PLEISTOCENE AND PREHISTORIC BIRDS OF SOUTH-WEST BRITAIN

by

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ABSTRACT

Recently re-examined Pleistocene bird material from south-west Britain is summarized. The sites yielding material include sixteen caves, together with an early Holocene and five Iron Age/Roman sites to complete the record into the Holocene. The area covered is from south Wales to Wiltshire, with cave sites clustered in the Gower Peninsula, Mendip and south Devon areas. The sites are roughly grouped as Late Wolstonian Glaciation, Ipswichian Interglacial, Devensian Glaciation, End of Devensian, Devensian/Holocene Transition, and Holocene. There are 136 species with a possible additional five where species-pairs cannot be separated on the specimens available. The possible significance of species occurrences is discussed within each group of sites. Comparisons are made with a list of species from the Pleistocene of south-east England. In general, in the range of species present, the variation between warmer and colder periods is less marked than might be expected. Although data are sparse, correlations between a number of sites are apparent, notably in the occurrence of grouse species and Common Shelduck.

INTRODUCTION

The records of birds occurring in Britain during the Pleistocene tend to be scattered through publications relating to specific sites. Records from sites in East Anglia and south-east England have already been summarized (Harrison, 1985). The present paper brings together lists of species identified or re-identified from sites in the south-west.

The area covered is roughly that of south Wales, Somerset, Devon and Cornwall, together with a cave in the Wye Valley, in Hereford and Worcester. Early Holocene material from a south Wales cave, and several small Iron Age sites including one in Wiltshire, together with more extensive collections from the lake villages of Meare Lake and Glastonbury in Somerset, have been included to give as comprehensive a picture as possible of the southwestern British bird fauna of the prehistoric past on the basis of osteological specimens.

The material available for study and on which this work is based is bird bones, usually individual and well-separated from any with which they might have formed the original skeleton. They have been identified by comparison with the very large range of osteological specimens in the collections of the Sub-department of Ornithology of the British Museum (Natural History) and with comparable early specimens already satisfactorily identified.

Where birds are concerned there has been a tendency to assume that it is possible to extrapolate from what is present in a region today to what should have been present during glacial or interglacial periods; and some published lists have been influenced by this. Objective identification done by direct comparison may result in the inclusion of some slightly unexpected species. These cannot be omitted merely because they appear unlikely, nor assigned to the nearest similar species, as seems sometimes to have occurred.

The use of more comprehensive comparative material has resulted in reidentifications of a number of specimens (Harrison, 1980b). Since there have clearly been errors in past works, earlier lists of birds based on material no longer available for restudy have been omitted. An example of the latter is the specimens collected by T. F. Hewer in Merlin's Cave, and identified by E. T. Newton (1925) but destroyed by wartime bombing in Bristol.

The south-east England sites, with the exception of the Ightham Fissures, are generally sands and gravels of fluvial origin and the avian remains appear to be of birds that died in watery or waterside habitats. These are natural open-air sites belonging to the Middle and Late Pleistocene. In contrast, the Pleistocene bird remains from the south-west are found in caves. This material is mostly from the latter part of the Pleistocene—the Ipswichian and Devensian.

A few species—owls, Swallow *Hirundo rustica*, Starling *Sturnus vulgaris*, Chough *P. pyrrhocorax* and Jackdaw *Corvus monedula*, for example—may have entered caves deliberately, but the majority will have been carried there by natural predators, including early man. Not surprisingly this creates a bias in the species found. In the south-eastern sites waterbirds predominate and constitute about half the species recorded (Harrison, 1985). The birds from caves also include a large number of waterbirds, mostly geese and ducks, but other groups are also strongly represented; such as the gamebirds, particularly the grouse family Tetraonidae, and the thrushes.

The present list of south-western records comprises 136 species, of which two are extinct, and the presence of inseparable species pairs makes another five possible. 75 species appear on this list only in the Devensian/Holocene transition or early Holocene. However, the list of birds from south-eastern sites (Harrison, 1985) confirms that 21 of the latter also occurred in Britain earlier in the Pleistocene and it also includes a further 13 species, of which three are extinct, that have not yet been identified from south-western sites

(see pp. 96-97 and Table II, pp. 100-102).

Most mammalian predators large enough to carry birds into caves tend to destroy bird bones, although some, such as foxes and otters, may accumulate larger bones. The other predators most likely to have carried these bird remains into caves are the Eagle Owl *Bubo bubo*, the White-tailed Eagle *Haliaeetus albicilla* and Man *Homo sapiens*. All three will take a large range of prey, from those so large that they may be difficult to carry away to quite tiny species. Other avian predators which might have played some part at times are the Barn Owl *Tyto alba*, and possibly the Tawny Owl *Strix aluco* and Long-eared Owl *Asio otus*. Most diurnal birds of prey are reluctant to enter caves, although they may nest or roost on vegetation or outcropping rocks around a cave entrance.

The dating of remains in caves has always presented a problem, and the correlation of one cave fauna with another is difficult. It has been further complicated by a change in the concept of Pleistocene climatic fluctuations. Until recently it was assumed that Britain had six successive major periods of glaciation, with intervening warm interglacials. More recent studies indicate the existence of a pattern of some seventeen glacially cold periods with intervening warmer interglacials in a Pleistocene epoch of c. 1.6 million years (Sutcliffe, 1985). The length of these periods varies but particularly in the later Pleistocene there is a pattern of c. 100,000 year stages, each consisting of an interglacial of about 10,000 years followed by a long glacial period. The pattern is thought to be continuing, with the Holocene period coincident with the milder Flandrian Interglacial.

Until new divisions and terminologies are worked out it is convenient to group these more numerous climatic fluctuations within the framework used

for the earlier six-phase concept, and to use the older names.

In the period with which we are concerned the last interglacial maximum, the Ipswichian, occurs as a well-marked warm period a little over 100,000 years b.p. (before the present); but as the cooling of the longer last glaciation, the Devensian, begins there are two further warm periods less extreme in

their amelioration than the full Ipswichian but seemingly of similar duration. There is also a briefer, and at one point very dry, warmer Windermere or Allerød Interstadial about 12,000–10,800 years b.p., in the final stages of the Devensian. During the Holocene the climate warms to its interglacial optimum, the Atlantic Period, about 7,000–5,000 b.p. and the Iron Age settlements occur in the cooler Sub-boreal period subsequent to this.

At times, more particularly in the transitional periods between glacials and interglacials, and possibly within the glacials themselves, the annual climatic pattern appears to have been closer to what we now know as the continental type. This tends to have more distinctly cold winters contrasting with shorter hot summers. This may result in periods in which winter temperatures might be consistently below those experienced at present, but where summer temperatures might be warm enough to support migrant bird species that would not be expected were one thinking in terms of the smaller annual seasonal variation now experienced in the north-west oceanic zone of Europe.

