Proceedings of

The Postglacial Colonization Conference

University College Cork,
15-16 October 1983.

Editors

D.P.Sleeman, R.J.Devoy and P.C.Woodman.

**OCCASIONAL PUBLICATION
OF THE
IRISH BIOGEOGRAPHICAL SOCIETY**

NUMBER 1

OCCASIONAL PUBLICATION

OF THE

IRISH BIOGEOGRAPHICAL SOCIETY

NUMBER 1

Date of Publication: 1986

ISBN 09511514 01

Abbreviation: Occ. Pub. Ir. Biogeog. Soc.

The Society desires it to be understood that it is not answerable for any opinion, representation of facts, or train of reasoning that may appear in the following papers. The authors of the several essays are alone responsible for their contents and for the correctness of references.

PREFACE

On 15-16 October 1983, a Postglacial Colonization Conference was held in University College, Cork. The meeting was a most successful one and the various speakers presented many original and stimulating views on this aspect of Irish Biogeography. The Irish Biogeographical Society is delighted therefore, to publish the proceedings of the Conference in its new series of Occasional Publications. Our congratulations are due to the organisers, both for their initiative in arranging this worthwhile meeting and for preparing the presented papers for publication.

J.P. O'Connor,
General Editor,
Irish Biogeographical Society.

CONTRIBUTORS

Dr. R.J. Devoy,
Department of Geography,
University College,
Cork,
Ireland.

Dr. A.J. Stuart,
Department of Zoology,
University of Cambridge,
England.

Dr. T.K. McCarthy,
Department of Zoology,
University College,
Galway,
Ireland.

Dr. L.H. van Wijngaarden-Bakker,
Albert Egges van Giffen,
Protohistoire, Universiteit van
Amsterdam,
Netherlands.

Professor G.F. Mitchell,
School of Botany,
Trinity College,
Dublin,
Ireland.

Professor W.A. Watts,
Provost,
Trinity College,
Dublin,
Ireland.

D.P. Sleeman,
Department of Zoology,
University College,
Cork,
Ireland.

Dr. J.P.F. Wilson,
19 Beaumont Road,
Chiswick,
London W4 5AL,
England.

Dr. M.C.D. Speight,
Forest & Wildlife Service,
Research Branch,
Department of Fisheries & Forestry,
Bray,
Co. Wicklow,
Ireland.

Professor P.C. Woodman,
Department of Archaeology,
University College,
Cork,
Ireland.

Dr. D.W. Yalden,
Department of Zoology,
University of Manchester,
England.

CONTENTS

TABLES

FIGURES

ACKNOWLEDGEMENTS

We would like to express our thanks to the many participants in the conference, to the Departments of Archaeology, Geography and Zoology, University College, Cork, for their support, and to those who helped on the day, in particular Mary Corkery, Desmond Murphy and Richard Fitzgerald. We are grateful to University College Galway for financial support. We also wish to thank the editorial staff of the Irish Biogeographical Society for their help and encouragement while putting this together, and the staff of University College Cork typing pool.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

INTRODUCTION

P.C. Woodman, R.J.N. Devoy and D.P. Sleeman

Any casual perusal of the literature on Ireland's native mammals quickly reveals that Ireland has a very restricted native mammalian fauna; no more than fourteen native mammals (Table 1). This and the fact that Ireland has been an island for at least 9,000 years, has given rise to speculation as to how Ireland acquired its postglacial fauna and flora. Even the 7th century Irish monk Augustine speculated on how animals could have reached Ireland. In order to discuss this problem, with particular reference to mammals, a one day public conference was held in University College Cork on 15th October 1983. This was followed by a half day discussion session.

This conference was the result of the mutual interest of three members of University College Cork in the problems of the colonization of Ireland during postglacial time. Professor P.C. Woodman (Department of Archaeology), concerned not only with the human colonization of Ireland but also with the habitat in which Ireland's initial colonists had found themselves, had suggested in 1978 that the arguments in favour of a landbridge as a mechanism for colonization were rather weak. Mr D.P. Sleeman (Department of Zoology) was concerned with the problems of survival of newly arrived groups of animals and found it difficult to accept colonization without a landbridge. Dr R. Devoy (Department of Geography), focusing on the problems of Quaternary sea-level and coastal change, was more concerned with the geological/geomorphological evidence for the existence of a landbridge(s) and in palaeogeographic reconstruction.

The organisers were in part stimulated by Dr Derek Yalden's (1982) paper on postglacial faunas in the British Isles. They felt that, although a conference could be organised round the topic of mammalian colonization, this alone would be too limiting as other areas of research might provide important indicators. Therefore, this conference tried to draw upon as many different fields as possible. Thus, many eminent workers engaged upon research in the same area of study were not asked to contribute, as it was felt that an overall picture should be obtained and that time, finance and a need for a balanced view necessitated their exclusion.

Initially, the Conference was intended to be little more than a public forum for discussion, identification of problem areas and paradoxes. There was no intention of publication, but shortly before the meeting took place we were approached with the idea of publishing the proceedings. As many contributors had felt that they had already stated factual detail in print, there seemed little point in arranging the publication of major papers. Therefore, we have compiled a series of shorter contributions which form a review discussion and varied interpretation of available data. A number of papers may be seen as containing a measure of overlap. Because of the differing approaches and opinions, both between and also within the disciplines involved, we feel that these highlight and contain valuable insights into the nature of the problems under study.

To the editors the papers appeared to fall naturally into certain groups:

1. Introduction
2. Environmental setting and Palaeogeography
   Two papers by Watts and Devoy constitute this section. Watts' paper presents a resume of environmental change in Ireland during the Quaternary, focusing in particular on plant colonization. Devoy discusses the possibilities of landbridges in the context of current geological knowledge.
3. Colonisation by Mammals
   This section concerns itself not only with the mechanism(s) of colonization but also with the survival and distribution of mammalian species. Stuart's paper shows that the impoverished fauna of Ireland is not something confined to the postglacial as similar trends can be documented on two other earlier occasions. The four following papers essentially concern themselves with the postglacial mammalian evidence. Woodman's paper, besides discussing the arrival of man, shows that the archaeological evidence is exceptionally limited and, due to human factors, may not always reflect accurately the range of

native fauna. Van Wijngaarden-Bakker's paper documents the appearance of various mammals in the archaeological record. Sleeman discusses problems with not only the arrival but also the survival of Ireland's mammalian predators. Finally, Yalden's paper, besides examining the various mechanisms by which mammals could get to Ireland, suggests that the anomalous occurrence of pygmy shrews in Ireland could be an indication that a low, rather wet landbridge existed in early postglacial times.

4. The record from Fish Amphibians and Reptiles

Wilson shows that amongst the freshwater fish, amphibians and reptiles there is also a relatively restricted range. While at least one fish species may be a glacial relict some of the other fish are certainly introduced, as may be the amphibians and reptiles.

5. Colonization by Invertebrates

McCarthy and Speight have drawn attention in their papers to the relative richness of the invertebrate fauna. They have also noted many anomalies, including the weakness of the traditional concept of the Lusitanian elements and that man must have significantly influenced our present range of invertebrates. Mitchell also shows that questions must be asked about the appearance of the range of mollusca found in the lateglacial and postglacial contexts.

The editors have provided two tables. The first contains a list of Ireland's postglacial mammals, reptiles, amphibians and fresh water fish (Table 1), the second (Table 2) contains the correlations of Late Quaternary stages in the British Isles. In addition a table on lateglacial flora and climate (Table 3) has been provided by Professor Watts.

References

Yalden, D.W. (1982) When did the mammal fauna of the British Isles arrive? Mammal Review. 12: 1-57.

TABLE 1

A list of Ireland's postglacial terrestrial mammals, reptiles, amphibians and fresh water fish.
Bats; marine species: seals, whales, turtles; and domestic species omitted. Probable status is indicated by N, native; I, introduced; E, extinct; ?, native status uncertain. The sequence N, E, I implies a native form, becoming extinct and then reintroduced (as in Yalden, 1982). Currently accepted endemic Irish subspecies are indicated with an asterisk.

MAMMALS		STATUS
Hedgehog	*Erinaceus europaeus* L.	N or I?
Pygmy shrew	*Sorex minutus* L.	N
Brown hare	*Lepus europaeus* Pallas	I
*Irish hare	*Lepus timidus hibernicus* (Bell)	N
Rabbit	*Oryctolagus cuniculus* (L.)	I
Red squirrel	*Sciurus vulgaris* L.	N, E, I
Grey squirrel	*Sciurus carolinensis* Gmelin	I
Bank vole	*Clethrionomys glarsolus* (Schreber)	I
Musk rat	*Ondatra zibethica* (L.)	I, E
Wood mouse	*Apodemus sylvaticus* (L.)	I
Black rat	*Rattus rattus* (L.)	I
Brown rat	*Rattus norvegicus* (Berkenhout)	I
House mouse	*Mus musculus* L.	I
Wolf	*Canis lupus* L.	N, E
Fox	*Vulpes vulpes* (L.)	N
Brown bear	*Ursus arctos* L.	N, E
*Irish stoat	*Mustela erminea hibernica* (Thomas and Barrett-Hamilton)	N
American mink	*Mustela vision* Schreber	I
Pine marten	*Martes martes* (L.)	N
Badger	*Meles meles* (L.)	N
*Irish otter	*Lutra lutra roensis* (Ogilby)	N
Wild cat	*Felis silvestris* Scherber	N, E
Horse	*Equus caballus* L.	I ?

TABLE 1 CONTINUED

Wild boar	*Sus scofa* L.	N, E
Fallow deer	*Dama dama* (L.)	I
Sika deer	*Cervus nippon* Temminck	I
Red deer	*Cervus elaphus* L.	N
REPTILES		
Viviparous lizard	*Lacerta vivipara* Jacquin	N
Slow worm	*Anguis fragilis* L.	I
AMPHIBIANS		
Smooth newt	*Triturus vulgaris* (L.)	N
Frog	*Rana temporaria* L.	I
Natterjack toad	*Bufo calamita* Laurenti	N or I?
FRESHWATER FISH		
Euryhaline species		
*Pollan	*Coregonus autumnalis pollan* (Regan)	N
*Goureen	*Alosa fallox killarniensis Regan*	N
Three-spined stickleback	*Gasterosteus aculeatus* L.	N
Charr	*Salvelinus alpinus* (L.)	N
Anadromous species		
Sea lamprey	*Petromyzon marinus* L.	N
River lamprey	*Lampetra fluviatilis* (L.)	N
Salmon	*Salmo salar* L.	N
Trout	*Salmo trutta* L.	N
Rainbow trout	*Salmo gairdneri* Richardson	I
Allis shad	*Alosa alosa* (L.)	N
Twaite shad	*Alosa fallax* (Lacepede)	N

TABLE 1 CONTINUED

Catadromous species		
Eel	*Anguilla anguilla* (L.)	N
Stenohaline species		
Brook lamprey	*Lampetra planeri* (Bloch)	I
Pike	*Esox lucius* L.	I
Carp	*Cyprinus carpio* (L.)	I
Gudgeon	*Gobio gobio* (L.)	I
Tench	*Tinca tinca* (L.)	I
Minnow	*Phoxinus phoxinus* (L.)	I
Dace	*Leuciscus leuciscus* (L.)	I
Roach	*Rutilus rutilus* (L.)	I
Rudd	*Scardinius erythrophthalmus* (L.)	I
Bream	*Abramis brama* (L.)	I
Stone loach	*Noemacheilus barbatulus* (L.)	I
Ten-spined stickleback	*Pungitius pungitius* (L.)	I
Perch	*Perca fluviatilis* L.	I

Occ. Pub. Ir. Biogeog. Soc. No. 1.

