,000 - 26,000 BP)
The sequence of stadial and interstadial events during the Middle Devensian period is more complex than the preceding stage. At no time during this period was northern Europe re-forested, however, and for the greater part of the period the area appears to have been dominated by open, treeless shrub-tundra.

Over the past twenty-five years three distinct interstadial events have been recognised from a series of sites in The Netherlands. In the absence of a continuous stratigraphic sequence the relationship between these events was established on the basis of radiocarbon determinations. The accepted sequence placed the Moershoofd interstadial between 43,000 and 50,000 BP and the Denekamp interstadial at ca 30,000 BP (Shotton 1977). The Hengelo interstadial was placed between these two events at ca 39,000 BP.

More recently Behre (1989) has suggested that the status of these interstadials should be considered with caution. Many more radiocarbon dates have now been obtained from The Netherlands and these combine to form a more or less continuous scatter between 50,000 and 30,000 BP. Behre has suggested that these interstadial events may not represent genuine climatic improvements. His alternative interpretation is that the greater part of the Middle Weichselian period was represented by relatively mild conditions during which time closed tundra vegetation formed at edaphically favourable locations.

Behre has recognised two previously unknown early interstadial events from the site of Oerel in northwest Germany, however (Behre and Lade 1986, Behre 1989). This site has produced a continuous pollen profile which covers a time span from the last interglacial through to the early part of the Middle Weichselian period. Behre has compared these interstadials with those already identified in The Netherlands but has concluded that the vegetation characteristics are sufficiently dissimilar to merit their recognition as distinct events. The earlier of these two events, the Oerel interstadial, has been correlated with
known interstadial events in southern Europe. The second episode, the Glinde interstadial, has no known correlates at present, but falls within the earlier part of the Middle Weichselian period and is thought to be stratigraphically earlier than the Dutch interstadial complex.

The sequence of known Middle Devensian interstadial events in Britain is somewhat different. No evidence has yet been found of early interstadial events comparable with the Oerel and Glinde interstadials of northwest Europe. A short but significant interstadial event, the Upton Warren interstadial, has been dated to between 43,000 and 42,000 BP (Shotton 1977). As these dates are close to the limits of resolution of the radiocarbon method, it is possible that this warm interval covered a somewhat longer time-span.

The period between 40,000 and 26,000 BP has not produced evidence for distinct interstadials such as those recognised in The Netherlands. The analysis of coleopteran assemblages from numerous sites has indicated that later Middle Devensian environments varied between temperate and cold continental conditions (Coope 1975). This period is therefore sometimes referred to as the Upton Warren Interstadial Complex.

6.5 The Late Devensian (26,000 -10,000 BP)

The early part of the Late Devensian period is marked by the maximum expansion of ice sheets throughout northern Europe. The exact timing of the onset of glaciation is unknown but radiocarbon dates on organic material buried beneath Devensian tills suggest that much of Scotland was still ice free ca 27,000 BP (Sissons 1974). Changes in the composition of fossil coleopteran assemblages ca 26,000 BP indicate a marked climatic shift from the cold continental climates of the preceding phase to the polar climatic conditions of the Late Devensian period (Coope 1977).

The height of the last glaciation is generally considered to have been reached ca 18,000 BP when glacier ice reached its maximum extent. This period of maximum glaciation, known as the Dimlington stadial (Rose 1985), came to an end with a rapid rise in temperature around 13,300 BP (Atkinson et al 1987). Radiocarbon dates from several sites in northern Britain also indicate that the ice sheet had largely disappeared by that time (Sissons and Walker 1974).

In Britain, the succeeding warm phase, known as the Windermere or Lateglacial interstadial (Pennington 1977), has been identified as a single episode covering the time range ca 13,000 - 11,400 BP (Atkinson et al 1987). This warm phase was followed by a short cold period marked by the regrowth of glacier ice. This period, known as the Lateglacial or Loch Lomond stadial covers the time span from ca 11,400 to 10,500 BP.

The Late Weichselian stratigraphic framework of continental northwest Europe is slightly different from that outlined above. Lateglacial stratigraphic stages (13,000 - 10,000
BP) have largely been established from palynological studies which have revealed a more complex picture of events (Mangerud et al. 1974). The conventional interpretation of events began with an early warm phase, known as the Bølling, followed by a brief cold phase, known as the Older or Early Dryas. A second warm phase, the Allerød period, separated the Older Dryas from the Lateglacial stadial. The latter period is also known as the Younger Dryas. The conventional explanation for the lack of tree growth during the Older Dryas period has been that cold climatic conditions prevailed. More recent studies have shown that thermophilous plants were found in relatively high numbers in Older Dryas contexts indicating that temperature was not the major factor inhibiting tree growth. An alternative explanation has been proposed by Kolstrup (1982) who suggests that drought may have been the primary cause of the decline in birch woodland during the Older Dryas phase. This has led to the recent suggestion that the Bølling and Allerød phases may be regarded as a single interstadial episode, akin to the Windermere interstadial which has been recognised in Great Britain (Kolstrup 1991).
7.1 Introduction
Many deposits and geomorphological features throughout Britain are thought to be of Early Devensian age but, owing to the problems of dating, few can be placed firmly within any of the known stages of this period. As a result of these dating problems any reconstruction of Early Devensian environments must be severely limited in its extent.

7.2 Interstadial environments
The most detailed environmental information for this period has been obtained for the interstadial episodes. Vegetation patterns during the Chelford interstadial have been described from several sites. At the type site in Cheshire, analyses of pollen and plant macrofossils have indicated the presence of pine, birch and spruce forest (Simpson and West 1958). A modern analogue in the boreal forests of southern Finland has been suggested for this environment (Green 1991). The analyses of both the coleopteran and pollen assemblages at Chelford have also indicated a continental-type climate with mean annual temperatures in the region of 1 to 2°C (Coope 1959). Average temperatures during July have been estimated at around 12 to 16°C, while the mean temperature of the coldest month in February probably fell within the range of -10 to -15°C. The average annual precipitation is thought to have been in the region of 400 to 700 mm but, in contrast to present day conditions, little precipitation is thought to have fallen during the winters which were relatively long, cold and dry.

A similar environment has been described at the site of Roosting Hill, Beetle in Norfolk (Phillips 1976). Here an initial grass-dominated vegetation was succeeded by a phase of coniferous woodland development with subsidiary heath and wetland. Pine, birch and spruce formed the dominant vegetation, spruce being the most common species amongst the plant macro-fossils. The exact age of the woodland phase is unknown, but it has been correlated with the Chelford interstadial. A third vegetational phase followed the woodland stage and may represent the termination of the interstadial period. Pollen analyses indicate that the forest became increasingly open, allowing the expansion of heath and herbaceous vegetation.

An Early Devensian interstadial environment has also been recognised at the site of Allt Odhar near Inverness (Walker et al 1992). A series of peat beds has produced several lines of evidence, including pollen, coleoptera and plant macro-fossils, which indicate an expansion of birch woodland during the Early Devensian period. While birch formed the dominant vegetation, arboreal pollen counts from the Allt Odhar profile rarely exceeded
50% of total land pollen, indicating that extensive non-wooded areas were also characteristic of this interstadial environment. A uranium series date of ca 106,000 BP places this interstadial within \(^{18}O\) sub-stage 5c and suggests that this episode may also be correlated with the Chelford interstadial. Both the floral and insect evidence from Allt Odhar suggest that mean July temperatures fell within the range of 9 to 12°C. While this is a few degrees cooler than the temperatures estimated at Chelford, such a temperature gradient is not inconsistent with the latitudinal difference between the two sites.

The second Early Devensian interstadial episode is poorly understood in Britain and is known only from the type site of Brimpton in Berkshire (Bryant et al. 1983). Pollen evidence from this site indicates that the interstadial environment was dominated by birch and pine forest. Molluscan evidence provides further support for the interpretation of this episode as a temperate interval.

7.3 Stadial environments

Early Devensian stadial environments are less well understood than the corresponding interstadials. A general paucity of vegetation under stadial conditions increases the difficulty in drawing correlations between floral assemblages from different deposits. A few sites have produced evidence for Early Devensian stadial environments, however. One such environment has been described at the site of Wing in Leicestershire (Hall 1980). A sequence of deposits at this site covers the period from the last interglacial (Ipswichian Zone IIb) through to an Early Devensian stadial. As the sequence of deposits is continuous it appears that this stadial environment may be correlated with the Herning stadial of northwest Europe (\(^{18}O\) sub-stage 5d) and the Melisey I stadial which has been recognised in French pollen profiles. Pollen analyses have indicated an almost complete absence of trees and have suggested a tundra-like environment dominated by a combination of peatland and herb-rich grassland. Evidence from the deposits themselves suggests that they were formed as a result of solifluction. The presence within the pollen assemblages of a number of mosses, which would have been associated with bare soil and rock, is consistent with this interpretation of increasingly disturbed soils.

Similarly open environments have been described for the pre-Chelford-interstadial episode at the sites of Beetle and Brimpton. At the latter site pollen analysis indicates that grasses, sedges and other herbs formed the dominant vegetation.

Brimpton has also produced evidence for a second stadial episode, a possible correlate of \(^{18}O\) sub-stage 5b. Pollen evidence for this stadial indicates that grasses and sedges again formed the dominant vegetation. The molluscan assemblage supports this interpretation, containing several species which are found today in open, dry habitats or in association with herbs and dwarf shrubs.
In addition to the solifluction and disturbed soils which have been described at the site of Wing in Leicestershire (see above), the generally dry and open conditions during the Early Devensian stadials may also have resulted in wind erosion and the formation of aeolian deposits. A series of loessic deposits in southeast England have produced thermoluminescence (TL) dates which fall within the Early Devensian period (Parks and Rendell 1992). Aeolian silts at the site of Hope Gap have produced a TL date of ca 110,000 BP while at Lepe Point a date of ca 98,000 BP has been obtained on a loessic deposit. Somewhat later dates have been obtained on silts from the site of Sussex Pad, near Lancing. These silts have produced two dates of ca 88,000 and ca 73,000 BP. The earlier of these two dates may reflect aeolian activity during \(^{18}O\) sub-stage 5b, while the latter date may be indicative of renewed erosion and deposition at the onset of \(^{18}O\) stage 4.

Oxygen isotope stage 4 represents the major stadial episode of the Early Devensian period. Evidence from deep sea cores indicates a marked drop in temperatures, dated to ca 73,000 BP (Martinson et al 1987). This drop in temperatures was coincidental with the movement of the oceanic Polar Front to the south of the British Isles shortly after 75,000 BP (McIntyre et al 1972). Several authors have argued that this period also marked the onset of glaciation in upland areas of Britain.

Arguments in favour of an Early Devensian glaciation have been presented by Straw (1979a, 1979b) and are based on both morphological and lithostratigraphic evidence. Morphological differences observable in morainic landforms such as those at the eastern end of the Vale of Pickering in eastern Yorkshire are thought to be the product of two separate glacial episodes. Lithostratigraphic evidence in areas such as the lower Bain Valley in Lincolnshire also suggests the formation of proglacial lakes during the Early Devensian period.

Evidence for an Early Devensian glaciation has also been found in the Gower peninsula in Wales where a glacial till has been found overlying a raised beach deposit (Campbell et al 1982). The latter has been dated to the last interglacial period. Shells within the till have produced similar amino-acid ratios to those from the raised beach suggesting an Early Devensian age for the glacigenic material.

The severity of climatic conditions during \(^{18}O\) stage 4 may be indicated by the apparent cessation of speleothem formation at around 66,000 BP (Gordon et al 1989). Several factors affect speleothem growth, the most significant of which include water availability, temperature and vegetation cover (Kashiwaya et al 1991). Mean annual temperatures affect the development of vegetation cover which in turn governs the amount of carbon dioxide which is available to groundwater. A dearth of actively growing speleothems at ca 66,000 BP may reflect low annual temperatures and sparse vegetation.
A reduction in the availability of groundwater as a result of freezing conditions or widespread permafrost might also be responsible for this period of non-growth.

While there is a good deal of evidence for the existence of periglacial conditions during the Early Devensian period in Britain, few features can be dated securely to any of the known stadial or interstadial episodes (Williams 1975, Watson 1977). Features such as ground ice mounds and involutions are indicative of periglacial conditions, but ice wedge casts are the only definite indicator of continuous permafrost.

Early Devensian ice wedge casts have been found at several sites in Britain including the sands overlying the interstadial deposits at Chelford in Cheshire (Watson 1977) and in stadial deposits at the type site of Four Ashes in Staffordshire (Morgan 1973). The environmental conditions which are implied by these features include mean annual temperatures of -8°C or lower.

The zone of continuous permafrost during 18O stage 4 was not restricted to Britain but spread across northwest Europe. Ice wedge casts at a site near Eerbeek in The Netherlands appear to relate to a major stadial episode between the Moershoofd and Odderade interstadials (Van der Meer et al 1984). This period may be correlated with the Early Devensian stadial episode known as the Schalkholz stadial in northwest Europe.

7.4 Britain in relation to Europe

During the last interglacial period world sea levels are believed to have been several metres above their present height (Jelgersma 1979, Lambeck 1990). A eustatic lowering of sea-level at the onset of the Early Devensian is thought to have resulted in a retreat of marine waters from a large area of the Southern Bight of the North Sea. Evidence of a marine-freshwater contact in this area between The Netherlands and England, dated to the start of the Early Devensian, indicates that sea levels dropped to at least 40 metres below those of the present day (Jelgersma 1979, Zagwijn 1983). A drop of this magnitude would imply that large areas of the shallow North Sea shelf must have been dry land. As no marine deposits of Devensian age have yet been found in the North Sea at depths above -40 metres (Behre 1989), it is thought that sea levels did not exceed this height at any time during the last glaciation.

As Britain was connected to mainland Europe throughout the Devensian period, faunal movements were clearly possible between the two areas. Vegetation patterns in northwest Europe were broadly similar to those prevailing in Britain (Behre 1989). During the two major Early Devensian interstadials a zone of boreal forest spread westwards from southern England across north central Europe and southeast Scandinavia. A sharp vegetation gradient existed, however, between northern and southern Europe. In contrast to the coniferous forests of the north, the pollen records of south central Europe indicate
the presence of thermophilous forests, including such species as oak (*Quercus*), hazel (*Corylus*), lime (*Tilia*), elm (*Ulmus*) and ash (*Fraxinus*) (Woillard 1979, de Beaulieu and Reille 1984, 1992). The boundary between the two forest zones has been estimated to lie between the River Main and the northern edge of the Alps (Behre 1989).

Vegetation zones to the north of the boreal forest belt were also compressed latitudinally. In Scandinavia during the Jämtland interstadial (a probable correlate of the Brørup and Chelford interstadials) the boreal forest of south eastern districts gave way to birch woodland and finally to tundra vegetation in the northwest (Miller 1986). A similar vegetational shift from coniferous forests in southern England to open birch woodland in northern Scotland has already been discussed above.

As in Britain, European vegetation patterns during the Early Devensian stadial episodes are less well known than those of the intervening warm stages. Pollen analyses appear to indicate that the northern boundaries of the major vegetation zones were pushed far to the south and east. Evidence from sites such as Oerel in northwest Germany indicate that open tundra vegetation dominated the landscapes of north central Europe during the Herning and Rederstall stadials (Behre 1989). A marked forest decline has also been recorded during the Early Devensian stadials in south central Europe. Pollen analyses at the site of La Grande Pile in Vosges, eastern France indicate an opening of the woodland vegetation and the expansion of non-arboreal taxa, including grasses and steppe species. (de Beaulieu and Reille 1992).

### 7.5 Early Devensian faunas

Few faunal assemblages can be securely dated to the Early Devensian period or any of its known sub-stages. Stuart (1982) lists only two major collections, from the sites of Coston and Wretton in Norfolk, which may fall within this period.

The site of Coston, near Barnham Broom in Norfolk, consists of a series of organic sands and silts within a commercial gravel pit. The organic levels have produced remains of pollen, plant macro-fossils, molluscs and vertebrates. Stuart (1982) describes the result of preliminary pollen analyses which indicate a transitional phase between spruce/pine forest and an open treeless landscape dominated by grasses and sedges. It has been suggested that this period may be correlated with the end of the Chelford interstadial.

The faunal remains from Coston are dominated by bison, but woolly rhinoceros, mammoth, reindeer and red deer have also been recorded. All of these species were discovered *in situ*. No evidence of predators has been recovered from this site.

The remains of wolf and arctic fox were recovered from the site of Wretton in Norfolk, together with an abundant assemblage of large mammal remains. The palaeoenvironmental investigations at Wretton, and the interpretative problems which they
produced, have already been discussed in Chapter 5. Until the major discrepancies between the pollen-based and coleopteran-based interpretations have been resolved and the age of the faunal remains has been established, the Wretton assemblage can not be considered to be a reliable indicator of Early Devensian faunas.

A more securely dated faunal assemblage which may have accumulated during the Brimpton interstadial has been recorded more recently from the site of Stump Cross Cave in northern Yorkshire (Sutcliffe et al. 1985). This assemblage was sealed within a speleothem deposit which has been dated by uranium-series to ca 83,000 BP. The deposit was underlain by a second layer of speleothem which has produced five uranium-series dates ranging from 118,000 ± 12,000 to 108,000 ± 18,000 BP. Both speleothems are thought to have formed under interstadial conditions. The unweathered condition of the bones has led to the suggestion that they were buried rapidly by the speleothem deposit and that the assemblage probably accumulated during or very shortly before the onset of the Brimpton interstadial. The faunal assemblage includes the remains of wolverine, wolf, fox (arctic or red fox), reindeer and a bovid (Sutcliffe et al. 1985).