During the Pleistocene in Britain the avifauna does not differ markedly from the range of species found in north-west Europe at the present. Unlike mammals, birds need not change or adapt to changing conditions but may merely move away, very rapidly if necessary, and return equally quickly when conditions improve. As a result bird bones do not usually show significant size differences from those existing at present. While this aids species identification, it unfortunately also reduces the usefulness of birds as period and climate indicators. Sequential differences are slight or absent. Most birds recorded appear to have passed through the Pleistocene relatively unchanged. Possible exceptions are the Eagle Owl which has a more slightlybuilt form in the Cromerian Forest Bed series of eastern England (Harrison, 1979a) and may have stayed on as long as suitable prey was present and adapted to colder conditions, as suggested by an increase in size by the Hoxnian period (Harrison, 1979b); some Starlings from earlier sites which are a little larger than recent birds; and what appears to be a larger-billed form of the Red Grouse Lagopus lagopus occurring in northern England in part of the Devensian.

Climatic inferences from bird faunas must be drawn with caution. When a species such as the Ptarmigan *Lagopus mutus* occurs, it may be inferred from our knowledge that it does not move far annually, that conditions were colder than at present and almost certainly produced tundra-like conditions on higher ground. However, many of the species identified migrate, sometimes between the Arctic and the Tropics. Their presence gives little indication of the climate at the time. The number of bird species usable as climatic indicators is therefore limited, but the combination of species present in a locality may be an indication of some of the types of habitat present, and hence of the climate in general.

SITES AND FAUNAS

The 22 sites have been grouped (both in the text and in Table II on pp. 99–102) in a rough sequence which might segregate possible patterns of occurrence. Because of the changing views and new data on Pleistocene climate mentioned earlier, there may be some measure of doubt in attributing sites to particular climatic stages, and the earlier broad Pleistocene subdivisions have been used here. The deposits in some caves span several successive stages, and in order to fit them into this pattern some sites, such as Tornewton Cave, Gough's Cave and Soldier's Hole, occur at more than one place in the tabulated sequence.

Within the time range of the sites it has been possible to recognize the later warming stages of a glacial period, thought to be Wolstonian, and only represented here at Tornewton Cave, Devon. This is followed by the warm Ipswichian Interglacial, evidence for which is found at Tornewton and in certain caves of the Gower Peninsula. There is a subsequent colder period, apparently assignable to the Devensian Glaciation, with rather scanty material from a number of caves.

Towards the end of the Devensian, Gough's Cave and Soldier's Hole at Cheddar yield a more abundant and varied fauna, some species of which are associated with the presence of trees. Since some of this material is dated at about 12,000 b.p., it is presumably linked with the Windermere Interstadial, just before the end of the Devensian; while the material from Chelm's Combe and from Bridged Pot in Ebbor Gorge appears to date partly from the relatively short cold period of the Loch Lomond Readvance between the interstadial and the end of the Devensian.

Finally there are several sites, with Chudleigh Fissure in particular, yielding material which appears to be possibly Holocene in origin, but which also contain species indicative of an avifauna of an earlier cooler period. In the adopted sequence this is grouped at the end of the Devensian as 'transitional'. To complete the sequence and to provide a link with the recent avifauna, several south-western Holocene sites have been included. The Port Eynon Cave in south Wales is interesting in being the only site from the early Holocene prior to the final rise in sea-level and in being apparently unoccupied by man. The remainder are mostly Iron Age. In the final column of Table II indication is given of the Pleistocene periods in which some of the listed species have been identified in south-eastern England.

It is obvious from these comments that there are problems in the dating of various sites and strata. In some instances this has been made more difficult by the collecting methods of the last century and the early part of the present century, which did not usually discriminate carefully between the beds in which various species might occur. There may well be a need for later amendments, but the intention has been to provide some general basis and background to aid the study of Pleistocene birds, and hopefully to provide a framework into which subsequent avifaunal data can be inserted.

Wolstonian Glaciation

Tornewton Cave (1). (T1 in Table II. Sutcliffe and Zeuner, 1962; Sutcliffe and Kowalski, 1976; Harrison, 1980a)

This is one of a series of caves in the limestone on the west side of Torbryan Valley in south Devon, south-east of Dartmoor and about 10 km inland.

There is a series of three early stages in the cave that have been attributed to the later stages of the Wolstonian Glaciation, during the period of climatic amelioration leading up to the Ipswichian Interglacial. At the base of the sequence the Glutton Stratum contains evidence of severe frost conditions at times, while the overlying Bear Stratum shows evidence of warmer conditions. The stratigraphically related Otter Stratum, which is restricted to a small side chamber of the main cave, appears to show a mixture of terminal Wolstonian and early Ipswichian species.

The above climatic inferences are based on sediment and stalagmite material, and on the associated mammal fauna. Through most of the period Brown Bear *Ursus arctos* is the principal inhabitant. In the earliest stratum, Glutton or Wolverine *Gulo gulo* and the Reindeer *Rangifer tarandus* occur together with two tundra lemming species, the Common Hamster *Cricetus*

cricetus and Steppe Lemming Lagurus lagurus, which tended to occur in the past in colder, arid steppe conditions. The Otter Stratum has the extinct Clawless Otter Cyrnaonyx antiqua and the White-toothed Shrew Crocidura suaveolens, both indicating warmer conditions.

All three strata have a stork which appears to be the White Stork *Ciconia ciconia* rather than the Black Stork *C. nigra*. This is surprising for a relatively cold period and, assuming that the species was affected by the factors which appear to govern its distribution today, this would appear to indicate a continental-type climate with a summer temperature of c. 16.7°C.

Brent Goose *Branta bernicla* in the Otter Stratum and Goosander *Mergus merganser* in both Glutton and Otter Strata indicate little other than tundra to boreal breeding conditions or temperate wintering conditions. The Common Shelduck *Tadorna tadorna*, which at the present day is resident in the British Isles and a summer breeder north to the Arctic Circle on Scandinavian coasts, is present in all these strata. It would appear to indicate that either estuarine conditions or saline lagoons were present on that part of the south Devon coast.

The White-tailed Eagle *Haliaeetus albicilla*, for which there is evidence in the Bear Stratum, was probably the shelduck predator. The large northern form of the Eagle Owl *Bubo bubo* is present in the Glutton Stratum, and also the Kestrel *Falco tinnunculus* that may have been a summer visitor if conditions were cold.

There are two problem species. One is a crossbill of the size of the Common Crossbill *Loxia curvirostra* in the Glutton Stratum. One cannot be certain whether the Scottish Crossbill *L. scotica* or Parrot Crossbill *L. ptyoptsittacus*, that evolved as Scots Pine specialists in Scotland and northern Scandinavia respectively, had differentiated at this time. However, the important point is that the species is linked with the presence of conebearing conifers. The suggested tundra/steppe habitat would not provide these.

The other species is a small *Alectoris* partridge. This genus comprises birds occupying mainly montane habitats in warmer climates and undergoing speciation in isolation. The nearest extant species—the Redlegged Partridge *A. rufa*—of France and Spain has been introduced into Britain with limited success, preferring a warm temperate climate. The specimen from the Glutton Stratum is of a smaller bird apparently occupying a cold tundra and steppe environment, and it has therefore been treated as a new separate species—the Western Partridge *Alectoris sutcliffei*.

The remaining species are corvids. The Raven *Corvus corax* occurs in the Glutton Stratum, and in the Bear Stratum there is a crow. It is difficult to separate the Carrion Crow *Corvus corone* and the Rook *Corvus frugilegus* on any bones except the skull. Examination of a larger sample of recent specimens suggests that some criteria used for earlier separations may be invalid. However, since the Rook is basically a bird of temperate grassland and forest clearings, nesting in groups of trees, the former is the more likely species at this stage in the Pleistocene.