TABLE 2 Correlation of Late Quaternary Stages in the British Isles

<table>
<tr><th colspan="2">BRITISH REGIONAL STAGES
AND RELATED CLIMATIC UNITS</th><th colspan="2">IRISH REGIONAL STAGES
AND RELATED CLIMATIC UNITS</th></tr>
<tr><td colspan="2">FLANDRIAN
(WARM)</td><td colspan="2">LITTLETONIAN
(WARM)</td></tr>
<tr><td colspan="4">10,200 ± 200 B.P.</td></tr>
<tr><td rowspan="8">D
E
V
E
N
S
I
A
N

(Glacial)</td><td>LOCH LOMOND
STADIAL (COLD)</td><td>NAHANAGAN
STADIAL (COLD)</td><td rowspan="8">M
I
D
L
A
N
D
I
A
N

(Glacial)</td></tr>
<tr><td colspan="2">LATE</td></tr>
<tr><td>WINDERMERE
INTERSTADIAL
(WARM)</td><td>WOODGRANGE
INTERSTADIAL
(WARM)</td></tr>
<tr><td colspan="2">c. 14,000 B.P.</td></tr>
<tr><td colspan="2">c. 30,500 B.P.</td></tr>
<tr><td colspan="2">MIDDLE</td></tr>
<tr><td colspan="2">c. 50,000 B.P.</td></tr>
<tr><td colspan="2">EARLY</td></tr>
</table>

2. ENVIRONMENTAL SETTING AND PALAEOGEOGRAPHY

Occ. Pub. Ir. Biogeog. Soc. No. 1.

ORIGIN OF THE IRISH FLORA AND FAUNA

W.A. Watts

Pleistocene environmental change

The flora and fauna of Ireland today, leaving aside species introduced by man, is the result of survival, evolutionary change and migration during the approximately two million years which make up the Pleistocene epoch. The last million years has been characterised by strong cyclic fluctuations of climate, each of some 125,000 years duration. The cycles are related in a manner still not fully understood to variations in the earth's tilt and precession resulting in variation in summer radiation over long periods (Imbrie and Imbrie, 1979). In Northwest Europe each cycle contained a relatively short period, perhaps some 15,000 to 20,000 years long, characterised by climate similar to today's in the same latitude and longitude. These 'warm' phases are known as interglacials. Several deposits of interglacial Age are known in Ireland of which the most famous is at Peterswell near Gort, Co. Galway (Jessen, et al., 1959; Warren, 1979). It contains a flora rich in species, several of which no longer occur in Ireland. The 'cold' parts of the 125,000 -year cycle are not at all homogenous climatically. In Northwest Europe during the last 100,000 years there were periods of cold without ice-sheets when there were arctic floras and faunas and there were relatively warm periods during which boreal conifer forest became established. These short 'warm' periods, which were not as warm as today, are known as interstadials. At the other extreme actual ice sheets covered the landscape and modified it, as happened in Ireland between about 25,000 and 13,000 years B.P.

Much modern information about the detailed climatic/geological course of the last million years comes from the stratigraphic study of fossils in sediment cores from the bottom of the deep North Atlantic far to the west of Ireland (Shackleton, 1976; 1977). The cores contain fossil foraminifera and other invertebrate animals. Our knowledge of the ecology of the foraminifera today allows us to make estimates of the temperature of ocean surface waters and hence climate in the past, while direct measurement of oxygen isotopes in the fossils and sediments, together with radiocarbon dating and other forms of radiometric dating, allow us to assess the past climate further and to date the times at which climatic change took place (Boulton, 1978; Kellogg, 1976; Ruddiman & McIntyre, 1976). On this basis we know that the Last Interglacial was at its warmest about 125,000 years ago. It was followed by a series of interstadial events and a brief period of very cold climate at about 75,000 years ago. Subsequently there was a long phase with relatively little climatic change when the climate was arctic and dry with limited precipitation. This ended about 30,000 years ago, the time to which the mammoth and hyaena remains at Castlepook Cave near Doneraile have been dated (see Stuart, this volume) and from which dated sediments with an arctic flora and fauna are known from beneath drumlins at Derryvree, Co. Fermanagh. By 25,000 years ago ice sheets were forming, presumably after a period of greatly increased precipitation as snow, and a great ice sheet may have covered much of Ireland until about 18,000 to 13,000 years B.P. (before present) during which time it melted out (Mitchell, 1976). This ice covered the northern two-thirds of the country and there was a substantial local ice cap in the Cork-Kerry mountains. However, considerable areas of southern Ireland, especially in counties Cork and Waterford, were not ice-covered in this final phase of the last cold stage (Synge, 1981; Devoy, 1983). Almost certainly these areas would have a rather varied flora and fauna, because this is true today of such extreme arctic environments as ice-free northern Greenland north of 80° latitude.

The complex geological story of Northwest Europe, even of the last 125,000 years, is very incompletely known and much detail still remains to be discovered (Bowen, 1978). In Ireland this is expecially true because, apart from the events around 30,000 years ago already referred to, little is known at all of environments existing prior to 13,000 B.P. (see Devoy, this volume). Ice present between about 25,000 and 13,000 B.P. must have done much, however, to mould our present landscape, make our soil and decide where our rivers and lakes would be. Further, the plant and animal life which must have been present in the unglaciated areas when the ice sheets were established, were available to colonize the deglaciated landscape as the ice melted.

Lateglacial vegetation

We know the events between 13,000 and 10,000 B.P., the Lateglacial Period, in great detail, a detail which is almost absurd when set against our nearly total ignorance of the period which preceded it. After 13,000 years B.P. the first plants revealed by counts of fossil pollen from sediments in newly formed lakes and ponds were grasses, sedges and Rumex (docks). The flora was almost certainly more diverse than the pollen suggests, because many species produce very little pollen and are unrecorded or under-recorded. This first phase ended with an invasion of Juniperus (Juniper), a gorse-like shrub which must have covered the landscape with low thickets. Many lines of evidence suggest that this was a period of warm climate (Mitchell & West, 1977), but trees were absent, as they were throughout the Lateglacial in Ireland, except possibly for some birch. Probably trees had not had time to immigrate from the remote area to the south or east where they had survived the ice-sheets. This 'lag factor' has to be taken into account when interpreting Pleistocene floras and faunas climatically. The juniper phase ended relatively suddenly, and there is some evidence to suggest that this was due to a climatic deterioration which resulted in slope erosion. It was followed by a grass-dominated period with diverse herbs. The giant deer lived during the later part of the grass phase, so far as we can establish. Where is came from or how long it had been in Ireland is unknown. The climate of the grass phase is uncertain, except that it was probably colder and less conducive to biological growth than the juniper phase. As it came to an end a very marked climatic deterioration caused severe slope erosion or solifluction and a thinned cover of vegetation. Many herbs are found in this period, but pollen of Artemisia (sage) and fossil leaves and twigs of Salix herbacea L. (dwarf willow) are specially characteristic. Local ice formed once more in mountain corries. The Artemisia phase ended about 10,000 years ago. Its cause is well-known from ocean cores. The North Atlantic, which had warmed about 13,000 years B.P. to the west of Ireland suddenly became cold once more and polar water, probably with winter pack-ice and icebergs, reappeared briefly off our west coast to cause a severe cooling of the land climate (Boulton, 1978). As this episode came to an end a very strong and sustained climatic warming led us into our present interglacial. The invasion of forest trees such as birch, pine, hazel, oak and elm had taken place by 9,000 B.P. to result in a forested landscape for the first time in 100,000 years.

The lateglacial period was originally investigated in Ireland during the 1930's by Jessen. He produced a relatively simple and well-known climatic/botanic scheme for the lateglacial. Modern research shows that events were rather more varied than he had thought. His scheme and a more modern one are set out in Table 3 for comparison.

Conclusions

To gain a perspective on the Pleistocene history of any plant or animal species then, one must realise the immensely diverse climatic events which had to be lived through. The survivors had endured frequent and sometimes abrupt major climatic change, during which they had been exposed to rigorous processes of natural selection for evolutionary change. They must often have survived by migration, finding themselves with constantly changing companion species also under compulsion to migrate or become extinct. The exact origin or modes of desperal remain unknown.

References

Boulton, G.S. (1978) A model of Weichselian glacier variation in the North Atlantic region. Boreas, 8: 373-395.

Bowen, D.Q. (1978) Quaternary geology: A stratigraphic framework for multidisciplinary work. Pergamon, Oxford.

Devoy, R.J. (1983) Late Quarternary shorelines in Ireland: an assessment of their implications for isostatic land movement and relative sea-level changes. In D.E. Smith & A.G. Dawson (editors), Shorelines and Isostasy. Academic Press, London.

Imbrie, J.I. and Imbrie, K.P. (1979) Ice Ages. Solving the Mystery. Enslow Publishers.

Jessen, K., Anderson, S. T. & Farrington, A. (1959) The interglacial deposits near Gort, Co. Galway, Ireland. Proc. R. Ir. Acad. 60B: 1-77.

Kellogg, T.B. (1976) Late Quaternary climatic changes: evidence from deep-sea cores of Norwegian and Greenland Seas. In R.M. Cline and J.D. Hays (editors). Investigations of late Quaternary palaeoceanography and palaeoclimatology. Geol. Soc. Am. Mem, 145: 77-110.

Mitchell, G.F. (1976) The Irish Landscape. Collins, London.

Mitchell, G.F. & West, R.G. (1977) The changing environmental conditions in Great Britain and Ireland during the Devensian (Last) cold stage. Phil. Trans. R. Soc. Lond. B., 280: 103-374.

Ruddiman, W.F. & McIntyre, A. (1976) Northwest Atlantic palaeoclimatic changes over the past 600,000 years. In R.M. Cline & J.D. Hays (editors). Investigations of late Quaternary palaeoceanography and palaeoclimatology. Geol. Soc. Am. Mem., 145: 111-146.

Shackleton, N.J. (1976) The oxygen isotope stratigraphic record of the late Pleistocene. Phil. Trans. R. Soc. Lond. B., 280: 169-182.

Shackleton, N.J. (1977) Oxygen isotope stratigraphy of the middle Pleistocene. In F.W. Shotton (editor). British Quaternary Studies: recent advances. Clarendon Press, Oxford.

Synge, F.M. (1981) Quaternary glaciation and changes of sea-level in the south of Ireland. Geol. en Mijnbw. 60: 305:315.

Warren, W.P. (1979) The stratigraphic position and age of the Gortian interglacial deposits. Geol. Surv. Irl. Bull., 2: 315-332.

Watts, W.A. (1977) The Late Devensian Vegetation of Ireland. Phil. Trans. R. Soc. Lond., B280: 273-293.

Author's Address

Trinity College,
Dublin,
Ireland.

TABLE 3 THE LATE-GLACIAL FLORA AND CLIMATE

Radiocarbon Years	Jessen	More Recent	
after 10,000 B.P.	Post-glacial warmth	Post-glacial warmth	
ca. 10,000 to ca. 11,000 B.P.	Younger *Salix herbacea* Period	Younger *Dryas* Period	v. cold, polar water in ocean
12,400 to 11,000 B.P.	Birch Period (warm)	Grass Period (giant deer) erosion Juniper Period	progressive cooling, warm at first, sub-polar water
13,000 to 12,400 B.P.	Older *Salix herbacea* Period	*Rumex* phase	pioneer flora, climate uncertain
>13,000	ice present	ice present	

Sources of information

Imbrie, J.I. and K.P., 1979. *Ice Ages. Solving the Mystery.* Enslow Publishers.