A similar fauna has been described for the site of Picken's Hole in Somerset (see Chapter 5) and may also have been accumulated during an Early Devensian interstadial. The Unit 5 fauna is thought to have been the product of wolf denning activity in the cave and includes the remains of red deer, reindeer and a bovid. In addition to the taphonomic indicators of wolf activity, the faunal assemblage also includes bones of this species, together with the remains of brown bear and red fox.

### 7.6 Early Devensian reindeer

The reconstruction of reindeer behavioural ecology during the Devensian period may be based partly on the distribution of dated reindeer collections and partly on the model of relationships between behaviour and environmental conditions which was proposed in Chapter 3. Early Devensian environments appear to have alternated between two different extremes, an open tundra-like vegetation and a closed habitat boreal forest. During the stadial episodes, the Northwest European plain was a relatively homogeneous, open environment dominated by grasses and sedges and totally devoid of trees. The contemporary northern tree line was pushed well to the south and east of Europe. Given the open nature of the environment and the likely presence of predators such as wolf, it is probable that reindeer formed large groups, particularly during calving in the early summer. The very long distances that existed between the tundra environments of Britain and the boreal forests of southeastern Europe are outwith the range of modern reindeer migrations. This suggests that large herd formation and long distance migration were unlikely to have formed part of the behavioural ecology of the species. Unfortunately no
reindeer remains have been found which relate to any of the known stadial episodes. In the absence of such information on seasonal distribution it is impossible to predict the likely movement patterns of the deer.

Reindeer behaviour patterns during the Early Devensian interstadials are likely to have been very different to those of the intervening cold phases. Two alternative strategies may also have been adopted by populations in the north and south of the country.

Where boreal forest meets open tundra a unique opportunity exists for the seasonal exploitation of adjacent environmental zones. Such conditions have been found in Scandinavia during the Jämtland interstadial but do not appear to have existed in Britain at that time. Open birch woodland such as that described at Allt Odhar in northern Scotland would have provided a degree of environmental contrast, however, and would have offered alternative habitats for summer exploitation. The existence of the two woodland zones may therefore have encouraged a degree of seasonal movement on a north-south axis. Such movements would have reflected regional vegetation changes, however, rather than a purely latitudinal shift. The relative openness of the birch woodland may also have encouraged large group formation as an anti-predator strategy, particularly during the early summer at the time of parturition.

In the south of the country a combination of closed habitat boreal forest and the presence of predators such as wolf probably resulted in the formation of small group sizes and dispersed foraging activity. Under such conditions calving would have occurred on an individual basis and calving sites would have been dispersed throughout the forest. Annual movements may have followed predictable patterns, perhaps exploiting altitudinal or topographic variations. The dispersed nature of reindeer populations would have reduced the visibility of such patterns however, which would probably have appeared as entirely random movements.

The scarcity of dated faunal assemblages which may be assigned to the Early Devensian interstadials precludes more detailed analyses of reindeer distribution patterns. The discovery of several shed female antlers from a wolf denning site at Picken's Hole in Somerset, however, does appear to indicate spring or early summer exploitation of the area. Unworn deciduous teeth from neonatal calves also support the hypothesis that calving took place within the Mendip area. While such a small collection of antlers from a wolf denning site must clearly be treated with caution, it is nonetheless tempting to envisage these finds as the product of wolf predation on lone reindeer cows, hiding out in the boreal forest at the time of parturition.
8.1 Introduction
Much of the Middle Devensian period falls within the theoretical range of radiocarbon
dating, thus enabling a more precise understanding of the climatic events and episodes of
the stage. Floral and faunal assemblages have been investigated from many sites of Middle
Devensian age and have revealed a complex picture of climatic and environmental change.
Radiocarbon dates on organic material from these sites have enabled many assemblages to
be assigned a place within a relatively detailed chronostratigraphy. As has already been
indicated, however, much of this period must be considered to be close to the practical
limits of radiocarbon dating. While finite dates in excess of 40,000 years may be considered
as minima, it would be dangerous to place too high a stress on any individual absolute date
within this age range. The reconstructions of Middle Devensian environments which
follow should therefore be considered within a relative framework of events rather than as
part of an absolute chronostratigraphy.

8.2 The Upton Warren interstadial
The warm episode, known as the Upton Warren interstadial, was first identified at the type
site of Upton Warren in Worcestershire (Coope et al. 1961, see Chapter 5) and has since
been recorded at numerous sites throughout southern Britain. Radiocarbon dates have
placed this episode between approximately 43,000 and 42,000 BP (Coope 1975). Many of
these dates are infinite, however, and others have large standard deviations. The true age of
the episode may therefore be somewhat older than currently thought and its duration may
have been rather longer.

Studies of the floral and faunal assemblages from interstadial sites have enabled a
reconstruction of the climate during this warm period. In a summary of the analyses of
over twenty Middle Devensian sites, Coope (1975) has suggested that average July
temperatures at the thermal maximum must have been in the region of 18°C. Such
temperatures are 1 or 2°C higher than those recorded in southern and central England at
the present day. Mean January temperatures have been estimated at around 2°C to -2°C and
average annual temperatures were probably in the region of 7°C or 8°C (Lowe and Walker
1984). Precipitation levels have been estimated at between 450 and 650 mm per year
(Lockwood 1979).

Despite the high temperatures, the floral evidence from sites such as Earith in
Cambridgeshire (Bell 1970) and Isleworth in Middlesex (Coope and Angus, see Chapter 5)
indicates that the landscape remained open throughout the interstadial. Communities of
thermophilous herbs and grasses dominated the environment but some boreal and arctic-alpine elements have also been recorded (Coope et al 1961).

The almost complete absence of trees is particularly notable since the climate was clearly warm enough to support their growth. Several hypotheses have been proposed to explain the lack of woodland development. The very rapid nature of the climatic amelioration and the apparently short-lived nature of the episode have been compared with the time-span required for the reforestation of northern Europe from woodland refugia in the south (Coope 1977). The slow migration rates of arboreal species may have prevented them from reaching northern habitats before the subsequent climatic deterioration pushed the tree line southwards again.

A second contributory factor which may have been involved was the effect of browsing animals. Middle Devensian faunal collections indicate that the environment supported large numbers of open habitat herbivores. It has been suggested that these animals may have caused excessive browsing and inhibited the regeneration of woodland habitats (Coope and Angus 1975).

8.3 The post-Upton Warren cool stage

The Upton Warren interstadial is thought to have been a relatively brief episode and by shortly after 40,000 BP arctic conditions again prevailed across northern Europe. Coope (1977) has drawn upon the analyses of several coleopteran assemblages from sites in southern Britain in order to reconstruct the prevailing climatic conditions. The overall character of the faunas has been likened to the boreal or alpine faunas of Scandinavia or the Siberian arctic. This has been interpreted as the result of a continental climatic regime with mean annual temperatures in the region of -8° to -12°C. Estimates suggest average July temperatures of 10°C and winter temperatures of between -20° and -30°C. Mean annual rates of precipitation are thought to have been low, perhaps ranging between 250 and 350 mm (Lockwood 1979).

This reconstruction of the palaeoclimate is supported by evidence of periglacial activity at many sites of Middle Devensian age (Watson 1977). Fossil ice wedges, such as those found at Earith in Cambridgeshire and Four Ashes in Staffordshire, indicate the presence of continuous permafrost and suggest mean annual temperatures of -8°C or less.

Palaeobotanical evidence has been obtained from many sites and is indicative of an open tundra landscape. At the site of Oxbow near Leeds, for example, a treeless environment has been described in which grasses, sedges and dwarf shrubs formed the dominant species (Gaunt et al 1970). Mammoth remains from the site have been radiocarbon dated to ca 38,000 BP. A similar environment of somewhat later date has been described on the basis of plant macro-fossils from the site of Brandon near Coventry.
The floral evidence from this site suggests a tundra-like landscape, consisting of a combination of bare ground, grassland, heath and shrubland communities. A radiocarbon date on the organic material has indicated an approximate age of between 29,000 and 32,000 BP.

One exception to this image of an open treeless landscape has been described by Whitehead (1990). The discovery of exfoliated bark from a mature gymnosperm within the Cheltenham sands and gravels of Middle Devensian age has suggested that some tree growth may indeed have occurred in isolated relict pockets, in hill valleys or on inaccessible rock faces. No direct date has been obtained for this find but an existing radiocarbon date of ca 32,000 BP from a similar organic lens within the gravels suggests a relative age for this deposit.

The reconstruction of environmental conditions during the Middle Devensian period has not been limited to the southern half of the country but has also been possible for certain areas of Scotland. Pollen analyses of an organic palaeosol at the site of Teindland in Morayshire, for example, have indicated an environment dominated by grasses and heathers (Edwards et al 1976). The age of this palaeosol is uncertain, however, as several radiocarbon dates have been obtained, ranging from ca 28,000 to ca 40,000 BP (FitzPatrick 1965, Caseldine and Edwards 1982).

An organic deposit dated to ca 27,000 BP has also been recorded at Tolsta Head on the island of Lewis in the Outer Hebrides. The floral evidence from this site is also indicative of an open landscape dominated by grasses and heathers (Von Weymarn and Edwards 1973).

8.4 European environments

As has already been discussed in Chapter 6, the correlation of the Middle Devensian/Weichselian environments of Britain and mainland Europe has not been very successful. The two early Middle Weichselian interstadial episodes, the Oerel and Glinde interstadials, which have been identified in northern Europe, have no known British correlates at present. Environmental conditions in northwest Europe during these episodes consisted of essentially treeless landscapes dominated by open shrub tundra. Correlates of the Oerel episode in south central Europe indicate the development of coniferous forests at this time in areas such as southern France and Switzerland (Behre 1989).

Shrub tundra environments have been described for north central Europe during the Hengelo and Denekamp interstadials of the later Middle Weichselian period. The Moershoofd interstadial environments are thought to have been more open, with fewer shrubs and a generally cooler climate.
An apparent longitudinal zonation of vegetation during this stage of the Middle Weichselian in north central Europe has been suggested by West (1977). While the northwestern region of Europe was dominated by open tundra landscapes, forest-tundra and boreal forest environments are known to have developed further east in areas such as southern Poland.

8.5 Middle Devensian faunas

A great deal of information has been gathered together on the ecology of large mammal communities during the Middle Devensian period (Rackham 1982, Stuart 1982). River terrace deposits such as those uncovered at Willment's gravel pit, near Isleworth in Middlesex (Coope and Angus 1975, see also Chapter 5), have produced large faunal collections which are dominated by the remains of herbivorous animals such as bison, giant Irish deer, reindeer, woolly rhinoceros, horse and mammoth. Bison dominates the assemblage from this particular site and reindeer is the second most commonly occurring species. A date of ca 43,000 BP has been obtained on organic material within the sands and gravels and provides an approximate age for the accumulation of this faunal assemblage.

A similar fauna has been found within fluviatile sands and gravels at the site of Tattershall Castle in Lincolnshire (Girling 1974, Rackham 1982). Both reindeer and bison remains have been found in association with a silt band of Upton Warren interstadial age (radiocarbon dated to ca 43,000 BP). Most of the bones of other species were not found in situ, however, and their true age is uncertain. The large numbers of dung beetles which were recovered from this site indicate that herbivore populations were present in the area during the summer months. The discovery of large numbers of shed male reindeer antlers indicates that the area was also exploited by this species during the winter. Assuming that reindeer were migratory, Rackham suggested that Lincolnshire may have formed an area of overlap between the annual distribution patterns of bison and reindeer, representing the southernmost part of the annual territory of reindeer and the northernmost zone of bison habitat. The likelihood of such reindeer movement patterns is discussed in further detail below.

While many large faunal collections have been found within the river terrace deposits of southern and eastern England, the distribution of Middle Devensian faunal remains is not limited to the southern half of the country. Faunal remains which have been attributed to this period have also been found throughout northern England and Scotland, the northernmost collections having been recovered from the site of Reindeer Cave in Assynt, Sutherland (See Chapter 5).

While the Scottish faunal collections have not been the subject of any detailed study, it is clear that similar large mammal communities also existed in this area. Examples of such
material include a reindeer antler from Kilmaurs in Ayrshire which has been radiocarbon
dated to more than 40,000 BP and which was found beneath glacial till in association with
mammoth remains (Shotton et al 1970). A somewhat later date of ca 27,000 BP has also
been obtained for a woolly rhinoceros specimen from Bishopbriggs, near Glasgow (Rolfe

Most faunal collections which are derived from fluviatile sands and gravels are
dominated by the remains of large herbivores. While the remains of carnivores, such as
brown bear or wolf, do occur occasionally within these assemblages they are usually found
in much smaller numbers. Our knowledge of carnivore activity during the Middle
Devensian period is therefore derived mainly from cave sites, where taphonomic indicators,
such as patterns of bone breakage and gnawing, combined with evidence of in situ deaths,
enable the generation of information about former carnivore populations.

The faunal assemblage from Unit 3 of Picken's Hole in Somerset is an example of such
a collection (Scott 1986a, see Chapter 5). The fauna, which includes the remains of arctic
fox, bear, hyaena, and lion, together with herbivorous animals such as mammoth, woolly
rhinoceros, horse, red deer, reindeer and bison, is thought to have been the product of
hyaena denning within the cave. Two dates of ca 34,000 and 27,000 BP place the
accumulation of this assemblage within the latter half of the Middle Devensian period.

The faunal collection from the Reindeer Stratum of Tornewton Cave in Devon may
also have been accumulated by hyaenas or wolves (Sutcliffe and Zeuner 1962, see Chapter
5). This fauna, which is probably of Late Middle Devensian age, includes the remains of
woolly rhinoceros, horse, reindeer and a bovid.

8.6 Middle Devensian reindeer
The distribution patterns of Middle Devensian reindeer may be readily observed from an
analysis of faunal collections from sites throughout Britain (Fig. 8.1). The social
organisation and movement patterns of those reindeer populations may also be inferred
from the foregoing analysis of environmental conditions.

8.6.1 Social organisation
The two primary factors which affect group size are latitude and predation. The low
latitude tundras which existed in Britain and northwest Europe during the Middle
Devensian period would have received far higher levels of insolation than the arctic tundras
of the present day. The growing season would also have been longer resulting in a
relatively productive environment, capable of supporting a rich and varied mammal fauna.
The productivity of these environments would also have resulted in a tendency towards
large group formation.
Fig. 8.1  Reindeer distribution in Britain during the Middle Devensian (S = Spring, C = calving, Su = Late summer/autumn, A = Late autumn/winter, W = winter).
A similar tendency to large group formation would have resulted from the presence of predators in the open environments which prevailed throughout the Middle Devensian period in Britain and northwest Europe. Many predators and scavengers have been recorded from Middle Devensian assemblages including wolf, lion, hyaena, arctic fox and brown bear. Under such conditions reindeer populations would regularly have formed large fluid groups as part of an anti-predator defence strategy.

Secondary factors which have a seasonal effect on group size include harassing insects and reindeer breeding strategies. Insect harassment is temperature dependent, requiring July temperatures in excess of 7-13°C. Estimates of mean July temperatures during the Upton Warren interstadial have been in the region of 18°C. While predatory insects do not survive in the faunal record, these temperatures were certainly sufficient to facilitate their existence in large numbers. As reindeer respond to harassment during the fly season by milling together in large groups, the seasonal formation of large aggregations, numbering up to 2500 individuals, would not be unexpected.

During the post-Upton Warren cool period, harassing flies may not have been quite such a problem. Average July temperatures of ca 10°C would have been sufficient to enable mosquito activity but may not have been high enough for other parasites such as nosebot flies and warble flies.

Reindeer breeding behaviour is related to their anti-predator strategy in open environments. It is likely, therefore, that parturition occurred in large groups on communal, traditional calving grounds. Rutting in the autumn will also have occurred in open environments, thus facilitating the formation of large rutting groups.

**8.6.1.1 Summary of annual fluctuations in group size**

Reindeer group size during the Middle Devensian period was probably at its lowest during the late summer months when appropriate forage would have been evenly spread across the landscape. Group sizes at this time were probably relatively small, perhaps reckoned in tens of animals or even in single figures. Solitary individuals would have been rare, however, owing to the need for vigilance against predators. Towards the end of the summer, in September and October, the onset of the rut would have led to the reformation of large aggregations, possibly numbering several thousands of individuals. After the first snows in winter, group size would probably have dropped again to enable the exploitation of feeding craters or windswept patches. An increase in group size would have occurred in late spring in preparation for movement to the calving grounds. While females and yearling males probably formed large pre-calving groups, young bachelor males and solitary bulls would have been relatively dispersed at that time. Following parturition group size probably reached its annual peak as large, mixed post-calving aggregations, perhaps
numbering several thousands of individuals, formed in response to insect harassment in July and early August.

8.6.2 Movement patterns

The primary factor involved in the determination of annual range size is the differential availability of forage. Of particular importance in relation to long distance migration is the juxtaposition of two different environment types, most notably tundra and boreal forest, which would offer seasonally preferred habitats and would encourage long distance migration. Given the distances of several thousand kilometres between the open tundras of Britain and northwest Europe and the forested environments of southern and eastern Europe, long distance migration between these two vegetation zones would not have been possible. The implication that reindeer populations remained in the open tundra environments of Britain throughout the year has been confirmed through the analysis of reindeer remains from numerous archaeological and geological sites (Fig. 8.1).

While long distance migration was an unlikely behavioural feature during the Middle Devensian period, seasonal nomadic movements would nonetheless have been necessary in order to sustain the large group sizes which the open environmental conditions would have promoted. While it is impossible to establish seasonal movement patterns from an analysis of Devensian faunal remains, it has nonetheless been possible to demonstrate seasonal absence in at least two faunal collections of Middle Devensian age. A gap in the size distribution of male reindeer antlers from the site of Pin Hole in Derbyshire (Fig. 5.11) clearly demonstrates that reindeer were not present in the region during the mid-winter months. Similar gaps in the size distribution of juvenile long bones from the site of Sandford Hill in Mendip (Figs. 5.15-17) demonstrate that reindeer were not present in the immediate vicinity of the site during late winter and early spring.