Ipswichian Interglacial

Evidence within the south-west for this principal warm period of the Late Pleistocene comes from three localities. There are two adjacent cave sites on the south side of the Gower Peninsula in south Wales—Bacon Hole and Minchin Hole—and in south Devon there is a stratum in Tornewton Cave. *Bacon Hole*. (B in Table II. Stringer, 1975, 1977; Stringer *et al.*, 1986: Harrison, 1977).

Minchin Hole. (M in Table II. Sutcliffe and Bowen, 1973; Sutcliffe, 1981; Sutcliffe and Currant, 1984; Harrison, 1977)

These are two shallow coastal caves, a short distance apart on the south side of the Gower Peninsula, West Glamorgan, Wales. The deposits in both caves are rich in mammal remains but have yielded relatively few bird bones. It has been possible to differentiate a long sequence of deposits including fossiliferous horizons representing the Ipswichian Interglacial with cooler places towards the beginning and end, plus one of the colder periods of the subsequent Devensian. No bird bones are at present available for the last stage. During the Ipswichian these were coastal caves, but would have been fronted by dry land during glacial periods.

Tornewton Cave (2). (T2 in TABLE II. See p. 84 for references)

In this south Devon cave there is a distinct stratum indicating a warm interglacial period. It is called the Hyaena Stratum after the numerous remains of Spotted Hyaena *Crocuta crocuta* that appears to have been the principal species inhabiting the cave during this period.

Discussion

Bacon Hole offers the most interesting instance in this region of the potential effect of an interglacial on the regional bird fauna. There are two seabird species that, from the evidence of incompletely ossified and seemingly juvenile bones, appear to have used the cave for breeding at this period.

The Razorbill Alca torda is a crevice-nesting auk using the cave for breeding and one that might be expected to be occupying the same site at the present time were there less human activity. Briefly during the warmest period it appears to have been replaced by Cory's Shearwater Calonectris diomedea. This species now breeds on Atlantic islands from the Cape Verdes to Madeira, and in the Mediterranean. Birds may wander as far north as the British Isles outside the breeding season, but its presence as a breeding bird in this Welsh cave represents a conspicuous temporary northward shift of range.

In addition the cave provides in its warmer period evidence of an early Red Kite *Milvus milvus*. Dunlin *Calidris alpina* and Turnstone *Arenaria interpres*, probably from the shoreline, give little environmental information; but a combination of Skylark *Alauda arvensis*, Starling *Sturnus vulgaris* and Wheatear *Oenanthe oenanthe* suggest open grassy conditions nearby. The Starling may have used the cave for nesting; and the Swallow *Hirundo rustica* also occurs, with some of its bone fragments poorly ossified and suggesting that it too nested there. There are also two species representing birds from the pairs of apparently osteologically inseparable Blackbird/Ring Ousel *Turdus merula/torquatus*, and Crow/Rook.

In the cooling period towards the end of this interglacial other species occur, together with the Starling. The Hobby *Falco subbuteo* may have bred locally as a summer visitor; but Bean Goose *Anser fabalis* and Golden Plover *Pluvialis apricaria* were probably wintering birds from further north, both likely to require open, short-grass areas.

Minchin Hole birds confirm Razorbill, Dunlin, Skylark and Starling for

the period generally, but do not add other species.

The Hyaena Stratum at Tornewton shares with its preceding cooler stages of the terminal Wolstonian the Kestrel, Starling and Raven; and among the waterfowl, Brent Goose and Common Shelduck. In addition the Hyaena Stratum has a Ruddy Shelduck *Tadorna ferruginea*, which is the first good evidence of this steppe species. In general steppe species are absent in the south-west but there appears to have been an assumption that they should

be present, which may have led to many Common Shelduck bones being

originally identified as Ruddy Shelduck (Lydekker, 1891).

The Wigeon Anas penelope is present and, like the Brent Goose and Common Shelduck, might have existed on shore or estuarine mudflats. The only additional passerine species is the Tree Pipit Anthus trivialis. If this were breeding it would imply the presence of some trees or tall scattered scrub. In general, apart from the Hobby and Rook at Bacon Hole, there is little evidence in this Ipswichian assemblage of species that might require trees, as opposed to those of more open, grassy places.

Devensian Glaciation

There are relatively few sites that appear to date from the colder periods of the last major glaciation and which contain much in the way of bird remains. Most of the species involved are those breeding in tundra or arctictype conditions, but some are more typical of boreal conditions such as occur at the present day in Scandinavia north to the tundra edge.

Soldier's Hole (1).(S1 in Table II. Parry, 1929, 1931; Bramwell, 1960; Harrison, in press)

This is a large cave-shelter high on the side of the Cheddar Gorge in the Mendip hills of Somerset. Bird remains occur in many of the layers excavated. The earliest layers, spits 21-11, appear to be Early to Middle Devensian, with spits 15-12 dated at c. 50,000-30,000 b.p.

Tornewton Cave (3). (T3 in TABLE II. See p. 84 for references)

There are two strata of a later cold period. The Reindeer Stratum is named after the species which represents the bulk of the remains present. These indicate a summer presence only, and hence tundra conditions. The 'Eboulis' layer is a later one which might possibly relate to the final, Loch Lomond Advance, stage of the Devensian, in which case the 'Diluvium' of the cave would represent the Windermere Interstadial, or it may be an earlier cold period. Since it involves only a single, cold-climate species it has been included here.

Kent's Cavern. (K in Table II. Kennard, 1945, 46; Campbell and Simpson, 1971; Harrison, 1980b)

A cave near Torquay, south Devon. Bird bones occur in the Cave Earth layer which also contains remains of cold-period mammals such as Mammoth Mammuthus primigenius and Woolly Rhinoceros Coelodonta antiquitatis. Only three bird species have been found.

Cat's Hole or Cathole Cave. (C in Table II. Allen and Rutter, 1948)

This is a small cave on the Gower Peninsula, south Wales. Two bird species occur with mammal remains of cold Pleistocene faunas as at Kent's Cavern.

Brixham Cave or Windmill Hill Cave. (W in Table II. Prestwich, 1874; Harrison, 1980a)

This cave is on a hillside bordering the coast at Torbay, south Devon. Although the two bird species are from the Middle Devensian they suggest a more temperate or boreal climate and may have originated in interstadial conditions.

Discussion

Most of the birds recorded from these caves are non-passerine. Pelecaniform birds are relatively infrequent in caves, and the Shag *Phalacrocorax* aristotelis at Kent's Cavern seems to be the only southern Pleistocene record. Cold-climate tundra-breeding swans and geese are represented by Bewick's Swan Cygnus bewickii from Cat's Hole and the White-fronted Goose Anser albifrons from Kent's Cavern and Soldier's Hole. The Greylag Goose Anser anser of Soldier's Hole and the Teal Anas crecca from Tornewton Cave Reindeer Stratum breed from the temperate zone to the southern borders of the tundra; but the Common Shelduck from Brixham Cave would require milder conditions no worse than a south-boreal summer with warm coastal currents.