Watts, W.A., 1977. The Late Devensian vegetation of Ireland. *Phil. Trans. R. Soc. Lond.* B280: 273-293.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

POSSIBLE LANDBRIDGES BETWEEN IRELAND AND BRITAIN: A GEOLOGICAL APPRAISAL

R.J. Devoy

The possible routeways

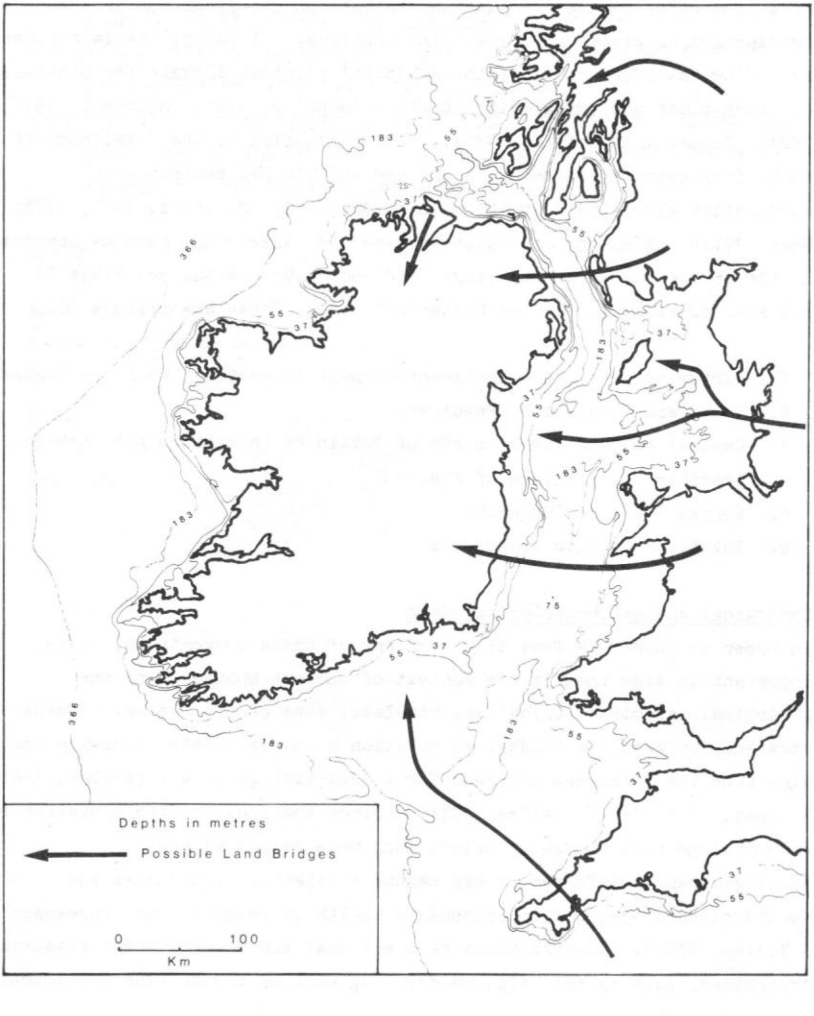
Biogeographers and other scientists working on the problems of environmental/-palaeoecological reconstruction have long found the concept of a landbridge between Ireland and Britain an expedient one in the explanation of plant and animal distributions. Globally, the landbridge mechanism has often provided the essential physical linkage for otherwise disjunct plant and animal distributions (Hopkins, 1967; Stoddart, 1978, 1981; Gentry & Sutcliffe, 1981). Past discussion of the likelihood of such links existing between Ireland and Britain has centred upon speculation about their location (Shotton, 1962; Mitchell, 1972, 1976; West, 1977). A number of routeways have been advanced; seen as operating at the end of the last cold stage (Midlandian-Devensian, see Table 2) and also possibly in earlier Quaternary time. These are (Figure 1):

1. Southward across the continental shelf to western, maritime Europe.
2. South east Ireland to Pembroke.
3. Central eastern areas, north of Dublin to Lancashire and Cumbria, possibly via the Isle of Man.
4. Across the North Channel.
5. Inishowen area to Islay/Jura.

Geological and geomorphological data

In order to judge the feasibility of any of these suggestions, it is important to view them in the context of current knowledge of the geological, geomorphological and sea-level data of the region. Recent work has reviewed the landbridge question more rigorously, throwing doubt even upon the existence and need for a land linkage at all (Corbet, 1961; Woodman, 1978, 1981; Yalden, 1982). Since the idea for the operation of a landbridge first became popular, much more sea-level and palaeogeographic information has become available. Individual and co-ordinated projects have produced a wealth of relevant data (Greensmith & Tooley, 1982). Contributions from national and international research programmes, such as the offshore drilling work of the British Geological

FIGURE 1. Bathymetry (after Atlas of Ireland, Royal Irish Academy, Dublin, 1979; Bickmore, D.P. & Shaw, M.A. (eds.) 1963. Atlas of Britain and Northern Ireland, Clarendon Press, Oxford) and location of postulated landbridge routeways.

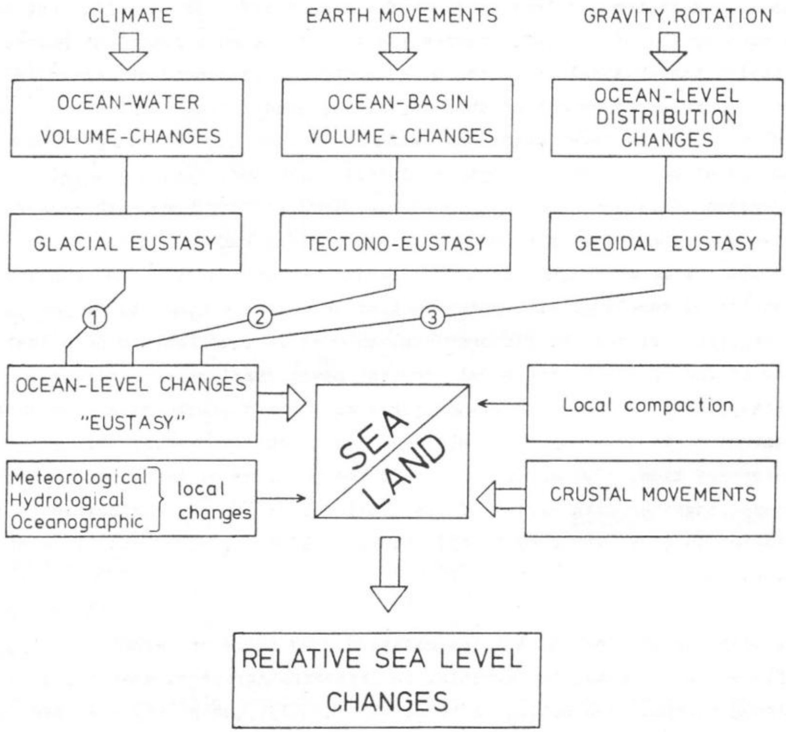


Survey (Institute of Geological Sciences, 1969-1984; Pantin & Evans, 1984; Davies et al., 1984) and of the International Geological Correlation Programme's Project 24 (Fannin et al., 1979) have been particularly productive.

Due to lack of space it is impossible to enter into the complexities of the region's Quaternary geology and readers are referred for more detailed discussion of the problems to the references cited. It is sufficient to examine by way of a brief commentary a few of the more important points. Firstly, the physical operation of a landbridge is dependent primarily upon the relative height of this transitory land surface to the contemporary sea-level position. Without a clear understanding of the factors at both local and regional levels which condition sea-level movements, together with an accurate knowledge of offshore bathymetry/palaeogeography, the problem of valid landbridge reconstruction is immense. A model (Figure 2) of the parameters determining the relative position of sea-level at a point in time shows the complexity of the interaction between the factors involved. It is important to note that many of the inputs to the model (crustal movements/isostasy, glacial eustasy, local meterological and hydrographic conditions) have been in a constant state of change in Ireland and neighbouring regions during Quaternary time. Fuller discussion of the problems of sea-level/land change, together with review of its implications for the landbridge question is given in Devoy (1985), Mörner (1976a, b, 1980) and Clark et al. (1978).

Secondly, within Ireland and its offshore zone there are great deficiencies in data, for example, in lithostratigraphic, sea-level, palaeogeographic and dating information. Lastly, Quaternary sea-level and other environmental changes within the region have been complex and spatially very different. Ireland's Quaternary environment seems to have been dominated by erosive processes, resulting in the destruction of environmental data predating the last glacial stage. Glacial evidence supports a pattern of repeated phases of ice mass growth/advance/decay across the land surface, Irish Sea and inner Scottish shelf areas, with accompanying erosion and reworking of sediments (Synge, 1977; Sissons,

FIGURE 2. Factors conditioning the position of relative sea-level at a point on the earth's surface (from Morner, 1979).



1976; Stephens & McCabe, 1977; McCabe & Hoare, 1978; Thomas & Summers, 1984. Fluvioglacial and fluvial action evacuated large quantities of sediment from the landsurface; primarily to the Atlantic ocean basin via extensive, but now buried, valley-canyon systems developed across the offshore and outer continental shelf zones (Hamilton & Smith, 1972; Andreieff & Le Font, 1972; Al-Saadi & Brooks, 1973; Whittington, 1977).

In these coastal and shelf areas sediment data indicates the existence of floating shelf ice/iceberg activity in Late Pleistocene time throughout the Malin, Irish and Celtic Seas (Synge, 1979, 1981; Davies et al., 1984; Pantin & Evans, 1984; McCabe et al., 1984). Based on this evidence and the known sea-level record (Devoy, 1983; Carter, 1982) there is a strong likelihood that marine conditions were present around Ireland from at least 20,000 years B.P. onwards.

Palaeogeographic reconstruction

As much of the physical data about the early to Middle Quaternary environment in Ireland is absent, discussion of the five suggested landbridge routes must be confined to their possible operation in Late Quaternary time only. Traversing the region from south to north, the first routeway for plant and animal migration lies directly across the southwest continental shelf (Figure 1). In the Celtic Sea and Western Approaches/English Channel and interconnected series of troughs and channels leads SW and W into submarine canyons on the outer continental shelf (Hamilton, 1979; Naylor & Shannon, 1980). Together these features form major areas of negative relief, reaching even today to >-100 m Ordance Datum (O.D.) effectively separating Ireland from areas to the south and east. The Celtic Sea channel systems are now largely infilled, but were probably active during the Quaternary at times of glaciation and consequent low relative sea-level (Hamilton & Smith, 1972; Wood, 1976), conducting meltwater and sediment into the Atlantic. Whatever the degree and timing of exposure of the continental margin, these areas constituted a highly mobile environment and would probably have formed barriers to organisms intolerant of water and unstable ground conditions.
The great difficulty for the landbridge question here lies in a lack of accurate knowledge of the interaction in time between changing land elevation and both the vertical and aerial extent of

relative sea-level change (Dingwall, 1975). The broad patterns are established (Pantin & Evans, 1984; Devoy, 1983; Heyworth & Kidson, 1982); however, for the operation of even a partial landbridge it is the detail of short term change (1 x $10^{2/3}$ years) that may be all important.

In the Irish Sea the three routeways, across the St. George's Channel, Central Irish Sea region and the North Channel, all appear somewhat illusory. A linear trough, reaching no higher than -90 m O.D. today and linked to the channel systems further south, runs the length of the area (Figure 1). Although subjected to repeated modification, this trough probably existed throughout the Quaternary. As a result, when the area was not blocked by ice, the trough facilitated early access to the sea after glaciation, if not its continued presence in the area. In any lag time between glacial retreat and marine inundation, sub-aerial erosion by meltwater systems would have created an inhospitable environment for plant and animal migration. Similarly, in the shallow areas between north-west England and the Isle of Man, marine incursion followed promptly on deglaciation (Pantin, 1977; Haynes et al., 1977; Tooley, 1977, 1978; Penney, 1983). Although phases of land emergence probably occurred here in the lateglacial, the surface would have been short-lived, interrupted frequently by shifting meltwater streams, sinuous lakes and lagoons.

Coring and bathymetric surveys support the probable occurrence of ridges of relatively high ground throughout the North Irish and Malin Sea areas, formed by till, glaciomarine and fluvio-glacial deposits. Across the southern end of the Irish Sea Dobson et al. (1971) have found similarly a submarine ridge composed of apparently glacial material. Today this lies at maximum heights of -75 to -80 m O.D. Formed probably at the end of the Midlandian stage, the feature, if ever continuous, was probably cut through and reworked immediately upon glacier retreat. Similarly, the ridge features as a whole found in the various offshore zones are unlikely to have been interconnected, high enough or resisted sub-aerial and marine erosion long enough to have acted as landbridges, or barriers to marine water movement, as some have suggested (Mitchell, 1963, 1976; Harris, 1979; Yalden, 1982).