8.6.2.2 Seasonal movement patterns

Foraging conditions which may have influenced reindeer movement patterns are extremely difficult to reconstruct. A major factor which would have influenced reindeer foraging behaviour during the spring and summer months, however, was the widespread distribution of permafrost across Britain and northwest Europe. Permafrost severely limits ground drainage and results in a relatively homogeneous foraging environment, with small patches of preferred forage dispersed randomly over a wide area. In the relatively flat and homogeneous regions of southeastern England, the dry North Sea bed and north European plain, this even spread of emergent plant growth would have resulted in highly unpredictable movement patterns during the spring and summer months.
The early spring and summer movement patterns of populations in upland Britain may have followed a rather more predictable pattern, exploiting altitudinal and topographic variations in forage availability. Patterns of movement may have included early spring distribution over south-facing slopes, followed by a move onto higher ground and more northerly-facing areas as the summer progressed.

Late winter, spring and early summer presence has been demonstrated at numerous sites in southern Britain where it is clear that there is no particular pattern in their distribution (Fig. 8.1). The general paucity of faunal collections from northern Britain (with the exception of calving grounds which are discussed in detail below) precludes any further assessment of spring or early summer distribution.

Few assemblages have been found which indicate reindeer presence during late summer and early autumn. This may have more to do with difficulties in identifying such seasonal presence, however, than with a genuine gap in the faunal record. Late summer and early autumn is one of the few seasons during which antler growth stages are difficult to identify. Late summer seasonal determinations are therefore dependent on the analysis of other types of evidence, most notably tooth eruption sequences and the size distributions of juvenile long bones. Middle Devensian assemblages which do indicate late summer and early autumn presence have been found at only four sites in Mendip, Devon and south Wales.

The low levels of precipitation which prevailed during the Middle Devensian period, particularly during the winter, would have reduced the effects of snow on the differential availability of forage. Open windswept areas would have been susceptible to crust formation, but, equally, ridges and hills would have been swept free of snow, facilitating winter foraging without the need to crater for food. Most areas would therefore have facilitated winter exploitation and there would have been no clear zone of preferable habitats.

This finding is supported by the faunal evidence for the distribution of reindeer wintering grounds. Late autumn and winter presence has been demonstrated at sites throughout southern Britain in Devon, (Kent's Cavern), Mendip (Banwell, Hyaena Den, Soldier's Hole, Sandford Hill), south Wales (Paviland Cave, Coygan Cave), north Wales (Ffynnon Beuno), the Midlands (Upton Warren), Derbyshire (Pin Hole), Lincolnshire (Tattershall Castle) and Middlesex (Willment's Pit, Isleworth).

8.6.2.3 Calving grounds
In addition to the differential availability of forage, a secondary factor which may affect reindeer movement patterns during the early summer months is the distribution of calving grounds. On the basis of the model of modern reindeer ecology, outlined in Chapter 3, it has been suggested that Middle Devensian reindeer populations exploited communal,
traditional calving grounds in high and exposed terrain. A distinct movement of cows and yearlings towards the calving grounds would therefore be expected in spring and early summer.

Calving grounds are readily identifiable within the zoo-archaeological record on the basis of the presence or absence of shed female antlers. At least four Middle Devensian calving grounds have been identified in Britain from the sites of Reindeer Cave (Assynt), Pin Hole (Derbyshire), Banwell Bone Cave (Mendip) and Tormewton Cave (Devon). Each of these sites has produced large collections of shed female antlers, usually in association with a smaller sample of shed yearling males. At two of the sites, Reindeer Cave and Pin Hole, the sample sizes were sufficiently large to enable an analysis of size distribution to be undertaken. Both these samples approximate the normal size distribution which would be expected if an entire female population were represented in the collection. The large size of these collections and the normal size distribution of the antlers suggest that both these calving grounds were used on a communal basis by large populations of female deer.

Radiocarbon dates are available for two of these collections. Several dates on shed female antlers from Reindeer Cave indicate that the area was used as a calving ground during at least two phases of the Middle and Late Devensian periods, between ca 43,000 and 48,000 BP and between 22,000 and 32,000 BP (Table 5.13). Two dates on shed female antlers from Pin Hole also indicate prolonged use of the area as a calving ground between ca 34,000 and 31,000 BP (Table 5.8).

This prolonged use of an area for calving over a period of several thousand years would suggest that Middle Devensian reindeer behaviour was very similar to that of their present day counterparts. The repeated use of communal, traditional calving grounds over a period of decades or centuries would have provided a highly predictable focal point within the annual pattern of movement.

While the collections discussed above have all included large numbers of shed female antlers, many other collections exist in which the sample size is considerably smaller. At several sites the sample size is reduced to a single specimen, which is either shed or on the point of shedding. While these collections do indicate female presence during the spring or early summer, it is not possible to be certain whether they are the product of barren or gravid females. In many cases the samples have been found within known calving areas, however, and would appear to support the interpretation of traditional calving grounds.

Amongst modern deer populations, the calving grounds are used almost exclusively by females and yearling males. Adult males never enter the calving areas during the period of parturition. An interesting feature of the collections from Banwell Bone Cave and Pin Hole, however, is the co-occurrence of male and female antlers within the same deposits. While no dates are yet available for the collections from Banwell Bone Cave, a series of
dates from Pin Hole suggest a degree of overlap between the use of the Creswell area as a calving ground and its use as a wintering area (Table 5.8). While there is no evidence to suggest that male deer were present in the area during the time of parturition, it does indicate that these areas were not used exclusively during the calving season but were also exploited during the winter months. This would also suggest that, while Middle Devensian reindeer populations were clearly nomadic creatures, they did not necessarily undertake extensive movements between their winter and summer range.

8.6.2.4 Summary of annual movement patterns

In conclusion, it has been demonstrated that Middle Devensian reindeer did not undertake long distance seasonal migrations but rather remained within Britain throughout the course of the year. Some degree of movement would have been necessary, however, in order to sustain large aggregations. For most of the year movement patterns within the relatively homogenous environments of southern Britain would have been rather unpredictable, reflecting the opportunistic exploitation of seasonally favourable habitats. Movements patterns within highland Britain may have followed a more predictable annual pattern, akin to those recorded amongst alpine populations. The general paucity of faunal assemblages from areas of upland Britain, however, prevents the more detailed modelling of movement patterns within these areas. One aspect of the annual movement patterns which was clearly predictable, however, was the exploitation of traditional calving grounds at the time of parturition. These calving grounds appear to have been re-used over considerable periods of time, perhaps covering a span of centuries or even several thousands of years.
9.1 Introduction
A great deal of research has been concentrated on the Late Devensian period and the significant environmental changes which occurred during that time span. As the period falls within the range of radiocarbon dating, the sequence of chronological events is relatively well understood. The recent expansion of dendrochronologies into the Late Glacial period, however, has indicated that major variations occurred in levels of atmospheric radiocarbon during this time span, resulting in plateaux of constant radiocarbon ages (Becker and Kromer 1991, Becker et al 1991). An example of the effect of these plateaux may be seen in the recent dendrochronological estimate of the Devensian/Holocene transition. This event, which has traditionally been placed at ca 10,000 BP, has now been dated to at least 10,970 dendro-years BP. In order to avoid confusion, the generally accepted time framework of Late Devensian events is used throughout this text, although it is clear that future research may result in the need for significant chronological alterations.

As the Late Devensian period can be subdivided into three distinct stages, the environmental conditions prevailing during each of these episodes will be considered in detail below. The likely effects of each set of environmental conditions on the social organisation and movement patterns of Late Devensian reindeer populations will then be considered in relation to the distribution of dated reindeer remains.

9.2 Dimlington stadial environments
The major event of the Late Devensian period was the development of the last British ice sheet and a great deal of research has been undertaken to establish its overall extent and duration. At its maximum, the ice sheet covered approximately two thirds of the present land area of the country, including large areas of Ireland, Wales and northern England and almost all of Scotland, the only significant exception in the latter case being a small enclave on the island of Lewis in the Outer Hebrides (Sutherland and Walker 1984, Hall and Bent 1990).

The western limits of the ice sheet are largely unknown. In northwest Scotland the ice sheet did not extend beyond the Outer Hebrides (Sutherland 1984) but the off-shore limit along most of the western continental shelf has yet to be determined. In the southwest of Scotland an ice stream radiating from the Firth of Clyde is known to have converged with ice flows from the Southern Uplands, Ireland, Wales and northern England to create the Irish Sea glacier, the largest ice stream draining and buttressing the Late Devensian ice sheet.
(Eyles and McCabe 1989). This glacier may have reached its maximum extent by 22,000
BP and it has been suggested that the rapid retreat of the glacier in response to iceberg
calving after 19,000 BP may have been a major factor in the subsequent deglaciation of the
entire British ice sheet.

The eastern margin of the British ice sheet has been the subject of much recent
research and two different reconstructions have been proposed. The first reconstruction,
made on the basis of sedimentological records along the North Sea coast, suggests that the
northeastern edge of the ice sheet terminated in the tidewater of a shallow northern sea
which separated the British ice sheet from that of Scandinavia (Cameron et al 1987, Sejrup
et al 1987, Hall and Bent 1990). According to this proposal much of the southern North
Sea would have been dry land at this time. An alternative reconstruction of the eastern
margin of the ice sheet is based on geomorphological features which have been recorded
beneath the North Sea bed (Ehlers and Wingfield 1991). Several series of channel-like
features have been recorded and are thought to have been formed by meltwater erosion
within the margin of the former ice sheet. This appears to indicate that the British and
Scandinavian ice sheets may indeed have met and that parts of the central and southern
North Sea may have been covered by ice during the height of the last glaciation. The
conflict between these two reconstructions has yet to be resolved.

The southeastern limits of the Late Devensian ice sheet were reached in eastern
Yorkshire, Lincolnshire and northern Norfolk. Radiocarbon dates on a series of silts
which underlie Late Devensian tills at the type site of Dimlington in eastern Yorkshire are
thought to provide a \textit{terminus post quem} for the maximum of the last glaciation (Rose
1985). The silts, which contain mosses and cold-climate coleoptera, have been dated to ca
18,500 BP (Penny et al 1969)\textsuperscript{1}. A similar, but slightly younger TL date of 17,500 ± 1,600
BP has been obtained on a solifluction deposit beneath a similar Late Devensian till at
Eppleworth near Kingston-upon-Hull (Wintle and Catt 1985).

The period of maximum glaciation appears to have been followed by relatively rapid
ice wastage, well in advance of the climatic amelioration of the Lateglacial period (Sissons
1981, Sutherland 1984). One of the earliest dates from a deglaciated deposit has been
obtained at Kildale, in the North York Moors. At this site till deposits are overlain by
lake sediments containing pollen. The latter deposits have yielded a radiocarbon date of
16,710 ± 340 BP (SRR-145) (Jones 1977), although it has been suggested that this early date
may have been affected by hard water error (Tipping 1991). An early date for the retreat
of the Late Devensian ice has also been obtained from a series of glaciomarine silts near the
village of St Fergus on the Buchan coast, northeast Scotland (Hall and Jarvis 1989, Hall and
Bent

\textsuperscript{1} 18,500 ± 400 BP (Birm-1372) and 18,240 ± 250 BP (Birm-108).
A single radiocarbon date of 15,320 ± 200 BP (Lu-3028) is thought to date the initial retreat of the Late Devensian ice margin in this area.

While several radiocarbon dates of between 14,000 and 15,000 BP have been obtained from sediments in deglaciated areas of Britain, it has been suggested that hard water error may have affected their validity (Tipping 1991). Radiocarbon dates from a large number of sites in northern Britain do appear to confirm, however, that the last ice sheet had largely disappeared by 12,800 BP (Sutherland 1980).

9.2.1 Climatic conditions in northwest Europe

Sea-levels during the height of the last glaciation are thought to have been somewhere in the region of 130m below their present day level (Jelgersma 1979). A drop in sea-level of this magnitude would have meant that the southern half of the North Sea, the English Channel, and substantial areas to the southeast of Ireland would have been dry land. The environmental conditions in the unglaciated areas of southern Britain should therefore be considered in their context as part of continental northwest Europe.

A study of the effects of insolation and glaciation on atmospheric circulation over the North Atlantic during the Dimlington stadial has suggested two prevailing wind directions for surface air flow over northwest Europe in winter (Harrison et al 1992). According to a series of climatic models, cold dry air would have been advected into western Europe from a deep cyclone over the North Atlantic and would have resulted in winds of a northerly or northeasterly direction. It is thought that the extensive sea ice in the North Atlantic would have cooled the air above it by as much as 30°C. The effects of this cold air flow would have been moderated to some extent, however, by a southerly flow of warmer air arising from the southeastern margin of the North Atlantic low. An anticyclone centred on the European ice sheet would have resulted in a northeasterly flow over much of central and eastern Europe and the winters in this part of the continent would consequently have been extremely cold and dry. A sharp north-south temperature gradient would also have existed from the ice sheet margin towards southern Europe and would have been particularly marked on the west coast.

During the summer months the atmospheric circulation models suggest that the low Atlantic sea surface temperatures may have cooled the air by as much as 10°C and may have resulted in low temperatures and precipitation levels over Europe. The subtropical anticyclone belt (associated with sinking air and dry, sunny conditions) would have been compressed, strengthened and shifted northwards of its present position, resulting in enhanced off-shore flow and dry conditions over western Europe. Northerly or northeasterly air flows arising from the European ice sheet would also have promoted dry conditions over central and eastern Europe.
9.2.2 Flora and fauna

Very few fossiliferous sites dating from the Dimlington stadial have yet been found in Britain and this situation is matched in many other areas of northwest Europe. Evidence of generally sparse vegetation cover can be found throughout the region in the form of aeolian deposits, including coversands and loesses. Coversands of aeolian origin were deposited over large parts of the flat and gently undulating landscape of northern Europe, in Belgium, The Netherlands, northern Germany, Poland and southern Denmark (Kolstrup et al 1990). Two coversand types have been recognised in The Netherlands and in Denmark, the earlier of which was deposited during the Upper Pleniglacial and early Lateglacial periods. Thermoluminescence dates on loessic deposits in southern Britain, between the Scilly Isles and Kent, indicate that similar aeolian sedimentation occurred in Britain throughout the Late Devensian period and, in particular, during the height of the last glaciation between 20,000 and 14,000 BP (Wintle 1981, Parks and Rendell 1992).

One floral and faunal assemblage which may have been accumulated during this period was found in the "Arctic Bed" at Barnwell Station, Cambridge. This assemblage was dated by radiocarbon to 19,500 ± 650 BP (Q-590), although there is some indication that this date may be too young (Bell and Dickson 1971, see chapter 5). The arctic plant beds indicate an open treeless landscape, dominated by herbaceous vegetation. Shrub taxa also occurred in small numbers, including arctic willows and dwarf birch.

Given the problems associated with the radiocarbon date from Barnwell Station, a more representative picture of Late Devensian environments in northwest Europe may perhaps be obtained from the site of Kobbelgård, on the island of Møn in Denmark (Kolstrup and Houmark-Nielsen 1991). The vegetation at this site was formed in an unstable environment and was dominated by grasses, sedges and Artemisia. Using thermoluminescence techniques the deposits have been dated to between ca 20,000 and 24,000 BP. This environment was one of repeated erosion and deposition, the result of a mixture of aeolian activity and slope processes. Various pioneer plants managed to grow, however, and a variety of herbs were found in relatively favourable locations such as sheltered moist and wet depressions, where snow could accumulate and protect the plants during the winter months.

Towards the end of the Dimlington stadial an early pioneer vegetation developed over much of northwest Europe as the ice sheets retreated. This period, known in Europe as the Oldest or Earliest Dryas, is marked by the development of herbaceous vegetation, dominated by grasses and sedges. At the site of Hjelm in eastern Denmark, for example, a vegetation cover of sedges, grasses, willows and Artemisia developed before the climatic amelioration of the Bølling episode (Kolstrup 1982). A similar pioneer vegetation has been described from several sites in The Netherlands where a heliophilous sedge-rich vegetation
intermingled with dwarf shrubs (Bohncke et al. 1988, Van Geel et al. 1989). Steppe-like elements also occurred frequently, including Artemisia, Thalictrum and Helianthemum.

As has already been discussed, there was little development of vegetation in Britain prior to the Late glacial interstadial and it has been assumed that southern Britain remained a polar desert-like landscape for much of the Dimlington stadial (Watson 1977).

Faunal remains dating from the height of the last glaciation are almost as sparse as the botanical remains. Barnwell Station in Cambridge is one of only two sites in Britain to have produced any evidence for the presence of large mammal faunas at this time but, as has already been discussed, the age of this assemblage is questionable (Stuart 1982). The combination of mammoth, horse, woolly rhinoceros and reindeer in this assemblage would not be out of place in the closing stages of the Middle Devensian period.

More secure dates have been obtained on a Dimlington stadial fauna from the site of Little Hoyle, near Tenby in south Wales (Green 1986b, Rae et al. 1987). Layer 3 of this cave site produced a remarkable fauna consisting of brown bear, reindeer, fox, arctic lemming, water vole (Arvicola terrestris), tundra vole and hare. Dates on this fauna are listed in Table 9.1.

A rather similar fauna has been recorded in continental northwest Europe from the site of Le Trou des Blaireaux à Vaucelles in Belgium (Bellier and Cattelain 1986). This fauna which includes the remains of reindeer and cave bear has been dated by radiocarbon to ca 16,200 BP.