Raptors are poorly represented. The White-tailed Eagle is present at both Soldier's Hole and Cat's Hole; and, although the Rough-legged Buzzard Buteo lagopus and Common Buzzard B. buteo are difficult and sometimes impossible to separate osteologically, the bird from Brixham Cave appears to be a small male, more probably of the latter species, and if so suggests

more temperate and possibly forested conditions.

The Ptarmigan, present at Soldier's Hole and in both the Reindeer Stratum and 'Eboulis' at Tornewton Cave, is a definite indicator of cold tundra-type conditions on high ground at least. Willow/Red Grouse Lagopus lagopus also occurs in the Reindeer Stratum. The occurrence of the Little Bustard Otis tetrax in the Reindeer Stratum at Tornewton is surprising. This is a species nesting in open grassland of the warmer parts of the temperate zone. Since it is migratory towards its northern limit it might represent a stray bird that had disastrously overshot its intended goal and fallen prey to a cave-dwelling predator, or suggest some admixture of strata.

The Long-tailed Skua Stercorarius longicaudus from Soldier's Hole is a migrant species breeding on higher, drier tundra and cold rocky plateaux and moorland. The Kittiwake Rissa tridactyla from the same cave is also a cold-climate breeder but is a small marine gull nesting on rocky shores and unexpected inland. The Snowy Owl Nyctea scandiaca occurs at Kent's Cavern. Although this is a species that must have been widespread and probably common in tundra conditions throughout the glacial periods, this is the only record of it from southern Britain in the Pleistocene. Presumably it was a bird unlikely to be predated by mammals or other large birds and carried into caves which, as an open tundra nester, it would not have entered of its own accord. However it appears to have been slaughtered extensively by cave-dwelling humans in France (Mourer-Chauviré, 1983).

The passerine species are all from the Reindeer Stratum at Tornewton Cave and include Skylark, Fieldfare *Turdus pilaris*, Starling, and Crow or Rook. Of these the Skylark would require open grassy areas. The Starling might feed in such areas but could nest in rocks or caves, and the Fieldfare will also feed in open grassy areas when not breeding, but requires trees or scrub of some kind in which to nest. The Crow is more likely than the Rook at this period and might nest on a rock ledge if a tree were not available.

End of Devensian

This period includes the final stages of the glaciation during which the climate warms to the Windermere Interstadial from c. 13,000-10,800 b.p. There is some evidence of woodland—Birch, Hazel and Alder—during the interstadial (Leroi-Gourhan, 1986) but it became arid and grassy towards its warmest middle period. There is a subsequent short, sharp cold stage to about 10,250 b.p. before the final amelioration. The range of species is more numerous and more varied. The bird faunas from the sites listed show a mixture of species, with some indicating evidence of a cooler climate and

others more typical of temperate conditions which were presumably typical of the interstadial.

Gough's Cave (1). (G1 in Table II. Jacobi, 1986; Harrison, 1980b, 1986)

This is one of the larger caves of Cheddar Gorge, Somerset; showing evidence of human occupation. The majority of birds from spits 19-11 date from about 12,000 b.p., during the interstadial, when man was also present.

Soldier's Hole (2). (S2 in TABLE II. See p. 87 for references)

The richer fauna from this cave shelter occurs during this later period, in spits 10-3, and ranges from tundra-type to woodland and grassland species.

Chelm's Combe Rock Shelter. (CC in Table II. Jackson, 1927)

This was a large rock-shelter high on the side of the Mendips near the entrance to Cheddar Gorge. It has recently been destroyed by quarrying. The material collected from it appears to date from the end of the Devensian, in the short cold Loch Lomond Readvance stage following the Windermere Interstadial.

Bridged Pot Cave Shelter. (E in Table II. Balch, 1928)

This is a cave shelter high on the side of Ebbor Gorge, Mendips. It has yielded a very small avifauna apparently dating from a similar period to that from Chelm's Combe. In both, the small number of species show evidence of both colder and more temperate climates, but on the basis of the present list the Chelm's Combe birds indicate rather colder conditions.

Discussion

The Whooper Swan from Gough's Cave is a boreal nester wintering further south; while Mallard *Anas platyrhynchos*, Teal and Wigeon from Soldier's Hole might breed or winter in both boreal and more temperate conditions. The Barnacle Goose *Branta leucopsis* from Chelm's Combe, and the Smew *Mergus albellus* from the Bridged Pot Cave-shelter, probably occurring in the colder terminal Devensian conditions, are respectively an arctic nester on rocky cliffs and a boreal forest nester using tree-holes.

Raptors are few but falcons better represented than usual. White-tailed Eagle is present at Soldier's Hole; Gough's Cave has a Peregrine Falcon Falco peregrinus possibly owing its presence there to human activity; Soldier's Hole also has a Merlin F. columbarius, a small moorland falcon; while

Chelm's Combe has the Kestrel more typical of cave sites.

Soldier's Hole has a full range of gamebirds. These include the Ptarmigan of tundra-type high ground, the Willow/Red Grouse of Willow and Birch scrub or Heather, the boreal woodland-edge Black Grouse *Lyrurus tetrix*, the woodland Hazelhen *Tetrastes bonasia* and the temperate grassland Common Partridge *Perdix perdix*. Gough's Cave has only the first two; the Bridged Pot Cave Shelter has all except the Black Grouse, while Chelm's Combe lacks both Black Grouse and Common Partridge. If these species were occurring serially they would indicate a gradual change in habitat with time, but if they were co-extant, as an alternative interpretation could suggest, then the nearest environmental equivalent would be that of the Scottish Cairngorms or southern Norway and Sweden at the present day.

The Black-tailed Godwit *Limosa limosa* at Soldier's Hole suggests moist grassland nearby, presumably on the lower ground now occupied by the levels, where the ducks are also likely to have occurred. The Barnacle Goose at Chelm's Combe mentioned earlier might have nested in the area, but the Little Auks *Alle alle* from the same cave are small marine birds nesting on coastal arctic screes, and their occurrence this far inland at a time when the

coastline was much further away is more likely to be the result of exhausted birds being driven inland in one of the intermittent 'wrecks' that this species suffers in stormy winters.

The probably cave-nesting Rock Dove *Columba livia* occurs at Soldier's Hole. The Stock Dove from Gough's Cave is a tree-hole or rock-crevice nester. Both indicate temperate conditions. The Long-eared Owl *Asio otus* and Short-eared Owl *Asio flammeus* of Soldier's Hole do not hunt in caves and were most probably brought in as prey by a predator such as the Eagle Owl, which is also recorded in the later part of this period from Chelm's Combe. The Long-eared Owl is a woodland species, and the Short-eared

Owl occurs in open, moorland-type habitats.

Of the passerines from these sites the Snow Bunting *Plectrophenax nivalis* from Soldier's Hole might have inhabited higher and colder ground with the Ptarmigan, as in the Cairngorms at present. The Skylark at Bridged Pot would need an open grassy space, probably replacing forest in the colder final phase; but the Song Thrush *Turdus philomelos* from Chelm's Combe as well as Soldier's Hole is a woodland species. Of other thrushes the Blackbird/Ring Ousels from Gough's Cave, Soldier's Hole and Chelm's Combe present a species pair problem, indicating either scrub and woodland or open rocky areas. The Fieldfares of Gough's Cave and Soldier's Hole might have been winter visitors to a warmer climate, but their relative abundance at the latter site together with the range of species present raises the possibility that they might have been nesting colonially in scrub or woodland.