The remaining possible landbridge location, as indicated by Mitchell (1976), West (1977) and Yalden (1982), lies in the Malin Sea area. At the south-eastern end occurs the major bathymetric depression of the North Channel. Filled for much of the Late Pleistocene by ice, it was occupied immediately by the sea on deglaciation. Further west higher relief is formed by the structurally determined NE-SW trending Middle Bank High and Donegal-Islay rock platforms. Survey of these areas show them to be covered variably by glaciomarine till, and postglacial marine sediments (Owens & Marshall, 1978). Dissection of the platforms, probably by glacial and sub-aerial erosion at times of low relative sea-level since the Late-Miocene (Dobson, 1979; Davies et al., 1984), has created deep channels and gullies to depths >-60 m O.D. In between these a series of relatively shallow areas, at depths of 25 to -46 m O.D., lie between the Inishowen Peninsular and the Jura/Islay area of Scotland. This initially unpromising topography may offer the best possibility for a former landbridge. If relative sea-level fell to a height of only -30 m O.D. in the area during the lateglacial (Jardine, 1982), then even these raised zones would not have been fully exposed. The original postglacial surface may, however, have been higher. Equally, relative sea-level may have fallen below -30 m O.D., or parts of these areas may have undergone more rapid isostatic uplift than those of northern Ireland. A larger factor of land uplift is indicated for the Islay/Jura end of the presumed link in lateglacial time (Jardine, 1982; Sissons, 1983); due presumably to its closer proximity to the assumed regional centre of ice loading. If this was the case, sea floor areas at this northern end would, in the short term, have been raised differentially higher than zones to the south-west near Inishowen. In any, or a combination, of these circumstances, the now submerged shallow water areas would have formed short-lived peninsulas and islands, separated by narrow straits perhaps with a fall of relative sea-level to between -40 to -46 m O.D., in the order of 2-6 km wide. On the basis of C^{14} dating of sea-level indicators (Carter, 1982) the timing of this possible exposure may have been sometime between 11,400 to 10,200 [200 B.P.]. Yalden's (1982) suggestion of an earlier emergence prior to 12,000 B.P. is not supported by the sea-level data available.

As many authors have formerly indicated, erosion has destroyed much of the pre-submergence landscape of the region. Working by analogy with modern coastal processes operating in this area (Carter, 1983), it is possible that the record of marine inundation of the Malin Sea coasts was accompanied by the creation of major beach ridge and other depositional sedimentary structures. It is unlikely that these would have linked any of the possibly emergent islands, though they could have formed the means for narrowing the distance between them. As is so often the case with a landbridge, it is likely that we shall probably never know for certain. If plant and animals did ever cross via this route they probably had to contend with a "low, soggy, possibly shifting and partially discontinuous linkage" (Devoy, 1985), open for a short time only prior to the postglacial.

References

Al-Saadi, P.H. & Brooks, M. (1973) A geophysical study of Pleistocene buried valleys in the lower Swansea Valley, Vale of Neath and Swansea Bay. Proc. Geol. Ass. 84: 135-153.

Andreieff, P. & Le Fort, J.P. (1972) Contribution a l'etude stratigraphique des terains secondaires et tertiaires affleurant en Manche Occidentale. Mem. Bur. Rech. Geol. Min. 79: 49-56.

Carter, W.G. (1982) Sea-level changes in Northern Ireland. Proc. Geol. Ass. 93: 157-170

Carter, R.W.G. (1983) Raised Coastal landforms as products of modern process variations and their relevance in eustatic sea-level studies: examples from E. Ireland. Boreas. 12: 167-182.

Clark, J.A., Farrell, W.E. & Peltier, W.R. (1978) Global changes in postglacial sea level: a numerical calculation. Quat. Res. 9: 265-287.

Corbet, G.B. (1961) Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. Nature, London, 191: 1037-1040.

Davies, H.C., Dobson, M.R. & Whittington, R.J. (1984) A revised seismic stratigraphy for Quaternary deposits on the linear continental shelf west of Scotland between 55°33'N and 57°30'N. Boreas, 13(1): 49-66.

Devoy, R.J. (1983) Late Quaternary shorelines in Ireland: an assessment of their implications for isostatic land movement and relative sea-level changes. In Smith D.E. & Dawson, A.G. (Ed.), Shorelines and Isotasy. Insitute of British Geographers Special Publication No. 16, Academic Press, London, pp. 227-254.

Devoy, R.J. (1985) The problem of a Late Quaternary landbridge between Britain and Ireland. Quaternary Science Review 4 to No. 1.

Dingwall, R.G. (1975) Sub-bottom infilled channels in an area of the Eastern English Channel. Phil. Trans. R. Soc. Lond. A, 279: 233-241.

Dobson, M.R. (1979) Aspects of the post-Permian history of the aseismic Continental Shelf to the west of the British Isles. In Banner, F.T., Collins, M.B. & Massie, K.S. (Editors), The Northwest European Shelf Seas: the sea bed and the sea in motion, I. Geology and Sedimentology. Elsevier, Amsterdam, pp. 25-41.

Dobson, M.R., Evans, W.E. & James, K.H. (1971) The sediment on the floor of the Southern Irish Sea. Mar. Geol. 11: 27-69.

Fannin, N.G.T., Dobson, M., D'Olier, B. & Harland, R. (1979) IGCP Project 24: Quaternary glaciations in the Northern Hemisphere working group 24.4 offshore deposits. Quat. Newsl. 29: 29-40.

Gentry, A.W. & Sutcliffe, A.J. (1981) Pleistocene geography and mammal faunas. In Cocks, L.R.M. (Editor), The evolving earth. C.U.P., Cambridge, pp. 237-251.

Greensmith, J.T. & Tooley, M.F. (Editors), (1982) IGCP Project 61: sea-level movements during the last deglacial hemicycle (about 15,000 years). Proc. Geol. Ass. 93, 1-125.

Hamilton, D. (1979) The geology of the English Channel, South Celtic Sea and Continental Margin, Southwestern Approaches. In Banner, F.T. (etc. see Dobson 1979 for details), 61-87.

Hamilton, D. & Smith, A.J. (1972) The origin and sedimentary history of the Hurd Deep, English Channel, with additional notes on other deeps in the western English Channel. Mem. Bur. Rech. Geol. Min. 79: 59-78.

Harris, C.R. (1979) The ontogeny, palaeocology, and palaeogeographical inference of the ostracod - Roundstonia globulifera. Boreas. 8: 297-307.

Haynes, J.R., Kiteley, R.J., Whatley, R.C. & Wilks, P.J. (1977) Microfaunas, microfloras and the environmental stratigraphy of the lateglacial and Holocene in Cardigan Bay, Geol. J. 12: 129-178.

Heyworth, A. & Kidson, C. (1982) Sea-level changes in Southwest England and Wales. Proc. Geol. Ass. 93: 91-111.

Hopkins, D.M. (Editor) (1967) The Bering landbridge. Stanford University Press.

Institute of Geological Sciences, (1969-1983) Report Numbers 69/8, 70/14, 71/19, 73/11, 73/2, 73/14, 74/7, 75/7, 76/7, 76/10, 78/20, 79/12, 81/12 and 82/11. Her Majesty's Stationery Office, London.

Jardine, W.G. (1982) Sea-level changes in Scotland during the last 18,000 years. Proc. Geol. Ass. 93: 25-41.

McCabe, A.M. & Hoare, P.G. (1978) The Late Quaternary history of east-central Ireland. Geol. Mag. 115: 397-413.

McCabe, A.M., Dardis, G.F. & Hanvey, P.M. (1984) Sedimentology of a late Pleistocene submarine-moraine complex, Co. Down, Northern Ireland. J. Sed. Petr., 54(3): 750-760.

Mitchell, G.F. (1963) Moranic ridges on the floor of the Irish Sea. Ir. Geogr. 4: 335-344.

Mitchell, G.F. (1972) The Pleistocene history of the Irish Sea: second approximation. Sci. Proc. Roy. Dubl. Soc., A. 4(13): 181-199.

Mitchell, G.F. (1976) The Irish Landscape. Collins, London, pp. 240.

Morner, N-A. (1976a) Eustasy and geoid changes. J. Geol. 84(2): 123-151.

Morner, N-A. (1976b) Eustatic changes during the last 8,000 years in view of radiocarbon calibration and new information from the Kattegat region and other Northwest European coastal areas. Palaeogeogr., Palaeoclimatol., Palaeoecol. 19: 63-85.

Morner, N-A. (1979) Eustasy and geoid changes as a function of core/mantle changes. In Morner, N-A. (Editor), Earth Rheology, Isostasy and Eustasy. John Wiley & Sons.

Morner, N-A. (1980) The Northwest European "sea-level laboratory" and regional Holocene Eustasy. Palaeogeogr., Palaeoclimatol., Palaeoecol. 29: 281-300.

Naylor, D. & Shannon, P. (1980) Geology of offshore Ireland and western Britain. Graham & Trotman, London.

Owens, B. & Marshall, J. (1978) Micropalaeontological biostratigraphy of samples from around the coasts of Scotland. Rep. Inst. Geol. Sci. 78/20: 1-35.

Pantin, H.M. (1977) Quaternary sediments of the Northern Irish Sea. In Kidson, C. & Tooley, M.J. (Editors), The Quaternary history of the Irish Sea, Seel House Press, Liverpool.

Pantin, H.M. & Evans, C.D.R. (1984) The Quaternary history of the central and southwestern Celtic Sea. Mar. Geol. 57: 259-293.

Penney, D.N. (1983) Postglacial sediments and foraminifera at Dundalk, Ireland. Unpublished thesis, submitted for the degree of Ph.D., University of Dublin, Trinity College, Dublin.

Shotton, F.W. (1962) The physical background of Britain in the Pleistocene. Adv. Sci. 19: 193-206.

Sissons, J.B. (1976) The geomorphology of the British Isles: Scotland. Methuen, London.

Sissons, J.B. (1983) Shorelines and isostasy in Scotland. In: Smith, D.E. & Dawson, A.G. (Editors), Shorelines and Isostasy. Academic Press, London, pp. 209-227.

Stephens, N. & McCabe, A.M. (1977) Late Pleistocene ice movements and patterns of late and postglacial shorelines on the coast of Ulster (Ireland). In Kidson, C. & Tooley, M.J. (Editors), Quaternary history of the Irish Sea, Seel House Press, Liverpool, pp. 199-222.

Stoddart, D.R. (1978) Biogeography. Progr. Phys. Geogr. 2(3): 514-528.

Stoddart, D.R. (1981) Biogeography: dispersal and drift. Progr. Phys. Geogr. 5(4): 575-590.

Synge, F.M. (1977) The coasts of Leinster (Ireland). In Kidson, C. & Tooley, M.J. (Editors), Quaternary history of the Irish Sea, Seel House Press, Liverpool, pp. 199-222.

Synge, F.M. (1977) Quaternary glaciation in Ireland. Quat. Newsl. 28: 1-18.

Synge, F.M. (1981) Quaternary glaciation and changes of sea level in the south of Ireland. Geol. en Mijnb. 60: 305-315.

Thomas, G.S.P. & Summers, A.J. (1984) Glacio-dynamic structures from the Blackwater Formation, Co. Wexford, Ireland. Boreas, 13(1): 5-12.

Tooley, M.J. (1977) The Isle of man, Lancashire coast and Lake District. In Bowen, D.Q. (Editor), X INQUA Congress Excursion Guides, Geo. Abstracts, Norwich, p. 60.

Tooley, M.J. (1978) Sea-level changes in Northwest England during the Flandrian Stage. Clarendon Press, Oxford.

West, R.G. (1977) Pleistocene geology and biology. Longmans, London.

Whittington, R.J. (1977) A lateglacial drainage pattern in the Kish Bank area and postglacial sediments in the Central Irish Sea. In Kidson, C. & Tooley, M.J. (Editors), The Quaternary history of the Irish Sea, Seel House Press, Liverpool, pp. 55-68.

Wood, A. (1976) Successive regressions and transgressions in the Neogene. Mar. Geol. 22: M23-M29.