Faunal remains from Oldest Dryas deposits have also been found in Belgium, at the sites of Presles and Le Trou des Blaireaux à Vaucelles. The microfaunas of these sites include the remains of arctic lemming and tundra vole, both of which are indicative of tundra-like environments (Cordy 1991). A large mammal fauna has also been found at

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Table 9.1 Uranium series and radiocarbon dates from Little Hoyle, Tenby (data from Rae et al 1987).

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<th>Specimen</th>
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<tbody>
<tr>
<td>Bear</td>
<td>$18.6 \pm 1.9$</td>
<td>$19,950 \pm 650$ BP (ANU-4350)</td>
</tr>
<tr>
<td></td>
<td>$17.3 \pm 1.9$</td>
<td>$20,050 \pm 900$ BP (ANU-4347)</td>
</tr>
<tr>
<td></td>
<td>$16.1 \pm 1.8$</td>
<td>$17,800 \pm 950$ BP (ANU-4348)</td>
</tr>
<tr>
<td>Reindeer</td>
<td>$15.7 \pm 1.5$</td>
<td>$17,350 \pm 850$ BP (ANU-4349)</td>
</tr>
</tbody>
</table>

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2. The fauna from this site was not available for study.
3. 16,270 ± 230 BP (LV-1385) and 16,130 ± 250 BP (LV-1558).
Vaucelles (Bellier and Cattelain 1986). This fauna, which was found in association with flint artefacts, includes reindeer, horse, ibex and fox. Three radiocarbon dates on this assemblage range from ca 13,730 to 13,930 BP.

9.2.3 Dimlington stadial reindeer

While several environmental factors may influence reindeer behaviour, forage availability was undoubtedly the primary factor responsible for the development of reindeer social organisation and movement patterns during the Dimlington stadial episode. As has already been discussed, there is an almost complete absence of botanical evidence from British sites for most of the period in question. Evidence from Denmark indicates that any vegetation which might have developed would have been very sparsely distributed, forming only in favourable areas where winter snow cover offered adequate protection.

The extreme patchiness of this environment would have resulted in very small group sizes and a highly dispersed population. Maximum group sizes amongst modern day populations of reindeer in the extremely patchy environments of the high arctic archipelago rarely reach double figures. Solitary animals or mother and calf pairs are the norm for most of the year.

The effects of predation on reindeer social organisation in low productivity environments are unclear. Many modern high arctic populations of reindeer occupy environments which are devoid of predators or where predators exist in very low densities. Reindeer usually respond to predation in open environments by increasing their group size. Given the limited productivity of the Dimlington stadial environments, it is unlikely that they would have been able to support large group formation. Reindeer and predators may only have been able to co-exist, therefore, in more stable environments with a higher degree of plant productivity.

The extremely patchy nature of Dimlington stadial environments would also have resulted in highly nomadic movement patterns amongst reindeer populations. Snow-bed communities in sheltered hollows would have offered the most productive patches of forage. The lack of floral diversity, and the relative homogeneity offered by this environment would have resulted in a high degree of unpredictability in reindeer movement patterns.

In all reindeer populations the time of parturition represents a fixed point within the annual cycle of movement. The low productivity of Dimlington stadial environments may also have discouraged the use of communal calving grounds, however. Indeed, in the absence of predators, it is likely that calving was a dispersed activity, enabling pregnant and lactating females to seek out the most productive patches within the environment.

4. 13,930 ± 120 BP (Lv-1433), 13,850 ± 335 BP (L-1309D) and 13,730 ± 400 BP (Lv-1434D).

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While the dated reindeer remains from Little Hoyle, south Wales, attest to the presence of this species in Britain during the height of the last glaciation, no evidence of seasonality has been obtained from this collection. Interesting evidence of reindeer seasonality has been obtained from the site of Le Trou des Blaireaux à Vaucelles in Belgium, however (Bellier and Cattelain 1986). Fragments of shed reindeer antler from the earliest levels at this site have been identified as those of females and juvenile males. This implies that the area was used as a calving ground during the height of the last glaciation. As the size of this collection has not been reported in full it is impossible to assess whether the antlers represent clumped social behaviour and the use of a communal calving ground, or whether they might fit with the model of dispersed calving behaviour which has been outlined above.

9.3 Lateglacial interstadial environments

The extreme paucity of floral and faunal remains dating from the Dimlington stadial is in stark contrast to the rich and varied biostratigraphic record of the succeeding warm episode. Studies of Late Devensian coleopteran remains indicate that the stadial episode came to an end with a rapid rise in temperature around 13,300 BP (Atkinson et al 1987). This period of rapid warming witnessed temperature increases of the order of 7-8°C in summer and ca 25°C in winter.

A similar picture of rapid temperature change has been obtained from analyses of patterns of marine circulation (Peacock and Harkness 1990, Lehman and Keigwin 1992). Radiocarbon dates on marine sediments indicate that polar waters were rapidly replaced by the warm waters of a weak North Atlantic drift between ca 13,500 and 13,100 BP.

While the entire interstadial episode was a period of relative warmth, temperatures were continually changing and did not stabilise at any time. Coleopteran remains dating from the first half of the interstadial (13,000 - 12,000 BP) have indicated that the climate of England and Wales was generally as warm as that of the present day but slightly more continental in nature. Temperatures peaked at ca 12,500 BP, reaching approximately 17°C during the warmest summer month and 0-1°C during the coldest winter month. This was followed by a gradual cooling from 12,500 - 12,000 BP and a period of relative stability from 12,000 - 11,400 BP. Average temperatures for the later period have been estimated at ca. -9°C during the winter and 15°C in the summer.

Models of atmospheric circulation at 12,000 BP indicate strong westerly winds during the winter months, but a pronounced off-shore flow during the summer months resulting in generally dry conditions throughout western Europe (Harrison et al 1992).
9.3.1 Flora and fauna

Considerable regional differentiation has been noted in the vegetation of this period and is thought to be the result of variation in such factors as altitude, latitude, aspect and soil development (Pennington 1977, Tipping 1991). During the early stages of the interstadiolar environments were predominantly open with a light pioneer vegetation of herbs, grasses and sedges. The earliest communities were characterised by *Artemisia* and rich grasslands containing *Rumex*. Open environments subsequently gave way to shrub vegetation characterised by juniper (*Juniperus*), willow and crowberry (*Empetrum*) and eventually to birch woodlands in those areas where edaphic conditions permitted.

Birch parkland has been recorded over much of England, Wales and southern and eastern Scotland. Two phases of maximum birch expansion have been recorded in northern England and have been radiocarbon dated to 12,500 - 12,000 BP and 11,800 - 11,000 BP (Pennington 1977). In southwest England and Wales the period of maximum birch expansion was rather later and occurred between 11,700 and 11,400 BP (Walker and Harkness 1990, Brown 1977). Scots pine has also been found in the woodlands of southeastern England and northwest Europe (Godwin 1975). Birch woodland did not develop in western Scotland or Ireland, however, and these environments were dominated by open grassland throughout the interstadiolar episode.

Thanks to a dating programme undertaken by the Oxford Radiocarbon Accelerator Unit, a great deal is now known about the Lateglacial faunas of Britain (Housley 1991). Assemblages dating to the Lateglacial interstadial include species which are characteristic of markedly diverse environments. Certain elements of the fauna such as elk (*Alces alces*) and beaver (*Castor fiber*) are typical of forest habitats while other species such as the saiga antelope and steppe pika are characteristic of dry steppe environments. A northern component is also present in the form of the arctic fox which is now restricted to arctic tundras.

One assemblage which illustrates this mixture of different elements is the interstadiolar fauna from Gough's Cave, Cheddar (Currant 1986, 1991). This assemblage includes a rich ungulate fauna with mammoth, horse, red deer, aurochs and saiga antelope. Carnivores also abound in the form of wolf, fox, arctic fox, brown bear and lynx. Surprisingly, reindeer is only recorded in the form of antler artefacts, although their presence in the Mendip area during the early part of the interstadiolar is attested by a directly dated specimen from the nearby site of Aveline's Hole (Housley 1991).

One possible explanation for the apparent mixture of arctic and temperate faunas is that the Lateglacial interstadiolar environments of Britain and northwest Europe represented a unique combination of conditions which permitted the co-existence of such diverse faunas.
species. An alternative explanation for these assemblages is that they represent a mixture of faunas dating from a succession of relatively short-lived climatic stages.

Such biostratigraphic phases are recognised by Cordy (1991) within the Belgian microfaunal record. Assemblages dating to the early interstadial (Bølling) are characterised by predominantly open-habitat microfaunas, with some elements suggestive of rather dry conditions, for example steppe pika and common hamster (*Cricetus cricetus*). During the following period arctic lemming increased considerably in number, and this phase has been interpreted as a correlate of the Older Dryas, representing a cold, dry, continental climate. The later interstadial (Algerød) microfaunas are marked by an increase in insectivores and woodland rodents and are thought to be indicative of a largely open herb-rich landscape with an increasing degree of woodland cover.

Few Lateglacial sites in Britain have been excavated with the precision necessary to produce such a detailed faunal sequence. In addition, almost all of the existing radiocarbon dates on British material of Lateglacial interstadial age fall within the time span from 13,000 to 12,000 BP. Few dates on faunal material fill the gap from 12,000 to 11,400 BP. It is therefore impossible, at present, to determine whether the interstadial macrofaunal assemblages represent a succession of environmental stages akin to those of the Belgian microfauna or whether they represent a response to the unique combination of environmental conditions prevalent at that time.

**9.3.2 Britain in relation to Europe**

World sea levels during the Lateglacial interstadial are thought to have been at least 60m and perhaps as much as 90m below that of the present day (Jelgersma 1979, Bard *et al* 1989). Relative sea levels in Britain during this time were greatly affected by the speed of isostatic recovery in previously glaciated areas. Estimates for the degree of isostatic depression in northern Britain caused by the weight of the Devensian ice sheet are in the range of 250-300m (Gray and Lowe 1977). Isostatic recovery is considerably slower than the eustatic rise in sea levels caused by melting ice sheets and consequently northern Britain witnessed a sudden rise in relative sea level and the flooding of firths and lochs. Evidence for this marine regression is now preserved in numerous raised shorelines around the coasts of Scotland and northern England. In contrast, those areas of southern Britain which were beyond the limits of the Devensian ice sheet were not subject to isostatic movement and sea level during the Lateglacial interstadial probably lay somewhere between the 75m and 90m depth contour. While this rise in sea level would have been sufficient to re-open the Irish sea, Britain would still have been connected to the European mainland across the southern half of the North Sea basin and the eastern English Channel.
Bohncke et al (1988) have summarised the patterns of vegetation change during the interstadial in The Netherlands and the neighbouring countries of northwest Europe. Between 13,000 and 12,000 BP a juniper-rich shrub vegetation developed in the western part of the region, while in Flanders, The Netherlands, Germany and Denmark dwarf birch intermingled with the juniper heath. By the end of the Bölling period an open birch forest was established in The Netherlands but juniper heath was still predominant in the west. The Bölling appears to have been followed by a brief interlude of deteriorating climate known as the Older or Early Dryas. In The Netherlands this period was marked by the development of a more heliophilous vegetation dominated by shrubs and herbs. As a result of this short climatic deterioration, the earlier distinction between the vegetation patterns of eastern and western regions became obscured. During the succeeding Allerød phase (11,800 - 11,000 BP), a grass-rich vegetation with some tree birches developed in Ireland, at the western end of the region, while in the east, a more diverse woodland developed in which birches and aspens (Populus) were predominant. In the central parts of the region, in Poland, The Netherlands, Flanders and Germany, the vegetation succession culminated in the development of boreal forest in which pine was the dominant genus.

As with the botanical record, there appears to have been considerable regional differentiation in the interstadial faunas of northwest Europe, particularly in relation to the distribution of reindeer. Faunal remains similar to those described from Gough's Cave, Cheddar, have been discovered at the site of Chaleux Cave in Belgium (Otte and Teheux 1986). In this assemblage horse predominates but woodland mammals such as red deer, roe deer (Capreolus capreolus) and wild pig are also prevalent. Saiga antelope is recorded but reindeer is again rare, representing only 3% of the total assemblage.

In contrast to the paucity of reindeer at Gough's Cave and Chaleux Cave, a number of sites in the Paris basin have produced evidence for large numbers of reindeer during the Lateglacial interstadial. The faunal remains at two open air sites, Verberie and Pincevent, are dominated by reindeer to the exclusion of most other species (Audouze and Enloe 1991). A similar abundance of reindeer has been found at the sites of Steilmoor and Meiendorf in northern Germany (Grønnow 1985).

The dominance of reindeer at these sites is not necessarily entirely representative of the faunal environment but may rather be the product of human hunting strategies. Other archaeological sites in the Paris Basin dating to the Lateglacial interstadial have produced a much more diverse fauna including horse, red deer, reindeer, bear, polecat (Mustela putorius) and wolf (Audouze and Enloe 1991). The large numbers of reindeer hunted by man in the Paris Basin are nevertheless indicative of the relative abundance of this species in the interstadial fauna of those areas.
9.3.3 Lateglacial interstadial reindeer

Modelling reindeer behavioural ecology during the Lateglacial interstadial is a rather more complex matter than during the preceding period. A very short time span, covering no more than two thousand years, witnessed environmental changes on a grand scale. Stable, climatic climax vegetation patterns did not have time to develop but significant changes did take place, their timing often depending on localised conditions such as soil cover and drainage.

In addition to the problems imposed by continual changes in vegetation patterns, there are also difficulties associated with assigning fossil assemblages to such short-lived episodes. While direct radiocarbon dating of fossils may enable determination of their age to within fifty or one hundred years, such resolution is still inadequate for the very short time span of an event such as the Older Dryas. While it is possible to use a model of reindeer behavioural ecology to draw generalisations about reindeer behaviour patterns during this period, it must be remembered that short-term changes in behaviour patterns may also have occurred in response to specific environmental conditions.

9.3.3.1 Social organisation

According to the model of reindeer behavioural ecology which was outlined in Chapter 3, the greatly enhanced productivity of Lateglacial interstadial environments would have resulted in a marked increase in mean group size. Group size is not only determined by latitude and environmental productivity, however, but is also greatly influenced by anti-predator strategies. During the Lateglacial interstadial reindeer were subject to predation by two major predators, wolves and lynx. The effects of such predation on reindeer social organisation are determined by the nature of the habitats in which the animals live.

While birch parkland developed over much of the country during the second half of the interstadial, extensive canopies were only attained on a regional basis. In many areas birches were limited to valley locations surrounded by a more open shrub vegetation. The extensive closed habitat conditions of boreal forest environments were never attained in Britain and the environment remained relatively open throughout the period. An anti-predator strategy based on clumping would therefore be expected amongst most interstadial populations.

Some regional variation in reindeer social organisation may also have occurred, however, particularly during the later stages of the interstadial. In those areas where birch woodlands were extensive an anti-predator strategy based on dispersal might have developed. Reindeer living in such habitats would have formed small groups or may have lived relatively solitary lives.
In open environments, a tendency to large group formation is heightened by seasonal factors such as biting insects and breeding strategies. With average July temperatures of 17°C during the first half of the interstadial and 15°C during the later stages of the period, conditions were ideal for high levels of insect activity and harassment. One strategy which reindeer adopt to counteract such harassment is the formation of large groups of up to 2,500 individuals. Such large aggregations would not have been unexpected in open habitats during the summer months of the Lateglacial interstadial.

Reindeer breeding strategies will also have resulted in seasonal fluctuations in group size. In open habitats calving is likely to have occurred communally on traditional grounds and to have resulted in the formation of large herds of pregnant cows, occasionally accompanied by yearlings. In contrast, calving in wooded areas may have resulted in dispersal and a lowering in mean group size. Reindeer behaviour during the autumn rut would have shown less variation from one habitat type to another. Mixed groups of all ages and sexes would have occurred, although rutting behaviour in open environments would have facilitated the formation of larger groups.

9.3.3.2 Movement patterns

Modern populations of reindeer are found in highly seasonal environments where forage availability is greatly affected by the length of the growing season and degree of winter snow cover. Reindeer have adapted to such environments by adopting an extreme form of nomadism, being constantly on the move in search of good quality forage. As has already been indicated, however, the rich floral environments of the Lateglacial interstadial are markedly different from the environments in which reindeer are found today. The slow development of vegetation patterns was out of step with the very rapid changes in climatic conditions.

During the first half of the interstadial (13,000 -12,000 BP) average winter temperatures are thought to have been in the region of 0-1°C. While precipitation may fall as snow at temperatures as high as 1.5°C, such temperatures do not result in the formation of persistent snow cover (Lockwood 1982). While the combination of lower temperatures and high levels of precipitation during the later stages of the interstadial would have resulted in a greater degree of snow cover, particularly in upland areas, continuous winter snow-cover is unlikely to have been a major factor influencing reindeer movement patterns for most of the interstadial episode.

Evidence suggests that the relatively snow-free birch parkland communities of the Lateglacial interstadial were capable of supporting sizeable ungulate populations on a year-round basis. While large group formation would have required a degree of movement, if only to counteract the effects of overgrazing, the movement patterns of interstadial reindeer
populations would have been rather different to any observed under modern environmental conditions. Seasonal movement patterns during the spring and summer months are likely to have been related to the phenological succession of new plant growth. Given the relatively heterogeneous environments of the Lateglacial interstadial these movements may have been fairly predictable, exploiting altitudinal differences or localised changes in vegetation. Winter distribution patterns are likely to have been highly variable, however, as most habitats would have been capable of supporting sizeable populations.