The Dunnock *Prunella modularis* at Soldier's Hole is another species that would have required scrub or woodland. The same site yields two corvids not recorded from earlier strata in southern Britain—the tree-nesting Magpie *Pica pica*, and the hole-nesting Jackdaw *Corvus monedula* which is a bird of temperate to warm-temperate zones.

Transitional

This group of sites contains those where problems of stratification or more casual early collecting may have resulted in inadequate data for dating; and where there appears to be an admixture of Late Devensian and Early Holocene material. To some extent it may overlap with the previous group and it is possible that some of the bird species that prefer temperate conditions may have originated in the Windermere Interstadial rather than the post-glacial/Holocene transition.

Torbryan Caves. (Tb in Table II. Sutcliffe and Zeuner, 1962; Walker and Sutcliffe, 1967; Harrison, 1980b)

This is a series of caves in the Torbryan Valley, about 10 km inland from Torquay, south Devon; and it includes Tornewton Cave which has otherwise been treated separately. The present material lacks data other than the fact that it originated from the caves as a group. It appears from its condition to have come from the upper and more superficial deposits. The number of temperate species involved make it reasonable to include it here.

Merlin's Cave. (M in Table II. Bate, 1901; Hewer, 1925; Harrison, 1980b)

This is a cave in the limestone of the Wye Valley, near Symond's Yat, Hereford and Worcester. Bate originally called it 'Wye Valley Cave'. Mammal remains date from the end of the Devensian and the bird fauna is boreal in character.

Neale's Cave, (N in TABLE II)

This is a small cave near the coast at Paignton, south Devon. Its lower layers, 2 and 3, were thought to date from the very early Holocene, but the presence of Reindeer among the mammals suggests that in part at least it dates from the transition from the Devensian.

Happaway Cave. (H in Table II. Cullingford, 1953; Sutcliffe and Kowalski, 1976; Harrison, 1980a)

This is a cave near Torquay. It contains birds, mammal and human remains; and the material appears to be of very late Pleistocene and post-Pleistocene origin.

Chudleigh Fissure. (Ch in Table II. Bell, 1915, 1922; Newton, 1923; Harrison, 1980b)

This is a fissure cave at Chudleigh, south Devon, the exact site of which is no longer known. Both Late Pleistocene and Holocene material occur in the cave. The long list of bird species might be suspected to be of recent origin, but includes species such as Ptarmigan and Hazelhen, indicating that some are of early, possibly terminal Devensian, origin.

Discussion

The Sooty Shearwater *Puffinus griseus* at Happaway Cave is a relatively complete skeleton of a migrant seabird that breeds in the southern hemisphere and would not normally come ashore here. Its presence in the cave suggests that it was carried in and then discarded, possibly by human hand. A Common Shelduck was present at Torbryan and at Neale's Cave; while Mallard is found at all except Happaway Cave.

The Goshawk Accipiter gentilis at Happaway is the earliest southern British record of the species; as is the Sparrowhawk A. nisus at Chudleigh, which was originally thought to be evidence of an early Little Owl Athene noctua

(Newton, 1923). Chudleigh also has a Kestrel.

The usual gamebirds are present. The cold-climate Ptarmigan occurs at Merlin's Cave, Torbryan and Chudleigh, and the Willow/Red Grouse at all except Neale's Cave. Chudleigh also has Hazelhen and Common Partridge, while Torbryan boasts the only Common Quail Coturnix coturnix, a temperate-zone nesting migrant. Common Snipe G. gallinago at Chudleigh and Jack Snipe Lymnocryptes minimus at Torbryan are also single records.

The Black Guillemot Cepphus grylle at Chudleigh is south of its present normal range and might relate to a colder Devensian period; and the same is true of the Shorelark Eremophila alpestris which as a present-day winter visitor is usually confined to the east coast, but might have nested on tundratype high ground in the colder period. However, the Woodpigeon Columba palumbus and Stock Dove from the same site relate to warmer climates and woodland habitats. The Rock Dove occurs at Neale's Cave.

The Barn Owl at Chudleigh may provide a clue to the origin of the large diversity of small passerine species occurring there. The only other owl from this group of sites is the Tawny Owl *Strix aluco*, a woodland species with its earliest southern British record from Happaway Cave where it may have been early Holocene rather than Late Pleistocene.

Among the passerines the Crested Lark Galerida cristata occurs at Torbryan and Chudleigh caves, and in south-eastern England (Harrison, 1985) is known from Ightham Fissures in north Kent during the Transitional period. It is a continental species which may indicate a continental-type climate at the end of the Devensian or in the Windermere Interstadial. Other species of open grassland-type habitats are Skylarks at Torbryan and

Chudleigh; Meadow Pipit Anthus pratensis from Neale's Cave; and a number of wagtails, pipits, and the osteologically inseparable Stonechat/Whinchat

Saxicola torquata/rubetra from Chudleigh.

The Swallow occurs at Torbryan, and the Robin *Erithacus rubecula* at Torbryan and Chudleigh. Thrushes are well represented. Blackbird/Ring Ousel is recorded for all five sites, Mistle Thrush *Turdus viscivorus* from Torbryan, Happaway and Chudleigh; and of the northern thrushes Fieldfare at Torbryan and Chudleigh, and Redwing *Turdus iliacus* at Neale's, Happaway and Chudleigh Caves. The woodland Song Thrush occurs at all except Merlin's Cave and Neale's Cave; but the latter has another woodland bird, the Blackcap *Sylvia atricapilla*, the only warbler so far identified from this area.

In addition to the above Chudleigh also has Dipper Cinclus cinclus, Wren Troglodytes troglodytes, Common Redstart Phoenicurus phoenicurus, Nightingale Luscinia megarhyncha, tits Parus species, Nuthatch Sitta europaea and buntings. Most of these would form a temperate Holocene fauna; but two possible exceptions are the Lapland Bunting Calcarius lapponicus and Snow Bunting Plectrophenax nivalis which are Arctic-breeding species that, like the Ptarmigan and Shorelark mentioned earlier, might relate to a colder part of the Devensian.

Among the finches there is a boreal, conifer-forest element, with Common Crossbill at Merlin's Cave and Pine Grosbeak *Pinicola enucleator* at Merlin's Cave and Torbryan. The temperate-zone Hawfinch *Coccothraustes coccothraustes* occurs at Torbryan, Happaway and Chudleigh, together with Goldfinch *Carduelis carduelis* and Linnet *Acanthis cannabina* at the last site.

The House Sparrow *Passer domesticus* is late in appearance, with first records at Merlin's Cave and Chudleigh; while the Starling is present at the last two sites and at Torbryan Caves. Among the corvids the woodland Jay *Garrulus glandarius* is present at Torbryan, Merlin's Cave and Chudleigh, as is the Jackdaw; while Crow or Rook occurs at Happaway Cave, and Raven at both Happaway and Torbryan Caves.