Woodman, P.C. (1978) The Mesolithic in Ireland: hunter gatherers in an insular environment. British Archaeological Reports, British Series, 58, Oxford.

Woodman, P.C. (1981) The postglacial colonization of Ireland: the human factors. In Ó Corráin, D. (ed.), Irish Antiquity: essays and studies presented to Prof. M.J. O'Kelly. Tower Books, Cork.

Yalden, D.W. (1982) When did the mammal fauna of the British Isles arrive? Mammal Review, 12: 1-57.

Author's Address

Department of Geography,
University College,
Cork,
Ireland.

3. COLONIZATION BY MAMMALS

Occ. Pub. Ir. Biogeog. Soc. No. 1.

Pleistocene Mammals in Ireland (pre-10,000 years B.P)

A.J. Stuart

Introduction

Fossil mammal remains occur fairly abundantly in the Pleistocene of Ireland, principally in 'bone caves' and in the deposits of former lakes. In comparison with Britain and most other parts of Europe, however, the Irish record is very restricted both in numbers of species and in stratigraphical range.

The lack of Irish fauna before 35,000 years B.P.

In England fossil mammals are known from the Lower Pleistocene, back to approximately 1.8 million years ago, and there is a rich sequence of faunas from the Cromerian Interglacial, perhaps 400,000 years ago, to the present-day. In marked contrast, so far there are no Irish records older than 35,000 years B.P., within the Middle Midlandian/last cold stage (Table 2).

Why are there no earlier faunas from Ireland? It would appear very unlikely that no mammals reached Ireland from Britain before the Midlandian, as even laying aside the possibility of former landbridges, Ireland could have been colonized by animals swimming across (large mammals) or floating over on drifting vegetation (small mammals). The answer is probably to be found in the scarcity of suitable fossiliferous sediments in the earlier Irish Pleistocene. The complete absence of vertebrate remains from the Irish Gortian Interglacial is not remarkable as vertebrate remains are scarce in such fine-grained non-calcareous lacustrine deposits elsewhere. Of particular relevance is the fact that most of Ireland was glaciated during the maximum of the late Midlandian cold stage and significantly 'pre-glacial' vertebrates are generally very scarce in those parts of Britain which were ice-covered at the same time. In Britain, glaciation resulted in the erosion or burial of most earlier terrace deposits. Nevertheless the deposits within caves generally remained protected from the ravages of glaciation and a few 'bone caves' in northern England and

Wales have yielded Ipswichian/Last Interglacial faunas, although they lie within the glacial limit (Stuart, 1983). Moreover, several Irish 'bone caves' are within the region of southern Ireland which probably remained ice-free throughout the Late Midlandian/Devensian and, as discussed below, Castlepook Cave has produced an extensive fauna dating from well before the main glaciation but not extending back as far as the Last Interglacial. Bearing in mind that several hundred British 'bone caves' have been excavated compared with only twenty or so in Ireland (in both countries mostly to a poor standard) the lack of Irish Last Interglacial, or earlier, faunas is probably more apparent than real. The discovery of such material could well await the efforts of a future investigator. The Irish Pleistocene mammal faunas known at present fall into two chronological groups, middle Midlandian and late Midlandian 'late-glacial'.

Middle Midlandian/Devensian

From comparison with stratified and/or radiocarbon-dated records from Britain, the few records of mammoth, Mammuthus primigenius Blumenbach from Ireland (Savage, 1966) probably pre-date the main Late Midlandian glaciation, i.e. are older than about 20,000 years B.P. By far the most important Irish Pleistocene mammal site is Castlepook Cave, Co. Cork, where a complex system of interconnecting galleries in Carboniferous Limestone contained a bed of sand, a metre or less in thickness, with abundant fossil bones and teeth. The site was excavated by Ussher in 1904 and described by Scharff, Seymour and Newton (1918).

No recent revision of the fauna has been made, but it appears to comprise: stoat; fox; wolf; brown bear; spotted hyaena, Crocuta crocuta L., Norway lemming; Lemmus lemmus; arctic lemming Dicrostonyx torquatus (Pallas); mountain hare; mammoth; reindeer Rangifer tarandus L.; giant deer, Megaloceros giganteus (Blumenbach) and various birds. Scharff et al. (1918) also record the wood mouse, a temperate forest animal quite out of place in this cold assemblage. Jaws and teeth of this species were however found by sieving sand from within the cave, which may well have suffered some contamination with younger material, and perhaps significantly, Scharff et al. (1918) state that no remains of this species were observed in situ.

Two radiocarbon dates on Castlepook material are now available:-

Material	Date 14C years B.P.	Lab. no.
Mammuthus primigenius	33,500 + 1200	(D-122)
Mammoth (molar)		
Crocuta crocuta	34,300 + 1800	(I-13, 256)
spotted hyaena		

The latter date was very kindly supplied by Prof. G.F. Mitchell. Taken together these dates are of considerable interest as they suggest that most or all of the Castlepook Pleistocene fauna may be perhaps of much the same age, dating from about 34,000 years B.P.

Many of the bones and teeth found in the cave were probably collected by spotted hyaenas and have been chewed extensively. Several species, notably spotted hyaena are known in Ireland from the Middle Midlandian only at Castlepook. The horse, a species not recorded from Castlepook, was found in apparent association with mammoth and other cold stage fauna at Shandon Cave, Co. Waterford (Brenan, 1860; Carte, 1860). This find needs further investigation or confirmation, however, especially as the absence of horse at Castlepook, appears significant in view of its abundance at British sites used as hyaena dens and the numbers of zebras killed or scavenged by modern African spotted hyaenas (Stuart, 1982). British faunas or broadly the same age are much richer in numbers of species (Stuart, 1982). Significant absences from the Irish faunas include: Coeldonta antiquitatis, woolly rhino; Bison priscus, extinct bison; Cervus elaphus, red deer,; perhaps horse (see above) all species of voles and Homo sapiens, man (not known in Ireland before the postglacial). The lack of Irish records for certain other species e.g. lion Panthera leo L., suslik Spermophilus sp., may be less significant, since these are relatively rare in the much more abundant assemblages from British sites. Although the Scottish Pleistocene faunas are also poorly-known, the records of woolly rhino from Scotland, strongly suggest that the absence of this and other species from Ireland is not due to their failure to reach a possible landbridge from south west Scotland to northern Ireland. It is possible that some of these animals were excluded by adverse climatic or vegetational conditions in much or all of Ireland, but it seems more likely that they were being filtered out by the nature of the migration route.

The marked impoverishment of the Irish middle Midlandian fauna is explicable, if there was not continuous land connection. Small mammals may have crossed small water gaps, perhaps between islands, either by swimming or perhaps by crossing over ice or on ice floes, whereas larger mammals in addition may have arrived by swimming across as much as several miles of sea. Which of the available species were successful in colonizing Ireland could have been partly a matter of chance depending both on the exact (Probably undeterminable) conditions along the migration route, or routes, and the dispersal abilities of the various potential immigrants. At the very least, of course, a pregnant female or two adults, one of each sex, is needed to make the crossing.

Late Midlandian/Devensian lateglacial

It is probably safe to assume that the Irish vertebrate fauna was virtually or entirely exterminated when most of Ireland was glaciated during the late Midlandian, so that the lateglacial fauna must have re-immigrated via Britain. Only two species, *Rangifer tarandus*, reindeer and *Megaloceros giganteus*, giant deer are at present known from the Irish late-glacial. Both are recorded over much of Ireland in calcareous lacustrine sediments dating from the Woodrange Interstadial (Mitchell, 1941; Mitchell & Parkes, 1949; also see Barnosky, 1985; 1986) found beneath postglacial peats. Much work remains to be done on the exact provenance of these finds, but radiocarbon dates on giant deer bones appear to support the available stratigraphical evidence that this species was extinct in Ireland by the onset of the Nahanagan Stadial, 10,500 years B.P. (Stuart & van Wijngaarden-Bakker, 1985;

Barnosky, 1986). As in Britain, however, the reindeer appears to have survived both the increasing cold and deteriorating vegetational conditions, becoming extinct only with ameliorating temperatures and the spread of forests at the end of the Midlandian, 10,000 years B.P. A single radiocarbon date of 10,700 + 110 years B.P. (Pta-2378) on a bone of reindeer from Kilgreany Cave, Co. Waterford demonstrates the presence of the lateglacial mammals in Irish caves. Bearing this in mind, it is clear from the total absence of records from Ireland, that the Irish fauna was again markedly impoverished in comparison with the late glacial fauna in Britain. In particular, Alces alces (L.), elk or moose, all species of voles and man are absent from Ireland (Stuart, 1982; Stuart & van Wijngaarden-Bakker, 1985). This again suggests that there was no continuous land connection.

General Conclusions

1. Although much work needs to be done on Irish Pleistocene mammals, it is clear that the faunas of Midlandian age are markedly less diverse than those from Britain. This implies only a tenuous link between Britain and Ireland, probably never a continuous land connection. The fact that only a few individuals of any one species are likely to have colonized Ireland and given rise to subsequent populations has interesting genetic implications ('founder effect'), which might be apparent in the fossil material.
2. The likely northerly position and tenuous nature of the migration route (see Devoy, this volume) would not have allowed free exchange of animals between Britain and Ireland, and so there would have been no opportunity for the Irish fauna to migrate elsewhere in response to changing climatic and vegetational conditions. Since such changes were a recurrent feature of the Pleistocene, in the long term Ireland must have been repeatedly a death-trap for its terrestrial vertebrate faunas.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

References

Barnosky, A.D. (1985) Taphonomy and herd structure of the extinct Irish elk, Megaloceros giganteus. Science. 228: 340-344.

Barnosky, A.D. (1986) "Big game" extinction caused by late Pleistocene climatic change: Irish elk Megaloceros giganteus in Ireland. Quaternary Research. 25: 128-135.

Brenan, E. (1860) Notice of the discovery of extinct elephant and other animal remains under limestone at Shandon, near Dungarven, County of Waterford. J.R. Dubl. Soc. 2: 344-350.

Carte, A. (1860) Description of the fossil discovery by Mr. Brenan at Shandon, near Dungarvan. J.R. Dubl. Soc. 2: 351-357.

Mitchell, G.F. (1941) Studies in Irish Quaternary deposits 3. The reindeer in Ireland. Proc. R. Ir. Acad. 46(B): 183-188.

Mitchell, G.F. & Parkes, H.M. (1949) The giant deer in Ireland. Proc. R. Ir. Acad. 52(B): 291-314.

Savage, R.J.G. (1966) Irish Pleistocene mammals. Ir. Nat. J. 15: 117-130.

Scharff, R.F., Seymour, H.J. & Newton, E.T. (1918) The exploration of Castlepook Cave, County Cork. Proc. R. Ir. Acad. 34(B): 33-72.

Stuart, A.J. (1982) Pleistocene Vertebrates in the British Isles. London, Longman. pp. 212.

Stuart, A.J. (1983) Pleistocene bone caves in Britain and Ireland; a short review. Studies in Spelaeology. 4(9): 9-36.

Stuart, A.J. & van Wijngaarden-Bakker, L.H. (1985) Quaternary vertebrates, Chapter 10. In Edwards, K. & Warren, W. (Eds.) The Quaternary History of Ireland. London: Academic Press.

Author's Address

Department of Zoology,
University of Cambridge,
England.

Now at:

The Castle Museum,
Norwich,
Norfolk NR1 3JU.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

MAN'S FIRST APPEARANCE IN IRELAND AND HIS IMPORTANCE IN THE COLONIZATION PROCESS.

P.C. Woodman

The Archaeological Evidence

At the moment, the earliest evidence for man in Ireland dates to just before 9,000 B.P. and, while there are indications of slightly earlier occupation, there is as yet nothing to suggest that man arrived here significantly earlier. As an intelligent adaptive being, it would not be surprising that man came by boat though, as Woodman (1982) has pointed out, even for man the problem would not have been one of colonization but rather one of establishing a viable population. In one particular sense, man is important to the broader topic of plant and animal colonization under discussion in that the organic remains found during archaeological excavations of his settlements provide most of the information about early faunas.