9.3.3.3 Reindeer distribution and abundance

While environmental conditions in Britain during the Lateglacial interstadial were theoretically capable of supporting large populations of reindeer, this is not reflected in the evidence from Lateglacial interstadial faunal collections. Indeed a general paucity of reindeer remains is one of the most remarkable features of many British collections of this age. Only one site, Pin Hole in Derbyshire, has produced evidence for the seasonal distribution of reindeer during the interstadial (Fig. 9.1). A single date of ca 13,000 BP was obtained on a shed female antler from this cave (see Chapter 5). As this specimen is part of a larger collection of shed female antlers, it suggests that the Creswell area of Derbyshire was used as a communal calving ground during the interstadial episode.

While dated reindeer remains have also been recorded at Aveline's Hole, Mendip (Housley 1991) and Victoria Cave, Yorkshire (see Chapter 5), neither of these pieces offer any indication of the animal's season of death.

The overall paucity of reindeer remains in Britain appears to be supported by evidence from the site of Gough's Cave, Cheddar. Despite a very rich and varied faunal collection at this site, reindeer is conspicuously absent from the interstadial levels. A similar scarcity of reindeer remains from the site of Chaleux Cave in Belgium appears to indicate their presence in very small numbers.

One explanation for the apparent scarcity of reindeer in the interstadial faunal communities of Britain may be related to the very diverse nature of those communities. Reindeer were subject to competition from several other species of browsers and grazers, including red deer, aurochs, elk, saiga antelope and horse.

All species are thought to occupy their own niche within a community. Reindeer are generally considered to be chionophiles and to have adapted to conditions of heavy snow cover. As has already been discussed, however, Lateglacial interstadial winters were relatively snow-free. As a result, reindeer may have lost their selective advantage over other ungulate species which cannot tolerate deep snow.

Direct interspecific competition with other browsers and grazers such as aurochs and red deer may have resulted in relatively low reindeer population densities. These low
Fig. 9.1 Reindeer distribution in Britain during the Late Devensian (S = Spring, C = calving, Su = Late summer/autumn, A = Late autumn/winter, W = winter).
densities would be reflected in the archaeological record by small numbers of reindeer kills. While reindeer population densities may have been low, their annual range size would not have decreased accordingly. Overall ungulate population densities would have been relatively high and, in order to reduce grazing pressure, the annual range of gregarious animals such as reindeer must have been quite extensive.

9.4 Lateglacial stadial environments
The Lateglacial stadial (also known as the Loch Lomond stadial) represents a short-lived return to glacial conditions spanning a period of ca 1000 years. According to the temperature curves established by Atkinson et al (1987), mean summer temperatures began to decrease from 11,400 BP, reaching a minimum of ca 10°C in southern England by 10,500 BP. Estimates of mean July temperatures in the northern half of the country are somewhat lower, ranging from 7.5°C in the Lake District to 6°C in the southeast Grampians (Sissons 1979a). Mean winter temperatures also decreased during this period from approximately -5°C at 12,000 BP to -17°C at 10,500 BP. This cold phase was followed by a rapid and uninterrupted rise in temperatures from 10,500 BP onwards.

The onset of the Lateglacial stadial coincides with the southerly movement of arctic waters (Ruddiman and McIntyre 1981, Peacock and Harkness 1990, Lehman and Keigwin 1992). During the Lateglacial interstadial episode two short periods of oceanic cooling have been recorded at ca 12,500 and 11,700 BP. These were followed by a sharp reversal in oceanic warming at ca 11,200 BP when all Atlantic waters north of 52-53°N returned to nearly full glacial temperatures. This transition was remarkably rapid and sea surface temperatures fell by over 5°C in less than 40 years.

9.4.1 Glaciation
Falling temperatures and increased snowfall during the stadial episode enabled the recrudescence of glaciers in many upland areas. The greatest accumulation of ice occurred in the western highlands of Scotland where a major ice-cap was centred on Rannoch Moor (Sissons 1979a). Smaller ice-caps formed in the central Grampians, and valley glaciers developed in upland areas throughout Britain, including the western Cairngorms, the islands of the Inner Hebrides, the northwest Highlands, the Southern Uplands, the Lake District, Snowdonia and the Brecon Beacons.

The predominantly western distribution of glacier formation seems to suggest that the principal snow-bearing winds were from a westerly or southwesterly direction. Sissons (1979a) has used alternative sources of evidence, however, derived from patterns of glacier dimension, altitude and orientation, to illustrate that the prevailing snow-bearing winds during this period were from a southerly or southeasterly direction. Patterns of glacier
formation also indicate the existence of a marked precipitation gradient between coastal and inland areas of upland Britain (Sissons 1979b). Estimated annual precipitation levels of 4000mm in the southwest Grampians, for example, can be compared with estimated values of 500-600mm per annum in the northwest Cairngorms. Precipitation levels at lower altitudes would have been somewhat lower, perhaps in the region of 200-300 mm per annum in low-lying areas of northeast Scotland such as the Spey valley.

9.4.2 Periglacial activity
While the distribution of glacier development was restricted, periglacial activity beyond the ice margins was widespread. Many periglacial landforms such as fossil scree, protalus ramparts and solifluction deposits are thought to date from this period. Widespread soil instability and incomplete vegetation cover are indicated by the deposition of minerogenic sediments in present and former lakes (Sissons 1979a). In many rivers, a reduction in peak discharge during the stadial episode, combined with the increase in sediment load, resulted in marked channel instability and the development of braiding (Rose et al 1980). Aeolian activity is also indicated by the renewed deposition of coversands in northern Europe (Kolstrup et al 1990) and of loesses in southern Britain (Parks and Rendell 1992).

9.4.3 Flora and fauna
The vegetation patterns of the Lateglacial stadial exhibit a marked deterioration from those of the preceding stage. Pollen analyses from samples throughout Britain indicate that the birch woodland and parkland environments of the Lateglacial interstadial disappeared and were replaced by herbaceous communities, dominated by grasses and sedges (Pennington 1977). Rumex and Artemisia were also common genera and are indicative of widespread bare ground and disturbed soil.

In Scotland, the proportions of Artemisia, together with Chenopodiaceae and Caryophyllaceae, increased steadily during the course of the stadial (Tipping 1991). Many species of the genus Artemisia are associated with arid conditions and the occurrence of three species in particular (A. norvegica, A. campestris and A. maritima) has been interpreted as evidence for increasing continentality of climate in Scotland during the course of the stadial.

In contrast to the large volume of information available on the vegetational history of the Lateglacial stadial, the fauna is very poorly researched and understood. While many individual specimens have now been radiocarbon dated (Housley 1991), few sites have been excavated to the standards necessary to ensure genuine association of vertebrate remains. Many early cave sites were excavated in horizontal spits with no record having been kept of the stratigraphic context.
One site, Ossom's Cave, in the Manifold Valley, Staffordshire, has produced a large collection of faunal remains from a single horizon (Bramwell et al. 1987, see Chapter 5). Reindeer represents 99% of the large mammal remains from this site, but a rich collection of small mammals includes arctic lemming, Norway lemming (*Lemmus lemmus*), and northern vole. The occurrence of these animals together with ptarmigan is indicative of an open tundra landscape. Radiocarbon dates of ca 10,500 - 10,700 BP on reindeer bone suggest that this fauna may be placed within the Lateglacial stadial. It should be noted, however, that significantly younger material was also obtained from this deposit. The occurrence of bank vole (*Clethrionomys glareolus*) within the collection indicates that at least part of the small mammal fauna may also belong to a younger context. The present day distribution of the bank vole extends throughout the taiga and deciduous woodland of the western palaearctic (Stuart 1982) and is usually indicative of interglacial conditions.

Directly dated remains from a number of Lateglacial sites indicate the occurrence of reindeer, red deer, aurochs, horse and pika within Lateglacial stadial environments (Housley 1991). As with Lateglacial interstadial faunas, there appears to be a degree of mixing, however, with more temperate elements such as red deer and aurochs occurring alongside faunal elements more typical of arctic environments (e.g. Norway and arctic lemming).

### 9.4.4 Britain in relation to Europe

Evidence from southern Britain and Ireland suggests that stadial sea levels lay somewhere between 35 and 50m below their present level (Sissons 1979a). A pronounced erosional shoreline has been found at a depth of 42m below sea level off the coasts of southwest England. A similar cliff has been recorded in Cardigan Bay at a depth of -35 to -40m and it has been suggested that these formations date from the Lateglacial stadial. In northern Britain, the effects of isostatic recovery have resulted in a slope in the main Lateglacial shoreline. This shoreline reaches a maximum height of ca 11m above sea level near Oban on the west coast of Scotland but has also been traced on the east coast at Berwick where it lies at a depth of 18m below present day sea level.

While this rise in sea level would have resulted in the flooding of the English channel, Britain would still have been connected to Europe across the dry North Sea bed. Vegetation patterns in northwest Europe during the stadial episode were also predominantly open. A rapid decline in the boreal birch-pine forest at the onset of the stadial episode was followed by the development of dwarf-shrub vegetation with juniper, dwarf birch and willow (Bohncke *et al.* 1988). It has been suggested, however, that stands of birch and pine may have been maintained in isolated favourable sites.
While open tundra or dwarf-shrub vegetation developed over much of northwest Europe, vegetation zones were not as greatly compressed as they had been during the Dimlington stadial. On the western coast of the continent the boreal forest zone lay far to the south in northern Spain and southern France. In central Europe, however, the tree line lay further north and the boreal forest zone extended into north central Germany, Poland and southern Denmark (Huntley and Birks 1983).

The Lateglacial stadial macrofaunas of northwest Europe are less well known than those of the preceding period. Few direct radiocarbon dates have been obtained on individual specimens, an interesting exception being a cave lion from the site of Lathum in The Netherlands, which has produced a radiocarbon date of 10,670 ± 160 BP (OxA-729) (Housley 1991). Archaeofaunal collections from sites in northern Germany and Belgium are dominated by reindeer but a more diverse fauna is also represented in small numbers and includes such species as bison, wild pig, horse, red deer, elk, ibex, arctic fox and lynx. (Dewez et al 1974, Gronnow 1985).

Studies of the microfaunal assemblages from the Lateglacial stadial in Belgium have indicated an increase in numbers of arctic lemming. It is notable, however, that the field vole (Microtus agrestis) and common vole (Microtus arvalis) remain predominant. The latter are generally indicative of temperate conditions. Woodland species of rodents and insectivores are also represented in small numbers and indicate that, while the environment was mainly open, it was nonetheless relatively heterogeneous, offering a mosaic of different habitat types.

9.4.5 Lateglacial stadial reindeer

The return of cold climate conditions during the Lateglacial stadial may also have been marked by changes in reindeer behaviour patterns. As in the preceding interstadial period, predominantly open environmental conditions would have resulted in large group formation throughout the year, and particularly at the times of calving and the rut.

Some differences in social organisation may have occurred, however, as a result of the fall in mean summer temperatures. While mosquitos may be active at 7°C, many parasitic insects require temperatures of 13°C or above. With very low mean summer temperatures of ca 6 - 10°C during the stadial episode, the activity of many parasitic insects would have been curtailed. Large post-calving aggregations would therefore not have been required.

Marked seasonal changes in the availability of forage would also have resulted from the short summer growing season and the intensely cold winters. This may have been reflected in changes in reindeer movement patterns. With average winter temperatures of -17°C, all winter precipitation must have fallen as snow, thereby restricting access to terrestrial food sources. Marked precipitation gradients also appear to have existed during the stadial, with
some upland areas subject to heavy precipitation while other lowland regions fell within a rain shadow. Reindeer may have sought out these lowland areas during the winter months as low levels of snow fall would have allowed easy access to terrestrial forage. Low-lying hills and ridges may also have been swept free of snow, facilitating winter foraging without the need to crater for food.

Confirmation of reindeer presence in Britain during the winter months has been found at two sites in the Mendips. Shed antler pedicles of male reindeer have been found at the sites of Chelm's Combe and Gough's Cave, indicating reindeer presence between the months of October and March.

As winter snow cover reduced the availability of winter forage, overall range size is likely to have increased. While some reindeer clearly over-wintered in Britain, long distance migration of southern populations to wooded environments in north central Europe would not have been beyond the bounds of possibility. Migration routes would have been channelled through the southeastern region of the country making use of the land bridge across the southern half of the North Sea.

While some populations may have undertaken long distance migrations, the movement patterns of other groups were clearly less extensive. Seasonal evidence from the site of Chelm's Combe in Mendip suggests that the area was used, not only as winter range, but also for calving and late summer pasture.

Movement patterns during the short summer growing season are likely to have been dominated by the search for high quality forage. Widespread permafrost would have resulted in poor drainage and relatively homogenous foraging conditions in the gently undulating environments of southeastern England. In such environments, spring and summer movement patterns are likely to have been opportunistic. In upland regions of the country, however, spring and summer movement patterns may have been more predictable, following the phenological succession of new plant growth.

One site in the Pennines appears to support this impression of spring movement onto high ground. Juvenile mandibles from the site of Ossom's Cave, Staffordshire, indicate that reindeer were present in the region during the spring or early summer months.

While reindeer calving grounds usually offer a highly predictable fixed point within the annual cycle of movement, little evidence of reindeer calving behaviour has yet been found for the Lateglacial stadial. This is almost certainly a function of the incompleteness of the archaeological record, however, rather than an indication of dispersed calving behaviour.
9.5 Summary

The significant environmental changes which took place during the Late Devensian period clearly influenced patterns of reindeer behaviour and distribution. While detailed environmental information is available for much of this period, regional variation during the Lateglacial episodes was such that models of reindeer behaviour cannot yet progress beyond broad generalisations. The effects of such regional variation and the rapidity of environmental changes during the Late Devensian period must be borne in mind, however, when attempting to utilise these models in discussions of human subsistence strategies and their related settlement patterns.
Reindeer and man during the Devensian period in Britain

10.1 Introduction
Archaeologically the Devensian period covers two chronological units known as the Middle and Upper Palaeolithic. Evidence for human occupation during this time span has been found in cave and open air sites, most of which are restricted in their distribution to the southern half of Britain. This evidence occasionally consists of artefact assemblages which were found in association with faunal remains and other settlement debris. Many Palaeolithic collections are of limited extent, however, and often consist of little more than an isolated find of a characteristic implement type.

Much of our knowledge of the Palaeolithic occupation of Britain is derived from the work of 19th century collectors and excavators. With the exception of Dorothy Garrod’s review of the Upper Palaeolithic period, published in 1926, little further research was undertaken until the late 1950s and 60s when Charles McBurney’s research excavations began to revive interest in the period (eg McBurney 1959). Over the last 30 years many caves have been the subject of further research, a few new sites have been uncovered and many older collections have been re-analysed. The results of this recent work have been published in numerous journals, monographs (eg Barton 1992, Jenkinson 1984), and collective volumes (Collcutt 1986, Roe 1986) and has also been incorporated into reviews of the period (Campbell 1977, Jacobi 1980, Roe 1981).

As Britain was connected to the European mainland throughout the Devensian glaciation, many parallels have been drawn between British artefact assemblages and their counterparts in the Palaeolithic traditions of northwest Europe. Evidence for Middle Palaeolithic occupation of Britain is largely restricted to assemblages of chipped stone tools. These assemblages have been compared with the Mousterian of Acheulian Tradition of southwest France (Mellars 1974, Roe 1981). As the greater part of the period lies outwith the range of radiocarbon dating, few of these assemblages have been accurately dated. It has been suggested that much of the material dates from the last interglacial (Ipswichian) and from the early stages of the Devensian. Radiocarbon dates on associated faunal collections appear to indicate that at least some of the assemblages may be rather younger, however, representing human settlement during the Upton Warren interstadial of the Middle Devensian period (Green 1986a).

The settlement history of Britain during the Upper Palaeolithic period (ca 38,000-10,000 BP) is rather better understood. At least four artefact traditions have been recognised on the basis of stone tool types, although different authors have assigned a variety of names to these industrial groupings (Fig. 10.1).
<table>
<thead>
<tr>
<th>Years BP</th>
<th>Jacobi</th>
<th>Campbell</th>
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<tr>
<td>10,000</td>
<td>Long blade industries</td>
<td>Creswellian</td>
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Fig. 10.1 British Upper Palaeolithic (after Jacobi (1980, 1991) and Campbell (1986)).
While there is a general agreement on the succession of industrial traditions, the dating of these phases is still largely problematic. Conventional radiocarbon dating techniques require large quantities of organic material, most of which has been obtained from faunal remains found in association with the stone tool assemblages. As many British Palaeolithic sites were excavated in the latter years of the last century and the early part of this century, often under conditions of poor stratigraphic control, the association between artefacts and faunal remains from these sites is rarely well recorded. The dates obtained from such faunal remains can only give an approximate guide, therefore, to the age of Upper Palaeolithic stone tool traditions. In recent years direct dating of humanly modified bone and antler remains (both tools and cut-marked bones) has been made possible by the accelerator technique of radiocarbon dating (Housley 1991). These dates provide firm evidence of human presence and will greatly enhance our understanding of Upper Palaeolithic chronology.

10.2 Subsistence strategies and settlement patterns

Given the difficulties in establishing an absolute chronology for human presence in Britain during the Devensian glaciation, little research has been conducted into the subsistence strategies and settlement patterns of those peoples. Discussion of these issues has usually been limited to comparison with models of the subsistence strategies and settlement patterns of hunting groups in continental northwest Europe.

As was discussed in Chapter 2, many of these models involve a degree of dependence on the exploitation of reindeer. While it is not yet possible to test any of these models against direct evidence from Palaeolithic sites in Britain, it is possible to assess the applicability of those models in the light of reindeer behavioural ecology during the Devensian period.

Before considering the question of Palaeolithic subsistence strategies, however, it may be useful to begin by considering the degree of continuity of human settlement in Britain during the course of the last glaciation.