Holocene

Records of birds from the prehistoric and early historic periods of the Holocene are usually based on bone fragments similar to those of Pleistocene birds, and hence are often treated as subfossil. As past information they tend to fall into a gap between palaeo-ornithology and recent ornithology and to be lost in broader-based archaeological studies. A number of such records, which have been examined during the course of this work have therefore been included here where they round off, albeit rather patchily, the picture of early bird life in south-west Britain.

Port Eynon Cave. (P in Table II)

This is a sea-cliff cave on the Gower Peninsula, South Wales. It is exceptional in that the bird and mammal bones found in it appear to date from c. 9,000-6,000 b.p., prior to the final rise in sea level and the climatic optimum; and in that there is no evidence of human use or occupation.

Glastonbury Lake Settlement. (G1 in Table II. Andrews, 1899; Bulleid and Gray, 1911-1917; Harrison, 1980b)

The Iron Age lake settlement at Glastonbury in the Somerset levels provides an assemblage of bird material used largely for food and limited to larger and mainly non-passerine species. Only those specimens for which the identification has recently been checked have been included here.

Meare Lake Settlement, (ML in TABLE II)

This is another Iron Age lake settlement in the Somerset levels yielding a similar range of species to those found at Glastonbury. The recently identified specimens were collected in 1936–1937, and the list given here is limited to these.

Soldier's Hole (3). (S3 in Table II. See p. 87 for references)

There are a few specimens from spit 2 which are thought to date from Holocene times.

Gough's Cave (2). (G2 in TABLE II. See p. 89 for references)

The upper spits, 9-1, show evidence of Iron Age/Roman occupation and the species in them are thought to date from about this period. The presence of Barn Owl and possible prey suggests that occupation of the cave by man may have been intermittent.

Woodbury Settlement. (WS in Table II. Harrison, 1980b)

This is an Iron Age site at Woodbury, Devon.

Hanging Langford Camp. (HL in TABLE II. Harrison, 1980b)

This is an early Iron Age site at Wylve, Wiltshire.

Hucclecote Roman Villa. (Hc in TABLE II. Harrison, 1980b)

This was a villa on the Ermin Way (now A417) just south-east of Gloucester. It has yielded two wild species in addition to domesticated forms of the Greylag Goose and Fowl.

Major Park Roman Villa. (MP in TABLE II. Harrison, 1980b)

This was a villa at Camborne, Cornwall.

Discussion

Although lacking the human hunting which presumably produced the large range of species at the marsh and freshwater sites at Glastonbury and Meare Lake, Port Eynon Cave on a rocky coast has a similar range produced by natural predators. It includes many seabirds and waterfowl presumably either taken at the water's edge by mammalian predators, or possibly off the sea itself by the White-tailed Eagle that was present.

All three divers were present, the Great Northern Diver *Gavia immer* and Red-throated Diver *G. stellata* at Meare Lake, and the Black-throated Diver *G. arctica* at Port Eynon. All were likely to have been winter visitors. Surprisingly the Dabchick *Tachybaptus ruficollis* from Meare Lake is the only grebe in these records from southern Britain. It was originally also listed from Glastonbury (Andrews, 1899) but the specimen has not been recently re-traced. The Manx Shearwater *Puffinus puffinus* now breeding on islands of western Britain occurs at Port Eynon Cave, and is another untraced specimen listed for Glastonbury by Andrews.

Among the pelecaniform birds the Gannet Morus bassanus is another British breeding seabird occurring at Port Eynon Cave. The Shag Phalacrocorax aristotelis also occurs at this site and incompletely ossified bones suggest that it bred nearby. The Cormorant Phalacrocorax carbo which also uses fresh water is absent from here, but recorded from both Glastonbury and Meare Lake.

However, the most interesting species of this group is the Dalmatian Pelican *Pelecanus crispus*. Glastonbury yields remains of this species indicating that it bred nearby. The bird nests in large colonies on isolated sites in large marshy areas but is intolerant of human disturbance and liable to desert the

colony even when there are young. It is probably this, rather than other changes, which has by now driven it right back to a small population in south-eastern Europe that is the nearest to us today.

Evidence of the heron family, Ardeidae, is scarce in these early avifaunas of south-western Britain. Grey Heron *Ardea cinerea* occurs at Meare Lake; and the Bittern *Botaurus stellaris* at Glastonbury where it may, together with species such as the Marsh Harrier *Circus aeruginosus* which occurs at both sites, be indicative of fen conditions with extensive reedbeds.

The Mute Swan *Cygnus olor* at Glastonbury might have been resident, but the Whooper Swan from Meare Lake was probably a winter visitor, as also would have been the White-fronted Goose and Barnacle Goose at both Meare Lake and Port Eynon.

The Mallard is the most widespread of the dabbling ducks present at Port Eynon Cave, Meare Lake and Glastonbury lake settlements, Gough's Cave and the Woodbury settlement. Wigeon is present at the first three; and Pintail Anas acuta at Meare Lake and Glastonbury. Meare Lake also has Gadwall Anas strepera, Garganey A. querquedula and Shoveler A. clypeata—all ducks of warmer temperate conditions. The Teal is unexpectedly not recorded.

The freshwater diving ducks Pochard Aythya marila and Tufted Duck A. fuligula are present at both Meare Lake and Glastonbury, and the Goldeneye Bucephala clangula at the former; while Port Eynon has the saltwater Long-tailed Duck Clangula hyemalis, Common Scoter Melanitta nigra and Velvet Scoter M. fusca, and the coastal Common Shelduck. Of the saw-billed ducks the Smew is present at both Port Eynon and the lake settlements, with Red-breasted Merganser Mergus serrator and Gooseander M. merganser only at Meare Lake.

Although in the south-west eleven of these duck species are identified only from the Holocene, eight of them also occur in the Middle Pleistocene of south-eastern England.

As already mentioned, Marsh Harrier occurs at Meare Lake and Glastonbury; and other raptors are White-tailed Eagle at Glastonbury and Port Eynon Cave, a smallish buzzard (probably Common rather than Roughlegged Buzzard and possibly juvenile) at Meare Lake, and Sparrowhawks at Port Eynon Cave and Soldier's Hole. A Peregrine at Port Eynon Cave is the only falcon.

Apart from a Black Grouse at Soldier's Hole gamebirds are surprisingly few; but the problem of the Junglefowl *Gallus gallus/europaeus* arises. Bones of the fowl have been found in a number of caves, usually where stratification was incompletely recorded, and are usually dismissed as those of later domesticated birds. This had occurred at Happaway Cave and Chudleigh Fissure in the Transitional list here, and at Gough's Cave in this Holocene list.

This fowl is usually assumed to be the domesticated form of the Red Junglefowl *G. gallus* originating in northern India and spreading westwards with early human cultures. It is thought to have arrived in Britain just before Roman times. There is evidence from Roman sites of domesticated birds varying considerably in size and usually much larger than the wild form. Where such large bones are found in British sites it is reasonable to suspect that domesticated birds of this type were involved.