It is rarely emphasised sufficiently how impoverished the prehistoric archaeological record actually is. There are approximately thirty stone age and Bronze Age sites with faunal remains, but less than ten have a significant concentration of animal bones. Many sites are ritual burial monuments or, as in the case of some of the Lough Gur sites, faunal remains were from multi-period sites (O'Riordain, 1954). Similarly, the fauna from many of the cave sites can only be, at best, divided into Pleistocene and post-Pleistocene components. It is sobering to realise that the Newgrange fauna (Van Wijngaarden-Bakker, 1974), is the only adequately published body of material for the whole of the Neolithic and early Bronze Age, a period of up to 3,000 years in duration. (Hopefully, the fauna from Doughty's unpublished cave excavation at Poul-na-Gollum, Co. Fermanagh and Bradley's ongoing excavation at Moynagh Lough, Co. Meath will help fill this gap).

The major problem for the archaeologist is whether his limited samples of bones genuinely reflect the range of animals available. This is particularly true of red deer. It is perhaps not surprising that this animal forms such a small percentage of the total fauna at the settlements of farmers, e.g. it occurs rarely in the lakeshore settlement of Ballinderry II but occurs frequently as skeletons of animals who died while enmired in the lake (Hencken, 1942). So far red deer has not been found on early mesolithic sites in Ireland. Is this rarity due to a positive choice by man as a hunter, a bias in the types of sites excavated or due to the fact that deer existed only in small numbers? If, as a result of an increased number of excavations, the third choice appears probable, then this rarity could be signalling something about the nature of Ireland's post-glacial colonization, i.e. red deer was a late introduction which took time to establish himself and that there was no convenient landbridge for him to cross.

The archaeological record can only, of course, provide information on a presence and absence basis. Thus, the occurrence of red deer, wild pig, wolf, brown bear and hare in Mesolithic contexts but the absence of other animals does not imply an absence from Ireland. Many of the other native mammals, e.g. squirrel, stoat, pygmy shrew, are animals which would not normally occur in quantities in an archaeological context, i.e. man would have little reason to bring them to his settlements. Similarly, many furbearing animals, such as pine marten, might be skinned at the point of capture, thus the numerous complete skeletons of pine marten which were chucked into the lake at Ringkloster in Denmark (Anderson, 1974). Therefore, natural accumulations of animal bones may be more important in revealing the range of Ireland's native mammals. In this respect, the accumulation of bones at Poul-na-Gallum, although dating to the Bronze Age, could represent one of the most important contributions to the study of Ireland's natural history.

Finally, it is important to remember both the length of time we are discussing and the role of man as an inadvertent agent of introduction. The process of human colonization was not a once-off event at 9,000 B.P. therefore, we cannot expect the rest of our fauna and flora to be a product of one short period of colonization alone.

Conclusions

We know that reindeer and giant Irish deer flourished in Ireland in a relatively warm period which lasted for perhaps more than 2,000 years down to 10,800 B.P. This period, the Woodgrange Interstadial, although within the lateglacial, occurred at a time when ice sheets had long since departed from Ireland. It was brought to an end by a short sharp cold snap, which we know had disastrous effect on Irish grassland ecology of that period; but did it wipe the slate clean? Authors such as Jacobi have argued that even man did not abandon southern Britain at this stage. Is it not possible that some of our mammals, like fish (see Wilson, this volume), could have survived this period? (see Watts, this volume).

Most of the mammalian fauna may have arrived in early postglacial times by a variety of means, though at this stage, it is unlikely that man acted as an unwilling agent while he was colonizing. We must, however, remember that there was a significant degree of contact between Ireland and Europe throughout later Prehistoric times. This is first evident in exchange systems in the Stone Age - notably Antrim porcellanite axes found in Britain but reaches its height in the Bronze Age when faience and amber objects are being brought to Ireland in exchange for copper and bronze artefacts. The Irish influence in the European Bronze Age cannot be overrated. The impact on Ireland's fauna of this constant movement to and from the island is epitomised by the late Dudley Waterman's discovery of a barbary ape Maca sylvaus (L.) in a late Bronze Age context at Emain Macha in Co. Armagh! (Waterman, pers comm.).

In summary, the archaeological record is, unfortunately, inadequate as an accurate repository of evidence on the colonization process. It is important that, in the context of colonization, we should not look for a simple, single explanation of the origins of Ireland's fauna.

References

Andersen, S. (1974) Ringkloster, en jysk inlands - boplads med Ertebolle Kulter. Kuml. 1973-74: 11-108.

Hencken, H. (1942) Ballinderry Crannog No. 2, Proc. R. Ir. Acad. 47 (C): 1-76.

O'Riordain, S.P. (1954) Lough Gur Excavations: Neolithic and Bronze Age Houses on Knockadoon, Proc. R. Irish Acad. 56(C): 297-459.

Van Wijngaarden-Bakker, L.H. (1974) The Animal Remains from the Beaker Settlement at Newgrange, Co. Meath: first report, Proc. R. Ir. Acad. 74(C): 313-383.

Woodman, P.C. (1982) The post-glacial colonization of Ireland: the human factors, in Irish Antiquity, Ed. D.O Corrain. Cork. 93-110.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

THE COLONIZATION OF ISLANDS. THE MAMMALIAN EVIDENCE FROM IRISH ARCHAEOLOGICAL SITES

Louise H. Van Wijngaarden-Bakker

The theory of island colonization

In general islands are characterized by an unbalanced fauna. Evolutionary biologists and ecologists have found island faunas a fruitful research basis for their studies on speciation, adaptive radiation, evolution of single species, etc. A theoretical background of island biogeography is provided by the MacArthur-Wilson colonization model (MacArthur and Wilson, 1967). The empirical basis for the model comes from observations that range from the eruption of Krakatao in 1883 to recent defaunation experiments on mangrove islands in Florida Bay. From these and other experiments MacArthur and Wilson conclude that the number of species on an island is a balance of immigration and extinction. Their model presents species diversity on a given island as a biotic, dynamic equilibrium.

At the specific level the immigration rate is a falling curve because as more species become established, fewer immigrants will belong to new species. The immigration rate is dependent on the distance of the island to the mainland. Successful immigrants may reach an island by passive dispersal or by their own means such as flying, swimming, drifting or by the use of natural rafts. Successful colonizers have a small death rate, a large birth rate, a cohesiveness of population and they are generally capable of habitat expansion.

Successful colonization can be prevented by the presence of either competitors and/or predators on the island, or alternatively by the small population size of the invading species. Theoretically, of course one pregnant female is sufficient to colonize an island, but in practice this seems rather unlikely. Apart from limiting enviromental conditions the number of species on a given island is approximately related to the area of the island.

The extinction rate is a rising curve, since the more species are present the more there are to become extinct. Causes for extinction encompass random population fluctuation, predation, competition, immigration of a new competitor, disease, habitat alteration etc. Immigration and extinction rates are difficult to define precisely and even more difficult to measure. However, in many cases a colonization curve can be drawn as a function of time, by integrating the difference between the time curves of immigration and extinction.

The mammalian evidence from Irish archaeological sites

For the postglacial period evidence on the time of immigration/extinction of Irish mammals comes from a great number of well dated archaeological excavations (Stuart and van Wijngaarden-Bakker, 1985). For the early Mesolithic period there is good evidence for the presence of wild boar and mountain hare. Both species are generally considered to be good colonizers. They have a high reproduction rate and are noted for their ecological expansion. By the end of the Mesolithic red deer and brown bear are certainly present. The brown bear is a large predator, but its feeding habits are not totally carnivore, bur rather diversivore. The evidence for the presence of a second predator, the wolf is more doubtful. One other mammal species that successfully invaded Ireland during the Early Mesolithic is man. Mesolithic hunter-gatherers found themselves in an environment devoid of most species of large ungulates. For their animal protein they may have relied heavily on the salmon runs in the Irish rivers. These anadromous fish constitute a highly predictable and abundant food resource.

In the Neolithic period we find, in addition to the already mentioned species, evidence for the presence of three more predators: fox, badger and wild cat. In the Bronze Age the otter can be added to the species list. The absence of evidence for this species in the earlier prehistoric periods is rather surprising as otters may be considered good colonizers (nowadays they frequently cross the Irish Sea). Presumably the absence of primary fresh water fish in the Irish rivers and lakes prevented their successful immigration. Either already in the Neolithic period or perhaps in the Bronze Age the wild boar

The woodmouse is first documented for an Iron Age site. But in the absence of an extensive sieving program, the bones of this mammal may have gone unnoticed in excavations of earlier periods. In the Early Christian period two more carnivores are documented: the pine marten and the stoat. Here again, the bones of these small species may have been overlooked in earlier excavations. Brown bear and wild cat may have become extinct during the Early Christian Period, while the wolf disappears by the beginning of the nineteenth century AD. In recent times the bank vole is a successful immigrant. Zooarchaeological data on the pygmy shrew and the red squirrel are still lacking.

A tentative colonization curve constructed from the available archaeological data indicates an equilibrium at circa ten to twelve mammal species, which may have been reached by the end of the Stone Age. By 7500 BC the whole English fauna was present including aurochs, elk, roe deer, wild horse, polecat and weasel. On the present evidence none of these species seems to have colonized Ireland.

In addition to the above mentioned indigenous mammals, the Irish fauna contains a large anthropogenic element. Firstly there are the deliberately introduced mammals: domestic stock, (dog, cattle, sheep, goat, pig, horse, cat, donkey, mink) and game (sika and fallow deer, brown hare, rabbit, grey squirrel). Secondly three species are typical 'culture-followers' and may be considered as accidental human introductions: housemouse, black rat and brown rat. Whether the introduction of the hedgehog was deliberate or accidental is still a matter of discussion.

When viewing the present Irish mammal fauna as a whole, human influence is considerable. Man has acted as an agent in the introduction of mammal species but probably also as a predator. With the introduction of agriculture man started to exert a profound influence on the landscape. On the one hand habibat alterations may have provided suitable biotopes for newly arriving species, but they could also have lead to the final extinction of species. Moreover, the introduction of domestic stock would have presented a competitive element for the then present indigenous (mammal) fauna.

disappears from the Irish archaeological record. Causes for its extinction could be hunting by prehistoric farmers wishing to protect their crops, habitat alteration by deforestation and/or the presence of a competitor, the domestic pig.

In the process of Irish postglacial colonization this pattern of profound human effect on the natural environment becomes more and more apparent. We hope that zooarchaeological, palynological and palaeobotanical monitoring of future excavations may deepen our insight in this process.

References

MacArthur, R.H. & Wilson, H.T. (1967) The theory of island biogeography. Princeton Univ. Press, Princeton.

Stuart, A.J. and van Wijngaarden-Bakker, L.H. (1985) Quaternary vertebrates. In Edwards, K.J. and Warren, W.P. (Eds.) The Quaternary History of Ireland. 221-249. Academic Press, London.

Author's Address

Albert Egges van Giffen,
Institut voor Prae-en
Protohistorie,
Universiteit van Amsterdam,
Netherlands.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

IRELAND'S CARNIVOROUS MAMMALS - PROBLEMS WITH THEIR ARRIVAL AND SURVIVAL

D.P. Sleeman

Introduction

There is an understandable tendency to think of mammals from the past as moribund creatures, patiently waiting to be turned into museum exhibits. However, to understand faunas of the past, in this case Ireland's postglacial fauna, we must think of these mammals as very much alive, as they once were, with ecological requirements not unlike their present day relatives.

To facilitate this approach we will define herbivores, carnivores and animals in general in a simplified ecological perspective, and then turn our attention to Ireland's postglacial flesh eaters.

Herbivores usually have an accessible and plentiful supply of their food. Plants don't run away if eaten, so herbivores usually have little difficulty in finding food. The drawback about being a herbivore is that plant tissue is difficult to digest and of poor nutritional value (in comparison to flesh). Hence herbivores have long and complex guts, grinding teeth and other adaptations to extract nourishment from plant tissue. Flesh, on the other hand is highly nutritious and relatively easily digested. Hence, carnivores have short guts, and the flesh eating role in any habitat is highly competitive. The major problem with being a carnivore is that the original owners of the flesh are never keen on giving it up, and will run away! Therefore, we get specialisation in carnivores. One example of such specialisation is the small long and thin shape of weasels and stoats, which, although energetically inefficient, allows them to specialise in hunting small mammals down their tunnels and runways (Brown and Lasiewski, 1972).