10.3 Continuity of human settlement

Gaps in the chronological succession of Palaeolithic industries in Britain during the course of the last glaciation have often been interpreted as evidence for discontinuity of human settlement (Mellars 1974, Campbell 1977, Jacobi 1980). These arguments have been supported by the suggestion that environmental conditions during the stadial episodes were so severe that the land would have been incapable of supporting human life. Campbell (1986) has recently argued against this "hiatus hypothesis", on the grounds that it is founded on an ethnocentric view of human tolerance. He suggests that many recent hunting
communities prospered in extremely harsh environments and under conditions which might have been considered intolerable by modern archaeologists. Otte (1990) has recently echoed this view by suggesting that it was culture rather than climate which prevented human occupation of the Northwest European plain during the height of the last glaciation.

While further archaeological research may ultimately resolve this matter, some indication of the potential for human settlement may be obtained from an analysis of environmental productivity. Large mammal faunas formed the basis of Palaeolithic subsistence strategies and the distribution and abundance of those faunas may therefore provide some clues as to the sustainability of human settlement during the course of the last glaciation.

Poor chronological resolution and a paucity of faunal evidence prevent the discussion of the settlement potential offered by Early Devensian environments. During the Middle Devensian period, however, the faunal record appears to indicate an extremely rich environment, capable of supporting a large and varied ungulate population. Large mammals such as mammoth and woolly rhinoceros would have provided occasional prey for human communities, but large populations of bison, reindeer, giant deer and horse would have formed the mainstay of human diets. While previous researchers have acknowledged the wealth of this Middle Devensian fauna, it has been suggested that the animal populations may have been migratory, leaving Britain during the winter months for richer pastures further south (Mellars 1974). Studies of seasonality indicate that this was certainly not the case with reindeer populations, which appear to have been present in Britain throughout the course of the year. On the evidence of the productivity of Middle Devensian environments, there is therefore no reason to suppose that human settlement would not have been viable on a permanent, year-round basis.

In contrast to the abundance and diversity of Middle Devensian faunas, the succeeding period is marked by the extreme paucity of large mammal remains. Botanical evidence for Dimlington stadial environments suggests that, at best, they may be described as cold deserts, with extremely low levels of productivity. While reindeer were clearly present within Britain at this time, no other large ungulates have yet been recorded. Environmental evidence suggests that reindeer population densities would have been extremely low and that the animals would have been highly dispersed. While such highly dispersed populations may have been able to support human settlement on a temporary basis, it is unlikely that they would have been capable of sustaining a permanent human presence. Campbell (1986) and Otte (1990) may have been over-optimistic, therefore, in their assessment of man's ability to colonise such harsh environments.

Environmental productivity increased markedly at the end of the Dimlington stadial and the large mammal fauna increased greatly in diversity. The re-colonisation of Britain
and northwest Europe appears to have coincided with this improvement in environmental conditions. With the return of glacial conditions during the Lateglacial stadial, however, some authors have suggested that settlement may only have been possible on a seasonal basis (Mellars 1974, Jacobi 1981). This suggestion echoes that of Clark (1938) who proposed the seasonal movement of Lateglacial men and reindeer herds between winter camps on the North European plain and summer pastures in southern Britain. While the Lateglacial stadial environments of Britain were not as productive as those of the Middle Devensian period, there is nonetheless clear evidence for the year round presence of reindeer populations in Britain. Permanent human settlement was therefore a perfectly viable possibility.

10.4 Herd-following, storage or seasonal relocation

The models of Palaeolithic subsistence strategies and their related settlement patterns which were reviewed in Chapter 2 all included reindeer as part of the primary resource base. These models envisaged three alternative scenarios in which the strategies of herd-following, storage or seasonal relocation enabled Palaeolithic groups to settle the Devensian environments of northwest Europe. The applicability of each of these models may now be assessed in relation to the Devensian environments of Britain.

Herd-following models are underpinned by two basic assumptions; firstly that Devensian reindeer populations undertook annual long-distance migrations between winter ranges and summer calving grounds; and secondly that Palaeolithic human groups were largely or entirely dependent on those migratory herds of deer, either as a result of necessity or through deliberate choice. The usefulness of this model clearly depends upon an ability to determine migratory behaviour amongst Devensian reindeer populations and to establish the relative importance of reindeer in Devensian faunal communities.

In contrast, broad-based models are based on the assumption that Palaeolithic groups would have attempted to minimise risk by utilising the widest possible resource base. In situations where there was a seasonal absence of prey, these models suggest that the strategies of storage and/or seasonal relocation may have enabled human populations to survive the lean season. The applicability of these models also depends on an ability to reconstruct the nature of the original extant faunal communities and to assess the degree of predictability in seasonal changes within those communities.

10.4.1 The Early Devensian period

Given the current difficulties in dating Early Devensian material, very little can yet be said about the relationship between men and reindeer which may have existed during the earliest stages of the last glaciation. A tentative model of reindeer behaviour has been
constructed for the Chelford interstadial, however, which suggests that reindeer movement patterns may have followed a relatively predictable pattern on a north-south axis. Potential winter ranges in the spruce pine forests of southern Britain would have been matched by summer range in the open birch woodlands of northern Scotland.

Under such conditions subsistence strategies based on herd-following or seasonal storage may both have been viable options. The relative importance of reindeer in the large mammal communities can not yet be assessed, however. While faunal remains from the site of Coston suggest a relatively diverse community of large mammals, this community is thought to have developed towards the end of the interstadial episode in environments which were already predominantly open.

Given these difficulties in assessing the relative importance of reindeer in the large mammal faunas, it is impossible to assess their likely importance in the subsistence strategies of Middle Palaeolithic groups.

10.4.2 The Middle Devensian period

Middle Devensian faunal communities are rather better understood than those of the preceding period. It is clear that reindeer represented one element of a diverse large mammal community which evolved to exploit the rich grassland environments of Britain and northwest Europe. While it is always difficult to establish absolute taxonomic abundances from zoo-archaeological collections, it appears that bison is often the dominant component of Middle Devensian faunas and that reindeer is often of secondary importance.

The diverse nature of Middle Devensian faunas suggests that human dependence on reindeer would have been highly unlikely and that herd-following would not have been a preferred subsistence option. The widely scattered settlement patterns which are associated with herd-following strategies would therefore be unexpected in the archaeological record of this period.

Broad-based models of Palaeolithic subsistence and settlement are perhaps more applicable to Middle Devensian environments. The social organisation and movement patterns of Middle Devensian reindeer are more likely to have encouraged small scale seasonal relocation, however, rather than large scale seasonal storage.

Subsistence strategies based on seasonal storage solve the problem of a seasonal absence of prey by building up large stocks of frozen or dried meat. Such strategies are only viable in environments where massive kills may be relied upon during certain seasons of the year. Reconstructions of reindeer behavioural ecology suggest that such large scale seasonal storage was neither necessary, nor necessarily viable, during the Middle Devensian period.

Evidence for the seasonal distribution of Middle Devensian reindeer populations suggests that the annual range of those populations may not have been very extensive.
Indeed there is some evidence to suggest that winter range and summer calving grounds may have overlapped. While Middle Devensian reindeer populations were mobile, it is likely that some groups would have remained relatively accessible to human populations throughout the course of the year.

Resource predictability is an essential pre-requisite of subsistence strategies based on large scale seasonal storage. Reindeer movement patterns during the Middle Devensian period are unlikely to have offered the high levels of predictability which would be required for such subsistence strategies to be viable. Movement patterns were probably most predictable during the late spring and early summer as herds of pregnant cows moved towards traditional calving grounds. As winter distribution patterns appear to have been widely dispersed, however, similar mass movements of deer would not have been expected during the autumn. While mass-killing techniques may have enabled the build-up of surplus meat during the early summer, no other season of the year would have offered similar opportunities for large scale storage of meat.

While the seasonal distribution of other large ungulates is currently unknown, the relatively small scale nature of reindeer movement patterns during the Middle Devensian period may have encouraged the development of localised settlement patterns involving short range relocations to exploit seasonally abundant resources. Seasonal changes in the social organisation of those ungulate faunas may also have been reflected in the hunting techniques employed.

Reindeer aggregation sizes may have varied considerably during the course of an annual cycle. Group sizes are likely to have been highest during the late spring, early summer and autumn. At such times mass-killing techniques involving drives and ambushes may have been employed. Given the unpredictability of reindeer movements, drives may have been relatively impromptu affairs making use of natural features such as ridges and valleys to funnel reindeer towards ambushes at river crossings. During late summer and early winter aggregation sizes may have dropped to double figures. At such times of the year smaller scale hunting techniques such as stalking or decoying may have been adopted.

10.4.3 The Lateglacial interstadial
The large mammal communities of the Lateglacial interstadial were very different from those of the Middle Devensian period. A highly diverse fauna appears to have developed, partly in response to rapid environmental change, and partly in response to the mosaic of habitat types which emerged during the course of the interstadial.

Given the very diverse nature of the large mammal fauna, human hunters are unlikely to have been dependent on the exploitation of any one species. Herd-following models
based on the exploitation of reindeer to the exclusion of most other species are therefore not applicable in this setting.

While reindeer populations did occur within the Lateglacial interstadial fauna, their densities appear to have been relatively low, possibly as a result of interspecific competition with other browsers and grazers. Human exploitation of reindeer is therefore likely to have occurred on a small-scale or seasonal basis within broad-based hunting strategies.

Most reindeer populations are likely to have been gregarious and mobile with fairly extensive annual ranges. While movement patterns may have resulted in the seasonal absence of reindeer, the year-round availability of other species with more localised distribution patterns, such as elk, aurochs and red deer, would have removed the need for seasonal storage or settlement relocation within human subsistence strategies. The preferred subsistence option may therefore have been based on the opportunistic exploitation of locally available fauna, resulting in the development of a relatively sedentary settlement pattern.

While reindeer population densities may have been relatively low, large aggregations would have facilitated the exploitation of this species in considerable numbers. Spring movements towards communal calving grounds would have been most predictable, following the phenological succession of new plant growth, perhaps along an altitudinal gradient. Such movement patterns may have facilitated the use of mass-killing techniques, whether in traps or ambushes in water. Winter distribution would have been widespread, however, and autumn movements would have been highly variable. Autumn and winter kills of reindeer are more likely to have been opportunistic, therefore, rather than predictable, planned hunts.

10.4.4 The Lateglacial stadial

The return of cold climatic conditions and predominantly open habitats during the Lateglacial stadial brought about a marked decrease in faunal diversity. While aurochs and red deer have been recorded during this period, most faunal assemblages appear to have been dominated by horse and reindeer. The relative importance of the latter species in human subsistence strategies is likely to have increased accordingly.

Two possible models of reindeer movement patterns have been presented for this period. These models, which are not mutually exclusive, involve nomadic movements within Britain or long distance migration to winter ranges in the boreal forest of north central Germany. These two models clearly offer opportunities for the development of alternative models of human subsistence.

A degree of dependence on migratory herds of reindeer may have encouraged the adoption of subsistence strategies based on herd-following. The resultant settlement
patterns would have consisted of limited seasonal settlement in southern and eastern areas of England. Sites of summer seasonality in these areas would be matched by sites of winter seasonality in north central Germany.

Unfortunately, in the absence of dated evidence for such seasonal movements of men and reindeer herds, this model can not yet be tested further. Clear evidence does exist, however, for the year-round presence of reindeer populations in Britain at this time. Such populations offered opportunities for human groups to settle within Britain on a more permanent basis.

Given the impoverished nature of the large mammal community, broadening of the resource base was not an option available to hunters during the Lateglacial stadial. The subsistence strategies of such human groups would therefore have been dependent, to a large degree, on the exploitation of reindeer. The annual ranges of those populations which over-wintered in Britain do not appear to have been particularly extensive, however, and some groups may have remained within reach of human populations throughout the course of the year. Reindeer movement patterns may also have been relatively predictable, particularly during the spring migration to calving grounds and during the autumn movements to winter range in areas of low precipitation. Aggregation sizes during the spring and autumn movements would have been relatively large and would have facilitated the use of mass-killing techniques and the accumulation of surplus meat for storage. Such stored meat supplies may also have been supplemented by the year-round availability of reindeer populations. While temporary relocation to exploit seasonally abundant populations of reindeer may have been a viable subsistence option, the opportunities which existed for seasonal storage during this period may have encouraged the adoption of more sedentary settlement patterns.

10.5 Summary
The behavioural ecology of reindeer populations in Britain varied throughout the course of the last glaciation, and its implications for human settlement, subsistence, and mobility have also been shown to have varied accordingly. While reindeer was an important element of Devensian large mammal faunas, other species were also available for human exploitation throughout this period. It seems unlikely, therefore, that human subsistence strategies were entirely dependent on reindeer at any stage during the last glaciation.

While some models of subsistence strategies in continental northwest Europe have suggested that human populations were highly mobile during the Upper Palaeolithic, the reconstructions of reindeer behavioural ecology which have been presented here suggest that such models are rarely applicable to the Devensian environments of Britain. The extensive settlement patterns which are associated with such herd-following models would
therefore be unexpected in the British archaeological record for most of the Devensian period. In contrast, the evidence for the distribution and behaviour of Devensian reindeer populations suggests that the subsistence strategies of Palaeolithic human groups may have resulted in relatively small-scale seasonal movements within Britain. These would be reflected in the archaeological record in the form of localised settlement patterns.
Conclusions and suggestions for future research

11.1 Conclusions

Reindeer was a major component of the subsistence strategies of human groups in northwest Europe during the last glaciation. Archaeological models of the subsistence strategies and related settlement patterns of those human groups are dependent upon assumptions about the nature of Devensian faunas, and, in particular, about the nature of reindeer behaviour. Previous attempts to reconstruct reindeer behaviour have been based on direct comparison between the behaviour of modern reindeer populations and that of their prehistoric counterparts. Studies of modern species have indicated that many aspects of behaviour are not fixed, however, but are adaptive to environmental conditions. Behavioural ecology attempts to unravel the complex relationships between animal behaviour and environmental conditions. This study set out to investigate the behavioural ecology of Devensian reindeer and to assess its implications for human settlement, subsistence and mobility during the last glaciation in Britain.

Behavioural ecology is an area of palaeoecological research which has considerable implications for the interpretation of the relationship between human groups and faunal communities. The reconstruction of many dynamic aspects of palaeoecology is problematic, owing to the incomplete nature of the data. Using models of modern behavioural ecology, however, it is possible to reconstruct former patterns of animal behaviour through the analysis of zoo-archaeological remains and the reconstruction of past environmental conditions. Reindeer is a particularly suitable subject for study as modern populations may be observed in a wide range of relatively undisturbed environments. By assessing reindeer behaviour patterns in a variety of habitat types, it has been possible to generate a model of the relationship between reindeer behaviour and environmental conditions.

In order to apply this model to the last glacial period in Britain, it has been necessary to analyse the seasonal distribution patterns of Devensian reindeer and to investigate the nature of Devensian environmental conditions. Existing zoo-archaeological techniques for the identification of seasonality have been employed in the analysis of Devensian faunal collections from both archaeological and geological sites. One previously unsubstantiated method of determining seasonality from shed reindeer antlers has been tested against a modern sample and has been found to be reliable. A new method of identifying seasonality in samples of juvenile reindeer bones has also been developed and employed where possible. Analysis of biological, lithological and geomorphological data, compiled from a wide variety of sources, has enabled the reconstruction of environmental conditions during
several stages of the last glaciation. Models of reindeer behavioural ecology which have been generated from these environmental reconstructions have been tested against zoo-archaeological collections of known age and seasonality. The reconstructions of reindeer behavioural ecology which have been generated by this study have thus enabled an assessment of the applicability of a range of archaeological models of human subsistence strategies and settlement patterns within the Devensian environments of Britain.

11.2 Problems encountered

Current difficulties with this research method include the problems of dating and association. Dating problems are particularly acute during the early stages of the Devensian period which are beyond the range of radiocarbon techniques. While significant environmental changes may be observed within this period, the dating of these events is still very uncertain. Correlations between different areas are tentative and, consequently, environmental reconstructions are, at best, rudimentary. An inability to assign faunal remains to the appropriate episode within this period further hinders any assessment of likely behaviour patterns.

For those collections of faunal remains which do fall within the range of radiocarbon dating techniques, indirect dates on associated material are of questionable value unless the degree of association between the dated samples and the reindeer collections can be demonstrated clearly. As many Devensian sites were excavated during the pioneering years of archaeological research, using somewhat crude techniques, genuine association between excavated faunal samples cannot always be assumed.