However smaller bones may present problems, for in eastern England bones apparently referable to *Gallus* were found in the Cromerian and Ipswichian Interglacials, with no evidence of human association. They have been assigned to a new extinct species, the European Junglefowl *G. europaeus*

(Harrison, 1978). In general size it was close to the wild Red Junglefowl. Some of the bones found in Devensian caves could have belonged to such a bird. A bone from Port Eynon Cave is also of this size and from a 9,000-6,000 year old site. Bones from Meare Lake are mostly of this size, with two leg bones very slightly larger.

When the European Junglefowl was first described it was assumed that it might have become extinct in the Devensian Glaciation; but on present evidence it might have continued to the time when the Indian bird is thought to have been introduced. This raises doubts about the identification of many of these late Pleistocene and early Holocene specimens. Did the European species become extinct with widespread human settlement, or were some domesticated? Was there interbreeding with the introduced birds, or did it even persist among the breeds of fowls? The situation at present raises more questions than it answers.

The Common Crane *Grus grus* is identified from Glastonbury and Meare Lake and from Woodbury settlement. Although it is usually said to have bred into historic times in extensive marshy areas, osteological evidence is scanty. A bone from Meare Lake appears incompletely ossified and suggests

breeding within the area, or nearby.

Another, larger crane was also present at the Somerset lake settlement sites. This was the extinct European Crane *G. primigenia*, a north-west European species similar in size to the Sarus Crane *G. antigone* of the Indian region (Harrison and Cowles, 1977). It appears to have been the representative in Europe of the larger cranes. The earliest record is from the Ipswichian Interglacial (Harrison and Walker, 1978). It also occurred in western Germany and northern France, and is known from western Scotland in the Bronze Age. Possibly the last record is from a Romano-British midden (G. Cowles, pers. comm).

Bones of an adult male Great Bustard *Otis tarda* at Port Eynon Cave must have been brought in by a predator from a carcase, probably on some open grassy area nearby, since that would be too large for most likely predators and a complete carcase should have left more evidence. The Corncrake *Crex crex* at this site may also have come from a similar area. Rails are otherwise represented only by the Moorhen *Gallinula chloropus*

and Coot Fulica atra at both Glastonbury and Meare Lake.

There are also few waders. Turnstone, Golden Plover and Grey Plover *Pluvialis squaterola* at Port Eynon Cave were probably migrants. A Lapwing *Vanellus vanellus* at Hucclecote Villa and Woodcock *Scolopax rusticola* at Major Park Villa were human food items, and are species likely to have occurred at earlier periods. They may represent deliberate selection in diet, especially since the Woodcock has also been found at Roman Villas in London and Hertfordshire.

At Port Eynon Cave the presence of incompletely ossified bones indicates that Great Black-backed Gull *Larus marinus*, Guillemot *Uria aalge*, Razorbill and Puffin *Fratercula arctica* nested nearby. The Little Auk, also occurring,

would have been a winter visitor to the area.

A Woodpigeon at Port Eynon Cave is the only pigeon recorded from these sites, and the only owl is the Barn Owl at Glastonbury and Soldier's Hole. However, some similar avian predator would have been responsible for the passerine remains at Port Eynon Cave, significantly numerous only at this site. Starling and Rock Pipit would almost certainly have nested in and around the cave. Stonechat/Whinchat, Wheatear and possibly White/Pied Wagtail *Motacilla alba* indicate more open and rocky conditions; but in addition all five thrush species are present, with elsewhere only a Song

Thrush at Glastonbury, and a Blackbird/Ring Ousel at Gough's Cave in the same spit as the Barn Owl.

An interesting occurrence at Port Eynon Cave is the Black Redstart *Phoenicurus ochrurus*. This was originally a cliff-nesting species. Although widespread on the European mainland, in Britain it is regarded as a species that gradually established itself in south-eastern England during the warmer first half of this century, only becoming well-established towards the end of that period in the 1940s. Its presence at Port Eynon Cave indicates that it, and others, may be species present in earlier warmer periods but temporarily lost during the cooler periods later in the Holocene.

It is perhaps surprising that the Chaffinch/Brambling *Fringilla coelebs/montifringilla* is only recorded from Port Eynon Cave in these south-western sites since the species pair is widespread in temperate to Boreal zones and might be expected to occur more frequently in these cave faunas.

Another isolated record from Port Eynon Cave is that of the Red-billed Chough *Pyrrhocorax pyrrhocorax*. Although a cave-nesting species it seems to have been rarely recorded. It is known from Kirkdale Cave in Yorkshire from what is now thought to be Ipswichian material. At present the species occurs in limited coastal and upland areas of south-west Britain; and its main species range is through the mountain areas of southern Eurasia. Its apparent absence for most of the Pleistocene apart from a warm interglacial and re-appearance in the early Holocene suggests that in spite of its mainly montane habitat it is more susceptible to cooler climate than might have been expected.

Other corvids are the Crow or Rook at Port Eynon Cave and Glastonbury, with the former species more likely in both instances; and the Raven at Port Eynon, Hanging Langford Camp, and Hucclecote Roman Villa. The latter species seems to occur with some frequency in the rather scanty bird material from British Roman Villas. It appears to have been kept or killed deliberately. Fisher (1966) suggested that it was kept as a pet but since it was a cult bird of the Mithraic religion it may have had some religious or ritual significance.

DIFFERENCES BETWEEN SOUTH-EAST AND SOUTH-WEST LISTS

The general difference between the types of sites yielding Pleistocene bird remains in the south-east and south-west of Britain has already been mentioned; and also the fact that this has resulted in differing species assemblages. In contrast to the 136 species from south-western sites the south-east has yielded only the 53 recorded in the published list (Harrison 1985) and a small number of as yet unpublished records.

TABLE I-Early bird species recorded from SE but not from SW Britain

North Atlantic Albatross Diomedea	Capercaillie Tetrao urogallus	W
anglica (extinct) RC	Spotted Crake Porzana porzana	D/H
Red-breasted Goose Branta ruficollis Ip	Green Sandpiper Tringa ochropus	Cr
Mandarin Duck Aix galericulata Cr	Storer's Black Guillemot Cepphus	
Red-crested Pochard Netta rufina Cr. An	storeri (extinct)	RC
Thick-legged Eider Somateria	Yellow Wagtail Motacilla flava	D/H
gravipes (extinct) Cr	Garden Warbler Sylvia borin	Но
Booted/Bonelli's Eagle Hieraeetus	Serin Serinus serinus	Но
pennatus/fasciatus D/H		110

Key: An = Anglian Glaciation, Cr = Cromerian Interglacial, D/H = Devensian/Holocene transition, Ho = Hoxnian Interglacial, Ip = Ipswichian Interglacial, RC = Red Crag, W = Wolstonian Glaciation

Of these 53 species a major part (40 species plus 3 unpublished occurrences) is shared with the south-west, and these species are indicated in the last column of TABLE II. Because the south-eastern sites cover a much longer time-span, their species records usually antedate those of the south-west at present. There remain 13 species known at present from the Pleistocene of the south-east but not yet recorded from the south-west. These are listed in TABLE I with indications of the period in which they were found.

FINAL COMMENTS

These data, when brought together, begin to give some general indication of Pleistocene and early Holocene British bird life. Comments have been included in the text on the sites and their birds, on instances where some correlations can be made between the species present, and on the likely

climatic and ecological conditions at the time.