Herbivores are the most rewarding prey for carnivores. This is because herbivores are next up in the food chains from the primary producers of biomass: plants. There must be many more herbivores than carnivores. If a rich carnivore fauna is to exist in a limited area, such as an island, there will have to be an adequate herbivore prey fauna present.

Animals don't exist on their own, they interact with each other, plants and inorganic environment. If an animal's ecological requirements are not met in a particular habitat, it will not be found there. A simple example of this is on an island. A predator cannot survive on an island without suitable prey species, a herbivore without suitable plant species; and the reverse should also be true. If one finds a predator or herbivore population on an island, its presence implies the presence of suitable prey or plant species.

The Irish Situation

Ireland is such an island now. This was not always so, as it is a continental island that at some time was connected to the European mainland via Britain. Whether or not Ireland's fauna and flora arrived across such a land connection is one of the major questions at issue.

Since the last glaciation a range of animals and plants have arrived in Ireland. We know that many of the animals were introduced by man, but we also know that some animals have been here long enough to evolve into distinct Irish forms . Among the mammals there are three accepted indigenous Irish subspecies; the Irish stoat, hare and otter (Table 1). All three are arctic mammals. They are darker than the same species in Britain. Two of these distinct indigenous forms are carnivores; the stoat and otter. Other mammalian carnivores that were present in the postglacial, and still exist here are the pine marten, badger and fox. We also know from historical records and bone remains that the wild cat, brown bear and wolf survived here in postglacial times. These three species are now extinct. We know that man deliberately hunted the wolf to extinction, and the same was the likely fate of the wild cat and bear. These three extinct predators provide examples of the problems surrounding Ireland's postglacial mammal fauna. They are only accepted as postglacial because they have been found on archaeological sites (Wijngaarden-Bakker, 1974).

There are, therefore, eight known postglacial Irish mammalian carnivores. This, in comparison to the ten mammalian carnivores found in Britain at the same time, is not an impoverished fauna. The two species present in Britain and absent in Ireland are the weasel *Mustela nivalis* L. and the polecat *Mustela putorius* (L.).

Given Britain's size, position and richer prey fauna, it is not unexpected that the polecat reached and survived on one island and not the other. The weasel's absence from Ireland has been termed "something of a zoogeographical mystery" by Corbet (1966). However, its absence can be explained by the fact that voles, until recently were absent from Ireland, and they are a principle part of the weasel's diet (Yalden, 1982). An interesting recent suggestion by King and Moors (1979) is that the weasel did occur here during the immediate postglacial, along with lemming, but became extinct along with the latter. We have no evidence, as yet, that weasels or lemmings ever occurred in Ireland in the postglacial. A good faunal sample from a postglacial context could solve this problem.

How did the carnivores get here? It has been speculated that some forms, the artic endemic forms in particular, might have survived the last glaciation, having crossed on an earlier landbridge. It has also been advanced that at least some of these carnivores were introduced by man. For example the wild cat, which Wijngaarden-Bakker (1974) has argued was probably accidentally introduced; or the fox and pine marten which Fairley (1975) has argued might have been introduced to be harvested for their fur. The discovery of the bones of a barbary ape in a Bronze Age context (see Woodman, this volume) shows that the idea of introduction by man may not be as far fetched as it sounds. The successful establishment of twenty two alien mammal species introduced to New Zealand by man (Gibb and Flux, 1973) shows how quickly modern man can introduce viable mammal populations to the remotest locations. However, we are not dealing with modern man in the Irish postglacial. The boats available would have been primitive. Carnivores are difficult to catch alive, handle and transport. If one is to start a viable population one has to introduce a number of animals, which indicates repeated introductions, not just an occasional introduction. Could or would Ireland's early colonizers have made the necessary journeys with such animals?

The possibility of some carnivores swimming or rafting into the country should also be considered, as well as a land connection, or partial land connection. All we can conclude definitely is that their journey was difficult, difficult enough to exclude other forms and that there is a probability that more than one method of transport was involved.

A more important problem, in the author's view, is how these carnivores survived after arrival? For they must have survived in order to have any likelihood of leaving remains behind. The carnivore fauna is not impoverished, yet the mammalian prey fauna certainly is (Table 1). Take for example the Irish stoat. It is smaller than stoats elsewhere and this has been ascribed to the absence of the weasel here (Hutchinson, 1959; Williamson, 1972). Given this suggestion we would expect the Irish stoat to hunt down tunnels more than stoats elsewhere. However, when we examine the list of suitable prey species we find that most are considered to have been introduced. Only three suitable mammal prey species are considered native; the Irish hare, pygmy shrew and the red squirrel.

The pygmy shrew is not believed to burrow, it tastes nasty and as a secondary consumer is in an unsuitable position in the food chain for a prey species. The Irish hare, as an adult, would be very big for a stoat to prey on, in particular for the small Irish stoat. Certainly young hares could have been prey, but they would only have been available seasonally. Red squirrels live in trees and their populations cycle erratically, which means that they would not have provided a constantly available food supply.

If we accept that the Irish stoat is ecologically adapted to, and dependant on, tunneling small mammal prey, there is a problem in explaining its survival, until man introduced suitable prey. A predator must have suitable available prey all year round, every year.

There is therefore a prey gap for the stoat in the postglacial. Were there other prey species present that we are, as yet, unaware of? Did the lemmings survive, filling this gap? As all the other eight species of carnivores are also known to eat small mammals (to a greater or lesser extent) they too would have been affected by (and indeed affect) the prey gap. The ecological effects of this prey gap, if it did exist, would be important in any ecological reconstruction of post glacial fauna.

How are we to go about solving these problems? The comparative study of the morphology, ecology and genetics of Irish, British and European mammals is one approach. The continuing study of bone remains is another - progress in our understanding of the postglacial would be greatly helped by a good faunal assemblage from a known postglacial site. Archaeological sites have served us well, mainly, for species associated with man. Investigation of a site (or sites) of bone accumulations not interfered with by man might solve some of our problems.

A rather neglected field of investigation in this area is parasitology. If an animal is introduced to a limited area in small numbers it is probable that at least some of its parasite fauna will not come with it, or survive in the new area. Can parasites tell us anything useful about how their hosts arrived, and survived, in Ireland?

For example. It is now widely accepted that the wood mouse is not native to Ireland and was accidently introduced by man (Corbet, 1961; Fairley, 1972). The rare rodent flea, *Rhadinopsylla pentacantha* (Rothschild) was recently rediscovered in Ireland on a wood mouse (Sleeman, 1983). A problem with the hypothesis that the wood mouse was introduced is that it is improbable that an uncommon nest flea, rarely found on its host's body, like *Rhadinopsylla*, could enter the island on mice introduced by man. It is of interest that *Rhadinopsylla* has been recorded on two islands of the Inner Hebridies, namely Eigg and Arran (George, 1974). These islands would have been connected to the putative land connection between Scotland and Ireland (Yalden, 1982).

References

Brown, J.H. and Lasiewski, R.C. (1972) The metabolism of weasels: The cost of being long and thin. Ecology. 53: 939-943.

Corbet, G.B. (1961) Origin of the British insular races of small mammals and the Lusitanian fauna. Nature (London). 191: 1037-1040

Corbet, G.B. (1966) Terrestrial Mammals of Western Europe. Foulis, London.

Fairley, J.S. (1972) The fieldmouse in Ireland. Ir. Nat. J. 17: 152-159.

Fairley, J.S. (1975) An Irish Beast Book. Blackstaff Press, Belfast.

George, R.S. (1974) Provisional Atlas of the Insects of the British Isles. Part 4 Siphonaptera: Fleas. Biological Records Centre, Monks Wood, Huntingdon.

Gibb, J.A. and Flux, J.E.C. (1973) Mammals. In The Natural History of New Zealand edited by G.R. Williams, A.H. and A.W. Reed, Wellington.

Hutchinson, G.E. (1959) Homage to Santa Rosalia or Why are there so many kinds of animals? American Naturalist. 93: 145-159.

King, C.M. and Moors, P.J. (1979) Coexistance, foraging strategies and biogeography of weasels and stoats in Great Britain. Oecologia. 39: 129-150.

Sleeman, D.P. (1983) Rhadinopsylla pentacantha (Rothschild) A rare flea from a wood mouse. Ir. Nat. J. 21: 191.

Williamson, M. (1972) The Analysis of Biological Populations. Edward Arnold, London.

Van Wijngaarden-Bakker, L.H. (1974) The animal remains from a Beaker settlement in Newgrange, Co. Meath: First report. Proc. R. Ir. Acad. 74C: 313-383.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

Yalden, D.W. (1982) When did the mammal fauna of the British Isles
arrive?
Mammal Review, 12: 1-57.

Author's Address

Department of Zoology,
University College,
Cork,
Ireland.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

HOW COULD MAMMALS BECOME IRISH?

D. W. Yalden

The Nature of the Problem

The Irish mammal fauna at present includes the mountain hare, stoat, pine marten, red fox, badger, otter, red deer, red squirrel and pygmy shrew, which are believed to be native mammals, and several others including wood mouse, house mouse, bank vole, hedgehog, brown rat and rabbit which are known or believed to be relatively recent human introductions (Table 1). Palaeontological or archaeological work suggests that reindeer, giant deer ("Irish Elk"), brown bear, wolf, and probably horse and wild cat should be added to the list of native mammals, but they have become extinct in the last 10,000 years.

There seems every reason to believe that in Ireland, as in the rest of the British Isles, the maximum spread of the last ice sheet, about 20,000 years ago, was accompanied by such severe conditions, even in the unglaciated regions of the south of these countries, that none of the present mammal fauna survived here. Just possibly the mountain hare and stoat might have occurred, along with high arctic forms such as arctic fox and lemmings, but there is no evidence that these survived in Ireland even in lateglacial times when conditions were improving. It seems certain that all of the present fauna has arrived since, say, 15,000 years ago. Some very common and widespread British mammals are missing from Ireland, however, some of them species which, in Europe, occur well north of the Arctic Circle: field vole, water vole, common shrew, water shrew, mole, weasel, polecat, roe deer, as well as the more southerly yellow-necked mouse, harvest mouse and dormouse are among the absentees. The problem, then, is to explain how the Irish native mammals arrived without, at the same time, these absentees also arriving.

There are three possibilities: human introduction; swimming; a selective landbridge.

Human Introduction

If such species as wood mouse and bank vole, not to say sheep and cattle, have been brought in by man, could other species have come the same way, either by accident (e.g. as stowaways in fodder for livestock) or design? Certainly red deer, wild boar and mountain hares would have been potential food animals and some of the others might have provided fur. However, some of the supposed natives are extremely unlikely to have been transported in this way - one cannot conceive of wolf or brown bear sharing a small Mesolithic boat, while the pygmy shrew is a very unlikely candidate for accidental transport when compared to the much more abundant (in Britain) common shrew. If these species arrived naturally, there is no reason to rule out a natural arrival of other natives.

Swimming

Red deer and wild boar, at least, are quite adept swimmers and even mountain (Irish) hares are recorded as regularly swimming to islands in loughs. If the Irish Sea were, in Late Glacial or early Postglacial times, narrower than now, it would have been easier to cross. Swimming across such a narrow sea would, of course, be less hazardous for larger mammals, and it is notable that most of the absentees are small mammals.

The problem with this hypothesis is that some absentees are surely better swimmers, and more likely to have swum across, than some of the native Irish mammals. The water vole and water shrew are more probable entrants this way than the pygmy shrew, while the beaver and moose are even more probable swimmers. Moose and beaver were well established in England by Mesolithic times, but have never been recorded from Irish archaeological sites.