11.3 Future research directions

Further research into the nature of Devensian environments, refinement of dating techniques, and the excavation and analysis of new material, using modern methods, will greatly enhance our ability to generate more accurate models of reindeer behavioural ecology during the Devensian period. Reindeer represents only one component of Devensian large mammal faunas, however, and future research should also be concentrated on the investigation of the behavioural ecology of other mammal species. An understanding of the distribution and behaviour patterns of the other major herbivores around which Palaeolithic exploitation strategies were built will greatly enhance our understanding of Palaeolithic subsistence strategies and their related settlement patterns. Finally, further archaeological research into the subsistence strategies of those early human groups, through the analysis of archaeofaunal collections, will enable the verification of the models of human subsistence potential which have been presented here.
Appendix 1: Antlers

The measurements recorded here are illustrated in Fig. 4.11. Museum names have been abbreviated as follows:

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<tr>
<th>Abbreviation</th>
<th>Museum</th>
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<td>Bristol City Museum</td>
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<tr>
<td>BGM</td>
<td>Bath Geological Museum</td>
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<tr>
<td>BU</td>
<td>Birmingham University, Department of Geology</td>
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<tr>
<td>BMNH</td>
<td>British Museum (Natural History)</td>
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<td>CUZM</td>
<td>Cambridge University Zoological Museum</td>
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<tr>
<td>KJHLA</td>
<td>King John’s Hunting Lodge, Axbridge</td>
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<td>MM</td>
<td>Manchester Museum</td>
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<td>NMS</td>
<td>National Museum of Scotland (Royal Museum of Scotland)</td>
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<td>NCM</td>
<td>Norwich Castle Museum</td>
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<td>OUM</td>
<td>Oxford University Museum</td>
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<tr>
<td>RISW</td>
<td>Royal Institution of South Wales, Swansea</td>
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<td>TTNCM</td>
<td>Taunton Castle Museum</td>
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<td>UBSS</td>
<td>University of Bristol Speleological Society Museum</td>
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**Banwell Bone Cave, Banwell, Somerset (continued)**

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**Banwell Station, Cambridgeshire**

A16 SM No acc. no. Gravel (Swann's Pit) 2. Location - Newmarket Rd - W of Barnwell Stalion 1916 Shed base Pedicle Male 25 22 31 29 27 24

**Black Rock Quarries, Tenby, Pembrokeshire**

|    | A17    | SM    | D2719 | T. Roberts' collection | 1. Tenby | Unshed antler | | 22 | 21 | 28 | 24 | 23 | 17 |
|    | A18    | SM    | D2720 | T. Roberts' collection | 1. Tenby R. | Unshed antler | -- | -- | -- | -- | 15 | 13 |
|    | A19    | SM    | D2721 | T. Roberts' collection | 1. Tenby | Unshed antler | 29 | 27 | -- | 31 | -- | -- |
|    | A20    | SM    | D2793 | T. Roberts' collection | 1. Tenby | Unshed antler | -- | -- | -- | -- | 14 | 11 |
|    | A21    | SM    | D2795 | T. Roberts' collection | 1. Tenby | Unshed antler | 28 | 26 | -- | 30 | 34 | 22 |

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### Appendix 1: Antlers (continued)

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Paviland Cave, Rhossili, Glamorgan

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## Appendix 1: Antlers (continued)

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continued over
## Pinn Hole, Creswell, Derbyshire (continued)

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## Appendix 1: Antlers (continued)

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### Appendix 1: Antlers (continued)

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### Pin Hole, Creswell, Derbyshire (continued)

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### Reindeer Cave, (Outer Chamber), Inchnadamph, Sutherland (continued)

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Sandford Hill, Mendip, Somerset

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**Upton Warren, Worcestershire**

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**Willment's Pit, Isleworth, Middlesex**

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Appendix 2: Skulls

The left and right antler/pedicle measurements listed here correspond with antler base measures 1 and 2 as illustrated in Fig. 4.11. Museum abbreviations are as listed in Appendix 1.
### Appendix 2: Skulls

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**Black Rock Quarries, Tenby, Pembrokeshire**

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<tr>
<td>SK10</td>
<td>ORM</td>
<td>Q3214</td>
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<td>Not visible</td>
<td>46  40  40</td>
<td>Male</td>
<td>Adult</td>
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<td>Picken's Hole, Compton Bishop, Somerset</td>
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<td>SK11</td>
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<td>Small fragment of frontal with pedicle, no measurements possible</td>
<td>Shed</td>
<td>Concave</td>
<td></td>
<td>42  Male</td>
<td>Adult</td>
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<tr>
<td>Pin Hole, Creswell, Derbyshire</td>
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<tr>
<td>SK12</td>
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<td>Fragment of skull with fronto-parietal suture</td>
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<td>Concave</td>
<td></td>
<td>40  37  41  38</td>
<td>Male</td>
<td>Adult</td>
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<td>SK13</td>
<td>MM</td>
<td>No acc. no.</td>
<td>Fragment of frontal and parietal bones</td>
<td>Shed</td>
<td>Concave</td>
<td></td>
<td>40  37  41  38</td>
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<td>Adult</td>
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<tr>
<td>SK14</td>
<td>MM</td>
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<td>Fragment of skull with fronto-parietal suture</td>
<td>Shed</td>
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<td></td>
<td>40  37  41  38</td>
<td>Male</td>
<td>Adult</td>
<td></td>
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<tr>
<td>Sandford Hill, Mendip</td>
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<tr>
<td>SK15</td>
<td>TTNOM</td>
<td>TTNOM:209/1985/1666</td>
<td>Rear of skull with shed antler pedicles</td>
<td>Shed</td>
<td>Convex</td>
<td>Fused/simple</td>
<td>Obtuse</td>
<td>18  15  18  16</td>
<td>Juvenile</td>
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<td>SK16</td>
<td>TTNOM</td>
<td>TTNOM:209/1985/1667</td>
<td>Parietal and two fragmentary frontal bones, unshed antler spikes</td>
<td>Unshed</td>
<td>Fused/simple</td>
<td>90°</td>
<td>12  10  13  11</td>
<td>Calf</td>
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<td>SK17</td>
<td>TTNOM</td>
<td>TTNOM:209/1985/528</td>
<td>Right frontal with shed antler pedicle</td>
<td>Shed</td>
<td>Convex</td>
<td>Fused/simple</td>
<td>90°</td>
<td>18  17</td>
<td>Juvenile</td>
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<tr>
<td>SK18</td>
<td>TTNOM</td>
<td>TTNOM:209/1985/139</td>
<td>Rear of skull with unshed antlers</td>
<td>Unshed</td>
<td>Fused/simple</td>
<td>90°</td>
<td>22  22</td>
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<tr>
<td>SK19</td>
<td>TTNOM</td>
<td>TTNOM:209/1985/535/536</td>
<td>In two pieces, parietal, 2 frontals with antler spikes</td>
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<td>Unfused</td>
<td></td>
<td>11  10  12  8</td>
<td>Calf</td>
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continued over
## Appendix 2: Skulls (continued)

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<th>Ref.</th>
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<th>Accession No.</th>
<th>Description</th>
<th>Antlers</th>
<th>Scar</th>
<th>Sutures</th>
<th>P/F Suture</th>
<th>A1 L</th>
<th>A2 L</th>
<th>A1 R</th>
<th>A2 R</th>
<th>Sex</th>
<th>Age</th>
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<td>SK31</td>
<td>CUZM</td>
<td>Wr60</td>
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<td>Shed/Unshed</td>
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<td>CUZM</td>
<td>Wr61</td>
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<td>Pused/complex</td>
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<td>46</td>
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<td>SK33</td>
<td>CUZM</td>
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<td>Rear of skull with part of occipital and right frontal</td>
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<td>Convex</td>
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<td>47</td>
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<td>CUZM</td>
<td>Wr201</td>
<td>Rear of skull</td>
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Appendix 3: Mandibles/Teeth

Tooth eruption sequences and wear patterns are described for juvenile mandibles and teeth. Museum abbreviations are as listed in Appendix 1.
### Appendix 3: Mandibles/Teeth

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Museum</th>
<th>Accession no.</th>
<th>Context</th>
<th>Marked?</th>
<th>Premolars</th>
<th>Molar 1</th>
<th>Molar 2</th>
<th>Age at death</th>
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<tbody>
<tr>
<td>M1</td>
<td>BGM</td>
<td>No acc. no.</td>
<td></td>
<td>Unmarked</td>
<td>Fully erupted, light wear</td>
<td>Fully erupted, no wear on posterior cusp</td>
<td>Tooth visible in crypt</td>
<td>5 - 10 months?</td>
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<tr>
<td>M2</td>
<td>KJHLA</td>
<td>No acc. no.</td>
<td>1952 excavations</td>
<td>Unmarked</td>
<td>Fully erupted, light wear</td>
<td>Half erupted, no wear</td>
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<td>3 - 5 months</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>1951A</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>M3</td>
<td>SM</td>
<td>D2618</td>
<td>T. Tenby T. Roberts</td>
<td>Fully erupted, moderate wear</td>
<td>Almost at full height, no wear</td>
<td></td>
<td></td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>M4</td>
<td>SM</td>
<td>D2614</td>
<td>1. Black Rock Tenby T.R.</td>
<td>Fully erupted, light wear</td>
<td>Fully erupted, no wear on posterior cusp</td>
<td>Crypt formed for tooth</td>
<td>5 - 10 months?</td>
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<tr>
<td>M5</td>
<td>SM</td>
<td>No acc. no.</td>
<td>1. Tenby T.R.</td>
<td>Missing</td>
<td>Almost at full height, no wear</td>
<td></td>
<td></td>
<td>3 - 5 months</td>
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<tr>
<td>M6</td>
<td>NMS</td>
<td>No acc. no.</td>
<td></td>
<td>Unmarked</td>
<td>Dps, no wear, hollow roots</td>
<td></td>
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<td>0 - 1 week</td>
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<td>M7</td>
<td>NMS</td>
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<td></td>
<td>Unmarked</td>
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<td></td>
<td>0 - 1 week</td>
</tr>
<tr>
<td>M8</td>
<td>WM</td>
<td>No acc. no.</td>
<td>Spit All</td>
<td>Unmarked</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<tr>
<td>M46</td>
<td>WM</td>
<td>No acc. no.</td>
<td>Spit A10</td>
<td>Unmarked</td>
<td>Fully erupted, light wear</td>
<td>Missing</td>
<td></td>
<td>3 - 5 months</td>
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Continued next
### Appendix 3: Mandibles/Teeth (continued)

<table>
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<tr>
<th>Ref.</th>
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<th>Accession no.</th>
<th>Context</th>
<th>Marked?</th>
<th>Premolars</th>
<th>Molar 1</th>
<th>Molar 2</th>
<th>Age at death</th>
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<tbody>
<tr>
<td>Kent's Cavern</td>
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<tr>
<td>M9</td>
<td>TNSHM</td>
<td>No acc. no.</td>
<td>1. 6009 (60297)</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<tr>
<td>M10</td>
<td>TNSHM</td>
<td>No acc. no.</td>
<td>1. 1/2246</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, light wear on anterior cusp only</td>
<td>Crypt formed for tooth</td>
<td>5 - 10 months</td>
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<tr>
<td>M11</td>
<td>TNSHM</td>
<td>No acc. no.</td>
<td>1. K.C. 6.3.33</td>
<td>Fully erupted</td>
<td>Fully erupted, light wear</td>
<td>Tooth visible in crypt</td>
<td>5 - 10 months</td>
<td></td>
</tr>
<tr>
<td>M12</td>
<td>SM</td>
<td>X8319</td>
<td>Cave earth</td>
<td>Missing</td>
<td>Fully erupted, light wear</td>
<td>Tooth visible in crypt</td>
<td>5 - 10 months</td>
<td></td>
</tr>
<tr>
<td>Pickem's Hole</td>
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<td>M13</td>
<td>UBSS</td>
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<td>Unit 5</td>
<td>1. As acc. no.</td>
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<tr>
<td>Reindeer Cave (Inner Chamber), Inchnadamph</td>
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<tr>
<td>M14</td>
<td>NMS</td>
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<td>Top 12&quot;, 50-70' from shaft</td>
<td>Unmarked</td>
<td>Dp4, no wear, hollow roots</td>
<td></td>
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<td>0 - 1 week</td>
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<td>M15</td>
<td>NMS</td>
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<td>Top 12&quot;, 6' from shaft</td>
<td>Unmarked</td>
<td>Dp3, no wear, hollow roots</td>
<td></td>
<td></td>
<td>0 - 1 week</td>
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<td>Scree</td>
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<td>Dp4, no wear, no roots</td>
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<td></td>
<td>0 - 1 week</td>
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<tr>
<td>M17</td>
<td>NMS</td>
<td>No acc. no.</td>
<td>Scree</td>
<td>Unmarked</td>
<td>Dp2, no wear, hollow roots</td>
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<tr>
<td>M18</td>
<td>NMS</td>
<td>No acc. no.</td>
<td>Scree</td>
<td>Unmarked</td>
<td>Dp2-4, fully erupted, no wear</td>
<td>Tooth visible in crypt</td>
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<td>0 - 1 week</td>
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<tr>
<td>M19</td>
<td>NMS</td>
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<td>Scree</td>
<td>Unmarked</td>
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<td>Scree</td>
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<td>Scree</td>
<td>Unmarked</td>
<td>Dp3-4, almost at full height, no wear</td>
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<td>0 - 1 week</td>
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<table>
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<th>Premolars</th>
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<th>Age at death</th>
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<td>TTHCM</td>
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<td>Fully erupted, light wear</td>
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<td>3 - 5 months</td>
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<td>Half erupted, light wear</td>
<td></td>
<td>3 - 5 months</td>
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<td>1 S.H. B.</td>
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<tr>
<td>M27</td>
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<td></td>
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<tr>
<td>M28</td>
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<td>Fully erupted, light wear</td>
<td>Half erupted, no wear</td>
<td></td>
<td>3 - 5 months</td>
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<tr>
<td>M29</td>
<td>TTHCM</td>
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<td></td>
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<td>Missing</td>
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<td>Missing</td>
<td>Crypt formed for tooth</td>
<td>3 - 5 months</td>
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<td></td>
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<td>Missing</td>
<td></td>
<td>3 - 5 months</td>
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<td>Missing</td>
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<td>Missing</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<td>TTHCM</td>
<td>209/1989/1660</td>
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<td>1 S.H. B.</td>
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<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<tr>
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<td>209/1989/1660</td>
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<td>Tooth showing above the bone</td>
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<tr>
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<td></td>
<td>1. S.H. B.</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<td></td>
<td>1. S.H. B.</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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<tr>
<th>Ref. Museum</th>
<th>Accession no.</th>
<th>Context</th>
<th>Marked?</th>
<th>Premolars</th>
<th>Molar 1</th>
<th>Molar 2</th>
<th>Age at death</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sandford Hill, Mandip (continued)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>M40 TTNM</td>
<td>No acc. no.</td>
<td>1. S.H. B.</td>
<td>Fully erupted, moderate wear</td>
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<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
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</tr>
<tr>
<td>M41 TTNM</td>
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<td>1. S.H. B.</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, very light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
<td></td>
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<tr>
<td>M42 TTNM</td>
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<td>1. S.H. B.</td>
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<td>Missing</td>
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<td>5 - 10 months?</td>
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<tr>
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<td>Fully erupted, moderate wear</td>
<td>Missing</td>
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<td>5 - 10 months?</td>
<td></td>
</tr>
<tr>
<td>M44 TTNM</td>
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<td>Missing</td>
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<td>5 - 10 months?</td>
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</tr>
<tr>
<td>M45 TTNM</td>
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<td>Fully erupted, moderate wear</td>
<td>Missing</td>
<td>Missing</td>
<td>5 - 10 months?</td>
<td></td>
</tr>
<tr>
<td>Victoria Cave</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>M46 BMNH</td>
<td>No acc. no.</td>
<td>Tom Lord's collection</td>
<td>Unmarked</td>
<td>Dp4 fully erupted, light wear</td>
<td>Fully erupted with light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
</tr>
<tr>
<td>Wooking Role</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>M47 MH</td>
<td>No acc. no.</td>
<td>W. Boyd Dawkins collection</td>
<td>1. 1729</td>
<td>Fully erupted, heavy wear</td>
<td>Fully erupted, moderate wear</td>
<td>Half erupted</td>
<td>10 - 15 months</td>
</tr>
</tbody>
</table>
Tooth eruption sequences and wear patterns are described for juvenile maxillae and teeth. Museum abbreviations are as listed in Appendix 1.
## Appendix 4: Maxillae/Teeth