In general the variations between colder and warmer periods seem less clear-cut than might be expected. One must be cautious of comment on this because the generally poor standards of recording in earlier excavations make any accurate assessment of the age and span of occurrence of many finds very difficult. Thus a stratum yielding bird remains might have accumulated over a period when conditions were changing, and the range of species present is a sample of a range of climatic conditions. Alternatively, conditions at the time were such that a wide range of species could co-exist, obscuring the effect of climatic fluctuation.

The more interesting information on the birds is to be found in some of the individual occurrences discussed in the text. Even so, one or two points do become apparent from the table. There is the apparent persistence of the Ptarmigan in Devon and the Mendips through most, if not all, of the Devensian Glaciation. It should indicate arctic-type climate, but at most sites appears to occur in company with the Willow/Red Grouse which indicates the presence of some low shrubby growth or heather, and in some instances with species of more wooded conditions such as Hazelhen or Black Grouse, and with the grassland Common Partridge.

As suggested above, this might be the accumulating evidence of periods of climatic and vegetational change; but the relative frequency with which it occurs at various sites within the small group involved suggests that the habitat correlation might instead be closer to something resembling the present-day situation in the Cairngorm region of Scotland, where a mixture of habitats ranging from tundra conditions on high ground to boreal woodland and riverine grassland at low levels allows a range of species to

co-exist.

Another fact that emerges from the data is the long-term presence of the Shelduck in an area around Torbay on the south Devon coast. In several caves it forms the greater part of the bird material, and even though it may have been intermittent in its occurrence it extends over a period from Late Wolstonian to Holocene in this area; and yet it occurs only as odd single instances elsewhere.

Other inter-site correlations are likely to become apparent as information from new sites becomes available, and hopefully the present paper will provide a structure into which further information can be incorporated to

yield a clearer picture of British Pleistocene birdlife.

LOCATION OF SPECIMENS

The majority of the specimens on which the identifications used here are based are in the collection of the Department of Palaeontology, British Museum (Natural History). Some of the specimens from Chelm's Combe Cave Shelter are in the collection of Wells Museum, Somerset. The specimens from Soldier's Hole, Cheddar are in the collection of the Cheddar Caves Museum.

ACKNOWLEDGEMENTS

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Key to Sites in Table II (pp. 100-102)

WOLSTONIAN GLACIATION

Tornewton Cave, south Devon (N.G.R. SX 814674)

IPSWICHIAN INTERGLACIAL

- Bacon Hole, Gower Peninsula, south Wales (SS 561868) R
- Minchin Hole, Gower Peninsula, south Wales (SS 555868) M
- T2 Tornewton Cave, south Devon (SX 814674)

DEVENSIAN GLACIATION

- S1 Soldier's Hole, Cheddar Gorge, Somerset (ST 469540)
- Tornewton Cave, south Devon (SX 814674) T3
- K Kent's Cavern, Torquay, south Devon (SX 934641)
- C Cat's Hole or Cathole Cave, Gower Peninsula, south Wales (SS 538900) Brixham Cave or Windmill Hill Cave, Brixham, south Devon (SX 925560)
- w

END OF DEVENSIAN (mainly Windermere Interstadial?)

- G1 Gough's Cave, Cheddar Gorge, Somerset (ST 467539)
- Soldier's Hole, Cheddar Gorge, Somerset (ST 469540) S2
- CC
- Chelm's Combe Rock Shelter, Cheddar, Somerset (ST 463545) Bridged Pot Cave Shelter, Ebbor Gorge, Somerset (ST 526487) E

TRANSITIONAL

- Tb Torbryan Caves, South Devon (SX 815674 to 817675)
- Merlin's Cave, Wye Valley, Hereford and Worcester (SO 556153) Neale's Cave, Paignton, south Devon (SX 882593) M
- N
- H Happaway Cave, Torquay, south Devon (SX 921641)
- Ch Chudleigh Fissure, south Devon (SX 8678)

HOLOCENE (the last six of these sites are combined in a single column using the key initials)

- P Port Eynon Cave, Gower Peninsula, south Wales (SS 468844). 9,000-6,000 b.p. Glastonbury Lake Settlement, Somerset (ST 492408)
- G1
- Meare Lake Settlement, Somerset (ST 446423) ML
- Gough's Cave, Cheddar Gorge, Somerset (ST 469540) Woodbury Settlement, Devon (SY 032873) S3
- G2
- WS
- HL Hanging Langford Camp, Wylye, Wiltshire (SU 012353)
- Hucclecote Roman Villa, near Gloucester (SO 877176) Hc
- MP Major Park Roman Villa, Camborne, Cornwall (SW 425636)

Periods in which the same species occurred in south-east England

- An Anglian Glaciation
- Cromerian Interglacial Devensian Glaciation Cr
- D
- D/H Devensian/Holocene transition
- Ho Hoxnian Interglacial
- IC Icenian Crag
- Ipswichian Interglacial Ip
- Pastonian Interglacial Pa
- RC Red Crag
- Wolstonian Glaciation

(Symbols in brackets indicate unpublished occurrences)

Table II—Occurrence of bird remains at sites in south-west Britain

	TI	T																					
	11	В	M	T2	SI	Т3	K	С	W	GI	S2	СС	E	Tb	М	N	Н	Ch	P	Gl	ML		also in SE England
Red-throated Diver Gavia stellata	_	-	_	-	-	_		-	_	-			_	-		_			-			_	Cr
Black-throated Diver Gavia artica	_			-				1000			-						1000					_	Ci
Great Northern Diver Gavia immer		_	_			0.22	550	255	1000	-			200		-	-	888	-					
Dabchick Tachybaptus ruficollis	2	_	-	12			20	100	-		-	-	-		-	-	550	-		-		_	
Cory's Shearwater Calonectris diomedea		*	- 50			100		145	-	-	-	-	-	_			8000			-		_	
Sooty Shearwater Puffinus griseus		573	-	-	-	-	1000	555	-		-	-	-	- 3		7		7	-	7	-	-	
Manx Shearwater Puffinus puffinus	_	-	- 5	-	_		-	-	-	\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\	-	-	-	1.5	5.5			-	-	-	-	-	
Cormorant Phalacrocorax carbo	-		~	-	-	-	7	-	~	-		177	-	-	-	7	-	77		7	-	-	
Shag Phalacrocorax aristotelis		-	-	-	-	1.7	-	-	-	-	-	-	-	-	-	**	-	-		•		-	Cr Ip
	: -		-	-	-	-	<u></u>	-	-	-	-	-	-	-	-	===	-	=		-	-	-	
Gannet Morus bassanus		-	=	-		-	-	-	-	-	-	**	-	-	-	-	-	-		-	-	-	
Dalmatian Pelican Pelecanus crispus	-	-	-	-	-	-	-	- 00	-	-	-	-	-)	-	-	-	-	-	*	-	-	
Grey Heron Ardea cinerea) -	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	_	*	-	
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Blackcap Sylvia atricapilla	-	·	-	-	-	_	-	-	-	-	-	_	-		-	-	•			-	-	-	
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Corn Bunting Emberiza calandra	-	-	**	-	-		-	-	-	=	177	-	-		-	120	-	*	-	-	-	-	
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