<table>
<thead>
<tr>
<th>Ref. Museum</th>
<th>Accession no.</th>
<th>Context</th>
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<th>Premolars</th>
<th>Molar 1</th>
<th>Molar 2</th>
<th>Age at death</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banwell Bone Cave</td>
<td>X1 UBB5</td>
<td>No acc. no.</td>
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<td>Missing</td>
<td>Fully erupted, moderate wear</td>
<td>Fully erupted, no wear on posterior cusp</td>
<td>5 - 10 months?</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Black Rock Quarries, Tamby</td>
<td>X2 SM</td>
<td>No acc. no.</td>
<td>Unmarked</td>
<td>Fully erupted, light wear</td>
<td>Fully erupted, no wear on posterior cusp</td>
<td>5 - 10 months?</td>
<td></td>
</tr>
<tr>
<td></td>
<td>X3 SM</td>
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<td>Fully erupted, light wear</td>
<td>Half erupted, no wear</td>
<td>3 - 5 months</td>
<td></td>
</tr>
<tr>
<td></td>
<td>X4 SM</td>
<td>No acc. no.</td>
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<td>Fully erupted, light wear</td>
<td>Almost at full height, no wear on posterior cusp</td>
<td>3 - 5 months</td>
<td></td>
</tr>
<tr>
<td>Chalk's Comb, Cheddar</td>
<td>X5 WM</td>
<td>No acc. no.</td>
<td>Spit A12</td>
<td>Unmarked</td>
<td>Fully erupted, light wear</td>
<td>Almost at full height, no wear</td>
<td>3 - 5 months</td>
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<tr>
<td>Paviland Cave</td>
<td>X6 RISW</td>
<td>Z836.6.66</td>
<td>Dillwyn and Talbot's 1823 collections</td>
<td>1. As acc. no.</td>
<td>Fully erupted, light wear</td>
<td>Almost at full height, no wear</td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>Fiddes's Hole, Compton Bishop, Somerset</td>
<td>X21 UBB5</td>
<td>No acc. no.</td>
<td>Unit 5</td>
<td>Unmarked</td>
<td>Dp2, no wear, no roots</td>
<td>0 - 1 week</td>
<td></td>
</tr>
<tr>
<td></td>
<td>X22 UBB5</td>
<td>M30.22/344</td>
<td>Unit 5</td>
<td>1. As acc. no.</td>
<td>Dp4, light wear on anterior cusp, no roots</td>
<td>0 - 1 week</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Age at death</th>
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<tr>
<td>5 - 10 months?</td>
</tr>
<tr>
<td>3 - 5 months</td>
</tr>
<tr>
<td>3 - 5 months</td>
</tr>
<tr>
<td>3 - 5 months</td>
</tr>
<tr>
<td>0 - 1 week</td>
</tr>
<tr>
<td>0 - 1 week</td>
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</table>

continued over
<table>
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<th>Accession no.</th>
<th>Context</th>
<th>Marked?</th>
<th>Premolars</th>
<th>Molar 1</th>
<th>Molar 2</th>
<th>Age at death</th>
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<tbody>
<tr>
<td>X7</td>
<td>NMS</td>
<td>No acc. no.</td>
<td></td>
<td>Unmarked</td>
<td>Dp3, no wear, no roots</td>
<td></td>
<td></td>
<td>0 - 1 week</td>
</tr>
<tr>
<td>X8</td>
<td>NMS</td>
<td>No acc. no.</td>
<td>2'-0&quot; below surface</td>
<td>Unmarked</td>
<td>Dp4, no wear, no roots</td>
<td></td>
<td></td>
<td>0 - 1 week</td>
</tr>
<tr>
<td></td>
<td>Sandford Hill, Mendip</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>X9</td>
<td>TTNM</td>
<td>209/1989/1653</td>
<td></td>
<td>1. S.H. B.</td>
<td>Fully erupted, light wear</td>
<td>Half erupted, no wear</td>
<td></td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>X10</td>
<td>TTNM</td>
<td>209/1989/1653</td>
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<td>1. S.H. B.</td>
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<td>Almost at full height, no wear</td>
<td></td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>X11</td>
<td>TTNM</td>
<td>209/1989/1653</td>
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<td>1. S.H. B.</td>
<td>Fully erupted, light wear</td>
<td>Almost at full height, light wear on anterior cusp only</td>
<td></td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>X12</td>
<td>TTNM</td>
<td>209/1989/1653</td>
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<td>1. S.H. B.</td>
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<td>Half erupted, no wear</td>
<td></td>
<td>3 - 5 months</td>
</tr>
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<td>TTNM</td>
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<td>Almost at full height, no wear</td>
<td></td>
<td>3 - 5 months</td>
</tr>
<tr>
<td>X14</td>
<td>TTNM</td>
<td>209/1989/1653</td>
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<td>1. S.H. B.</td>
<td>Fully erupted, moderate wear</td>
<td>Almost at full height, light wear on anterior cusp only</td>
<td>Tooth visible in crypt</td>
<td>3 - 5 months?</td>
</tr>
<tr>
<td>X15</td>
<td>TTNM</td>
<td>209/1989/1653</td>
<td></td>
<td>1. S.H. B.</td>
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<td>Fully erupted, light wear</td>
<td>Tooth showing above the bone</td>
<td>5 - 10 months</td>
</tr>
<tr>
<td>X16</td>
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<td>Tooth visible in crypt</td>
<td>5 - 10 months</td>
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<td>X18</td>
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<td>Fully erupted, moderate wear</td>
<td>Missing</td>
<td></td>
<td>5 - 10 months?</td>
</tr>
</tbody>
</table>

**Tormseaton Cave**

| X20  | BMNH | M26868 | Reindeer Stratum | Unmarked | Fully erupted | Almost at full height, light wear on anterior cusp only |         | 3 - 5 months |

*Appendix 4: Maxillae/Teeth (continued)*
Appendix 5: Crown heights of fourth deciduous premolars

The measurement recorded here is illustrated in Fig. 4.2.

<table>
<thead>
<tr>
<th>Ref.</th>
<th>Age</th>
<th>Posterior cusp (mm)</th>
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<tr>
<td>M6</td>
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<td>9.65</td>
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<tr>
<td>Cave No.1, Inchnadamph</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M8</td>
<td>0 - 1 week</td>
<td>10.2</td>
</tr>
<tr>
<td>M11</td>
<td>0 - 1 week</td>
<td>9.55</td>
</tr>
<tr>
<td>Ossom's Cave1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ii/iiiC</td>
<td>10 - 15 months</td>
<td>5.4</td>
</tr>
<tr>
<td>vC4'8&quot;</td>
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<td>4.8</td>
</tr>
<tr>
<td>vC4'8&quot;</td>
<td>5 - 10 months?</td>
<td>9.7</td>
</tr>
<tr>
<td>vC</td>
<td>5 - 10 months?</td>
<td>10.2</td>
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<tr>
<td>Reindeer Cave (Inner Chamber), Inchnadamph</td>
<td></td>
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</tr>
<tr>
<td>M20</td>
<td>0 - 1 week</td>
<td>10.5</td>
</tr>
<tr>
<td>M22</td>
<td>0 - 1 week</td>
<td>10.1</td>
</tr>
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<td>M23</td>
<td>0 - 1 week</td>
<td>10.25</td>
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<td>Sandford Hill, Mendip</td>
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<tr>
<td>M26</td>
<td>3 - 5 months</td>
<td>9.05</td>
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<tr>
<td>M27</td>
<td>3 - 5 months</td>
<td>9.6</td>
</tr>
<tr>
<td>M29</td>
<td>3 - 5 months</td>
<td>9.3</td>
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<tr>
<td>M32</td>
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<td>9.65</td>
</tr>
<tr>
<td>M33</td>
<td>3 - 5 months?</td>
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</tr>
<tr>
<td>M35</td>
<td>3 - 5 months?</td>
<td>8.75</td>
</tr>
<tr>
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<td>3 - 5 months?</td>
<td>8.9</td>
</tr>
<tr>
<td>M37</td>
<td>3 - 5 months?</td>
<td>9.3</td>
</tr>
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<td>M38</td>
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</tr>
<tr>
<td>M40</td>
<td>5 - 10 months</td>
<td>9.3</td>
</tr>
<tr>
<td>M41</td>
<td>5 - 10 months</td>
<td>9.75</td>
</tr>
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<td>M42</td>
<td>5 - 10 months</td>
<td>8.6</td>
</tr>
<tr>
<td>M43</td>
<td>5 - 10 months</td>
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<td>M44</td>
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<td>8.4</td>
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<td>M45</td>
<td>5 - 10 months</td>
<td>9.4</td>
</tr>
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<td>M46</td>
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</table>

1. Data from Bramwell, Scott, Stuart and Cook 1987
Appendix 6: Bone measurements

Most of the bone measurements used in this study follow the guidelines of von den Driesch (1976). These guidelines were designed to be used in the analysis of fused bones from adult animals. As the purposes of this study also required the analysis of juvenile bones, similar measures have been used to record the dimensions of these unfused specimens. The measures used are described in detail below.

As unfused bones lack epiphyses, the measurements of most juvenile bones are not directly comparable with those of fully adult specimens. In order to highlight this distinction, the measurements of juvenile bones which are recorded here are enclosed in brackets.

Direct comparisons between juvenile and adult bones are desirable, however, as they enable a more accurate assessment of growth patterns to be made. In order to make such comparisons between fused and unfused humeri a new measure has been devised. This measure records the length of the diaphysis and is illustrated overleaf (Fig A6.1).

Measurements used in this study

6a. Atlas
   GB: Greatest breadth over the wings
   GL: Greatest length
   BFcr: Greatest breadth of the cranial articular surface
   BFcd: Greatest breadth of the caudal articular surface
   GLF: Greatest length from the cranial articular surface to the caudal articular surface

6b. Axis
   LDe: Greatest length in the region of the corpus including the dens
   LAPa: Greatest length of the arch including the caudal articular process
   BFcr: Greatest breadth of the cranial articular surface
   BPac: Greatest breadth across the caudal articular process
   BPtra: Greatest breadth across the transverse processes
   SBV: Smallest breadth of the vertebra
   BFcd: Greatest breadth of the caudal articular surface
   H: Greatest height

6c. Calcaneus
   GL: Greatest length
   GB: Greatest breadth

6d. Centroquartal bone
   GB: Greatest breadth

6e. Femur
   GL: Greatest length
   GLC: Greatest length from caput
   Bp: Greatest breadth of the proximal end
   DC: Greatest depth of the caput femoris
   SD: Smallest breadth of the diaphysis
   CD: Smallest circumference of the diaphysis
   Bd: Greatest breadth of the distal end

6f. Humerus
   GL: Greatest length
   GLC: Greatest length from caput
Fig. A6.1  Length of diaphysis in humeri (DL)
6f. Humerus (continued)
Bp: Greatest breadth of proximal end
SD: Smallest breadth of diaphysis
Bd: Greatest breadth of distal end
BT: Greatest breadth of the trochlea
DL: Length of diaphysis

6g. Innominate
SB: Smallest breadth of the shaft of the ilium
GL: Greatest length of one half
LA: Length of the acetabulum including the lip

6h/i. Metapodials
GL: Greatest length
Bp: Greatest breadth of proximal end
Dp: Greatest depth of proximal end
SD: Smallest breadth of diaphysis
DD: Smallest depth of diaphysis
Bd: Greatest breadth of distal end

6j. Radius
GL: Greatest length
BP: Greatest breadth of proximal end
BFP: Greatest breadth of proximal articular surface
SD: Smallest breadth of diaphysis
Bd: Greatest breadth of distal end
BFD: Greatest breadth of distal articular surface

6k. Sacrum
GL: Greatest length on the ventral side
PL: Physiological length
GB: Greatest breadth across the wings
BFcR: Greatest breadth of the cranial articular surface
HFcR: Height of the cranial articular surface

6l. Scapula
HS: Height along the spine
DHA: Diagonal height
SLC: Smallest length of the neck
GLP: Greatest length of the glenoid process
BG: Breadth of the glenoid cavity

6m. Talus
GLI: Greatest length of the lateral half
GLm: Greatest length of the medial half
DL: Greatest depth of the lateral half
Dm: Greatest depth of the medial half

6n. Tibia
GL: Greatest length
Bp: Greatest breadth of proximal end
SD: Smallest breadth of diaphysis
CD: Smallest circumference of diaphysis
Bd: Greatest breadth of distal end
Dd: Greatest depth of distal end

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60. Ulna
GL: Greatest length
LO: Length of the olecranon
DPA: Depth across the Processus anconaeus
SDO: Smallest depth of the olecranon
BPC: Greatest breadth across the coronoid process
<table>
<thead>
<tr>
<th>Ref.</th>
<th>Accession No.</th>
<th>Marked</th>
<th>Part and condition</th>
<th>Age</th>
<th>GB</th>
<th>GL</th>
<th>BFCr</th>
<th>BFCd</th>
<th>GLF</th>
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<td>Broken on dorsal surface, in two pieces, worn</td>
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<td>57.10</td>
<td>51.15</td>
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<td></td>
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<tr>
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<td>Broken, dorsal are missing</td>
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<td>58.45</td>
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<tr>
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<td>S.H.</td>
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## Appendix 6b: Axis

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### Appendix 6: Femur

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### Appendix 6e: Femur (continued)

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### Sandford Hill, Mendip, Somerset

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### Appendix 6g: Innominate (continued)

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### Appendix 6h: Metacarpals (continued)

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<td>(135)</td>
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<td>14.00</td>
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### Appendix 61: Metatarsals

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### Pin Hole, Creswell, Derbyshire

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### Reindeer Cave, Inchnadhamph, Sutherland

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### Reindeer Cave (Inner Chamber), Inchnadhamph, Sutherland

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## Appendix 61: Metatarsals (continued)

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## Appendix 6J: Radius

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<td>Unfused</td>
<td>(114)</td>
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### Appendix 6j: Radius (continued)

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### Appendix 61: Scapula

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### Appendix 6a: Talus

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<td>L</td>
<td>Complete</td>
<td>Unfused</td>
<td>(248)</td>
<td>50.90</td>
<td>18.90</td>
<td>61</td>
<td>(35.60)</td>
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<td>L</td>
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<td>Unfused</td>
<td>(218)</td>
<td>47.65</td>
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<td>Complete</td>
<td>Unfused</td>
<td>(206)</td>
<td>43.70</td>
<td>17.95</td>
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<td>(31.40)</td>
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<td>Unfused</td>
<td>(188)</td>
<td>41.95</td>
<td>15.25</td>
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<tr>
<td>T42</td>
<td>TTNM:209/1989/1452</td>
<td>S.H. B</td>
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<td>Almost complete, both ends damaged</td>
<td>Unfused</td>
<td>20.90</td>
<td>65</td>
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<td>Unfused</td>
<td>18.60</td>
<td>59</td>
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<td>S.H. B</td>
<td>L</td>
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<td>Unfused</td>
<td>(222)</td>
<td>42.10</td>
<td>18.95</td>
<td>59</td>
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<td>T45</td>
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<td>S.H. B</td>
<td>L</td>
<td>Complete, ends worn</td>
<td>Unfused</td>
<td>15.40</td>
<td>50</td>
<td>(23.00)</td>
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Appendix 6a: Ulna

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<th>Marked</th>
<th>Side</th>
<th>Part and condition</th>
<th>Proximal epiphysis</th>
<th>GL</th>
<th>LO</th>
<th>DPA</th>
<th>SDO</th>
<th>BPC</th>
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<td>Bone Cave, Inchnadamph, Sutherland</td>
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<td>U14 No acc. no.</td>
<td>Unmarked</td>
<td>R</td>
<td>Proximal end</td>
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<td>(13.45)</td>
<td>13.80</td>
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<td>(12.00)</td>
<td>13.30</td>
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<td>Reindeer Cave (Inner Chamber), Inchnadamph, Sutherland</td>
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<td>Proximal end</td>
<td>Unfused</td>
<td>(13.70)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandford Hill, Mendip, Somerset</td>
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<td>Proximal end, gnawed</td>
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<td>36.25</td>
<td>25.15</td>
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<td>Proximal end, damaged</td>
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<td>U3 No acc. no.</td>
<td>S.H. B.</td>
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<td>Proximal end, slightly damaged</td>
<td>Unfused</td>
<td>(33.90)</td>
<td>36.15</td>
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<td>22.50</td>
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<td>65.00</td>
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<td>Pused</td>
<td>46.60</td>
<td>24.60</td>
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<td>S.H. B. Ulna</td>
<td>L</td>
<td>Proximal end, damaged</td>
<td>Unfused</td>
<td>37.60</td>
<td>23.35</td>
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<td>U10 No acc. no.</td>
<td>S.H. B.</td>
<td>R</td>
<td>Proximal end, damaged and rather worn</td>
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<td>39.40</td>
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<td>Pused</td>
<td>52.60</td>
<td>37.10</td>
<td>32.55</td>
<td>22.65</td>
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<td>U12 TTNCHM:209/1989/1650</td>
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<td>Proximal end, damaged</td>
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<td>(45.85)</td>
<td>39.20</td>
<td>35.80</td>
<td>21.05</td>
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Appendix 7: Zoological nomenclature of species referred to in text

**Mammals**

- aurochs: *Bos primigenius*
- arctic fox: *Alopex lagopus*
- arctic lemming: *Dicrostonyx torquatus*
- badger: *Meles meles*
- bank vole: *Clethrionomys glareolus*
- beaver: *Castor fiber*
- bison: *Bison priscus*
- brown bear: *Ursus arctos*
- cattle: *Bos sp*
- cave bear: *Ursus spelaeus*
- common hamster: *Cricetus cricetus*
- common vole: *Microtus arvalis*
- elk: *Alces alces*
- field vole: *Microtus agrestis*
- giant Irish deer: *Megaceros giganteus*
- hippopotamus: *Hippopotamus amphibius*
- horse: *Equus ferus*
- hyaena: *Crocuta crocuta*
- ibex: *Capra ibex*
- lion: *Panthera leo*
- lynx: *Felis lynx*
- mammoth: *Mammuthus primigenius*
- mountain hare: *Lepus timidus*
- northern vole: *Microtus oeconomus*
- Norway lemming: *Lemmus lemmus*
- otter: *Lutra lutra*
- polecat: *Mustela putorius*
- red deer: *Cervus elaphus*
- red fox: *Vulpes vulpes*
- reindeer: *Rangifer tarandus*
- roe deer: *Capreolus capreolus*
- saiga antelope: *Saiga tatarica*
- sheep: *Ovis sp*
- slender-nosed rhinoceros: *Dicerorhinus hemitoechus*
- steppe pika: *Ochotona pusilla*
- stoat: *Mustela erminea*
- straight-tusked elephant: *Palaeoloxodon antiquus*
- tundra vole: *Microtus gregalis*
- water vole: *Arvicola terrestris*
- wild pig: *Sus scrofa*
- wild cat: *Felis sylvestris*
- wolf: *Canis lupus*
- woolly rhinoceros: *Coelodonta antiquitatis*
- wolverine: *Gulo gulo*

**Birds**

- red grouse: *Lagopus lagopus*
- ptarmigan: *Lagopus mutus*
### Insects
- Warble flies: *Oedamagena tarandi*
- Nosebot flies: *Cephenomyia trompe*
- Mosquitos: *Culicidae*

### Trees and shrubs
- Ash: *Fraxinus sp*
- Aspens: *Populus sp*
- Birch: *Betula sp*
- Crowberry: *Empetrum sp*
- Docks: *Rumex sp*
- Dwarf birch: *Betula nana*
- Elm: *Ulmus sp*
- Hazel: *Corylus sp*
- Juniper: *Juniperus sp*
- Lime: *Tilia sp*
- Meadow-rue: *Thalictrum sp*
- Oak: *Quercus sp*
- Pine: *Pinus sp*
- Rock-rose: *Helianthemum sp*
- Spruce: *Picea sp*
- Willows: *Salix sp*
- Wormwoods: *Artemisia sp*


Lockwood, J. G. (1979) Water balance of Britain 50 000 yr BP to the present day. Quaternary Research, 12, 297-310.


Rutter, J. (1829) *Delineations of the North-Western Division of Somerset and of its Antediluvian Bone-Caverns.* London.