Selective Landbridge

I have argued elsewhere for the possibility of a low-lying, waterlogged, land bridge as the likely explanation for the presence in Ireland of the pgymy shrew, in the absence of the common shrew. The common shrew is more fossorial than the pygmy shrew, and about a third of its diet is earthworms. The absence of the mole, and perhaps also of other burrow-dwelling small mammals (water shrew, water vole), might be similarly explained. Given the evidence of relative sea levels and the deep channel down the centre of the Irish Sea, (see Devoy, this volume) any such landbridge must have been between S.W. Scotland and N.E. Ireland. The problem then is to decide when it existed, and for how long. Since the reindeer and giant deer were in Ireland in Allerod (Windermere) times, there was presumably a landbridge then. One possibility is that all other native Irish mammals also arrived then (though we have no fossil evidence of them) and survived the subsequent climatic deterioration (Younger Dryas Nahanagan times). Palynological and palaeoentomological evidence suggests that this was unlikely (that the Younger Dryas was too severe), but perhaps not impossible. Alternatively, there might have been a short-lived landbridge early in postglacial times. At present, evidence of relative sea-levels suggests that this was unlikely. Clearly there is an impasse here which can only be resolved by more evidence. We need archaeological evidence from lateglacial and Mesolithic sites in Ireland which will confirm when various species of presumed native species arrived; we also need geological evidence from the Irish sea floor, which will confirm when the Irish Sea became, indeed, a sea as opposed to a meltwater channel or lake. If possible, we also need geological evidence from the region(s) of the possible landbridge(s), to give us a better idea of whether, when, and for how long, it existed. Indeed, evidence on relative sea-levels around the western coasts and isles of Scotland is still insufficient to confirm or deny what is, at present, little more than conjecture.

I appreciate that this brief synopsis makes no acknowledgement of the enormous amount of work that has been synthesized to produce it; a full bibliography is appended to my recent review (Yalden, 1982), and the specific details relevant to the pygmy shrew are in Yalden (1981).

References

Yalden, D.W. (1981) The occurrence of the Pygmy shrew Sorex minutus on moorland, and implications for its presence in Ireland. J. Zool. (Lond.), 195: 147-156.

Yalden, D.W. (1982) When did the mammal fauna of the British Isles arrive? Mammal Review. 12: 1-57.

Author's Address

Department of Zoology,
University of Manchester,
England.

4. THE RECORD FROM FISH, AMPHIBIANS AND REPTILES

Occ. Pub. Ir. Biogeog. Soc. No. 1.

THE POSTGLACIAL COLONISATION OF IRELAND BY FISH, AMPHIBIANS AND REPTILES

J. P. F. Wilson

Introduction

The Irish fish, amphibian and reptile fauna includes only a small number of species known to be native. However, some of these species' locations pose fundamental questions about postglacial mechanisms of colonization, notably the pollan of Lough Neagh, the charr of Coomasaharn lake, and the natterjack toad, found only in the Dingle Peninsula. The occurrence of these species will be described in some detail below. The primary (non-migratory) freshwater fish and the amphibians and reptiles face problems of dispersal similar to those of mammals, as described by Yalden (1982).

Freshwater Fish

The species composition of the fish fauna of both Britain and Ireland has been markedly influenced by introductions, both from abroad and within each country, for economic, sporting and ornamental purposes. The Irish freshwater fish may be functionally divided into stenohaline (narrow salinity tolerance) and euryhaline (broad salinity tolerance) groups (Table 1). Salinity tolerance may vary with latitude; marine flounders Platichthys flesus L. enter fresh water in the northern parts of the British Isles, for example. This has implications for the distribution of charr and pollan, which are not salt-tolerant in these latitudes at present.

It seems unlikely that any of the present Irish stenohaline fish (all of them non-salmonid "coarse" fish) could have survived the last glaciation in any part of Ireland. Most cyprinids require relatively warm water for spawning, for example. This poses the question of how the present coarse fish colonized Ireland.

Southern Britain probably obtained its fish fauna near the beginning of the postglacial or Littleton Warm, when the rivers of south-eastern England were part of the Rhine system, but by this time it would have been too late for them to have reached Ireland by any lake or river connection (Wheeler, 1977). Giraldus Cambrensis noted the presence of salmonids, eels and lampreys in Ireland in the 12th Century, but specifically pointed out that pike, perch, roach, minnow, loach and bullhead were absent (O'Meara, 1951). This and other historical evidence, along with the patchy distribution of many coarse fish in Ireland, indicates that all the present coarse species were introduced in historical time. In some cases the introductions have been documented (Went, 1978).

Of our three lamprey species, the brook lamprey is stenohaline and may have been introduced by anglers as livebait. Both of the other species are anadromous, i.e. they spawn in fresh water but go to sea to feed. The three-spined stickleback is found in the sea, especially in northern regions. The ten-spined stickleback is much less salt-tolerant and has a restricted distribution in Ireland: it was probably introduced.

The group known as salmonids includes salmon, trout, charr, whitefish and grayling Thymallus thymallus L. In general salmonids are euryhaline, inhabit cold water and exhibit a high degree of phenotypic plasticity. The grayling is perhaps the least salt-tolerant of salmonids and this is probably why it did not colonize Ireland.

Atlantic salmon live and feed in the sea, entering rivers to breed. Payne et al. (1971) found two races of salmon, identifiable by characteristic transferrin allelic frequencies and named Celtic and Boreal races. These are now present in north-western and southern Ireland respectively. They were probably separated by the last glaciation.

Many isolated populations of brown trout exist. Ferguson and Fleming (1983) used electrophoretic analysis of the enzyme lactate dehydrogenase or LDH to show that reproductively isolated populations, known as gillaroo, sonaghen and ferox trout, exist sympatrically in Lough Melvin. They also propose that genetically distinct trout colonized Irish freshwater successively after the last glaciation.

Rainbow trout in the wild in Ireland are farm excapes; the species was first introduced in the late 19th century but does not breed in the wild.

The charr is anadromous in the subarctic from Oslo Fjord (59^{o} N) northwards. It is widely accepted that the potentially anadromous charr and whitefish exist in more southerly lakes at present because in glacial times they lived near the edge of the ice sheet and went into fresh water to breed; as temperatures rose postglacially, the fish became isolated in fresh water. The charr of Lough Finn, Co. Donegal and L. Coomasaharn, Co. Kerry are dward charr, but the Coomasaharn population is unique in the British Isles in having 18-19 gillrakers, rather than the usual 13-15, on the lower arch. Behnke (1972) has proposed that the Coomasaharn population is a relict of a pre-glacial stock, although there is no direct evidence for this as the degree of electrophoretic distinctness of European and Siberian charrs is not known (Ferguson and Fleming, 1983).

It may be that in its origin and possible Siberian ancestry, this charr is paralleled by the pollan. Although most authors have chosen to regard pollan as conspecific with one or other of the British coregonines, Ferguson _et al_. (1978) have shown that electrophoretic patterns of pollan are identical with those of the anadromous Arctic whitefish _Coregonus autumnalis_ Pallas, whose geographically nearest representatives are in northern Finland. The two whitefish are apparently identical, and probably separated only since the last glaciation. Maitland (1970) proposed the existence of a postglacial Lough Hibernia, where the Irish Sea is at present, from where the British and Irish coregonines colonised their present lakes. Ferguson _et al_. (1978) argue that if this were the case, pollan would be found in British lakes at present. They suggest that _C. autumnalis_ colonized Ireland from the south-west, which was the first part of Ireland to become ice-free, and entered the Shannon. By the time the British lakes were ice-free, other species had colonized that island from the Continent.

Two anadromous species of shad are found in Irish waters; the rare Allis shad and the twaite shad. The goureen of Lough Leane, Killarney was described as a subspecies of the twaite shad, named A.f. killarniensis, distinguished by a high gillraker number. Unlike charr and pollan, shad are not Arctic fish. It seems likely that the goureen did not arrive until well after the glaciation, and that the population became isolated for generations, until it became freshwater adapted. Freshwater populations of A. fallax are also found in the Rhone and in some Italian lakes.

Amphibians and Reptiles

Although there are 19 species of native amphibians and reptiles in France, and 12 species in Britain, Ireland has only one undisputed native amphibian - the smooth newt Triturus vulgaris - and one native reptile - the viviparous lizard Lacerta vivipara. Amphibians are not salt-tolerant, and the newt probably arrived in Ireland by whatever land connection may have existed postglacially. The species is widespread in Europe, and found throughout the British Isles.

The frog Rana temporaria is similarly widespread, but there is evidence from early writings that there were no frogs in Ireland in mediaeval times. The frog's introduction to Trinity College, Dublin in the 17th century had been documented, but it may have been introduced by the Normans (O'Rourke, 1970).

Of the three species of Bufo toads in Europe, the common toad Bufo bufo L. is the most widespread, but is not found in Ireland. The natterjack Bufo calamita occurs in northern and western Europe, has a discontinuous distribution in Britain and is restricted to the Dingle Peninsula in Ireland. Its presence in Ireland is surprising, and its distribution almost equally so. It has been regarded as a member of the Lusitanian fauna, but it is unlikely to have moved northward as rapidly as other Lusitanian organisms such as beetles. Yalden (1982) has pointed out that the natterjack would have been prevented from getting to Ireland postgalcially by the deep freshwater channel which existed where the Irish Sea is at present. Macdougald (1942) reports an old tradition that a ship once landed a number of natterjacks at the head of Dingle Bay. While the frog could have been introduced as a food item, it is unlikely that introduction of toads would have been deliberate. It might be that a ship or ships took natterjacks on board in Britain or the Continent with sand used as ballast, and unloaded them on a beach as cargo was loaded in Kerry (Frazer, 1983).

The viviparous lizard is a northern European species, extending beyond the Arctic Circle. Like the newt, its presence here is best explained by a post-glacial land connection.

A recent addition to the Irish fauna is the slow worm Anguis fragilis apparently introduced quite recently (McCarthy, 1977). The species is widespread in Europe, as are the native viviparous lizard and smooth newt, and it is difficult to account for its previous absence from Ireland.

References

Behnke, R.J. (1972) The systematics of salmonid fishes of recently glaciated lakes. Journal of the Fisheries Research Board of Canada. 29: 639-671.

Ferguson, A., and Fleming, C.C. (1983) Evolutionary and Taxonomic significance of protein variation in the Brown Trout (Salmo trutta L.) and other salmonid fishes. Systematics Association Special Volume No. 24: Protein Polymorphism: Adaptive and Taxonomic Significance edited by G.S. Oxford and D. Rallinson. Academic Press.

Ferguson, A., Himberg, K.J.M. and Svardson, G. (1978) Systematics of the Irish pollan (Coregonus pollan Thompson): an electrophoretic comparison with other Holarctic Coregoninae. J. Fish Biol. 12: 221-233.

Frazer, D. (1983) Reptiles and Amphibians in Britain. Collins, New Naturalist, London.

MacDougald, T.J. (1942) Notes on the habits of the natterjack in County Kerry. Ir. Nat. J. 8: 21-25.

McCarthy, T.K. (1977) The slow-worm, Anguis fragilis L., A reptile new to the Irish fauna. Ir. Nat. J. 19: 49.

Maitland, P.S. (1970) The origin and present distribution of Coregonus in the British Isles. pp 99-114 In Biology of coregonid fishes. C.C. Lindsey and C.S. Woods, University of Manitoba Press, Winnipeg.

O'Meara, J. (1951) Giraldus Cambrensis' Topographica Hibernica - translation. Dundealgan Press, Dundalk.

O'Rourke, F.J. (1970) The fauna of Ireland. Mercier Press, Cork.

Payne, R.H. Child, A.R. and Forrest, A. (1971) Geographical variation in the Atlantic salmon. Nature (London). 231: 250-252.

Went, A.E.J. (1978) The zoogeography of some fishes in Irish waters. Fisheries Leaflet no. 93, Dublin.

Wheeler, A. (1969) The Fishes of the British Isles and Northwest Europe. MacMillan, London.

Yalden, D.W. (1982) When did the fauna of the British Isles arrive? Mammal Review. 12: 1-57.

Author's Address

19 Beaumont Road,
Chiswick,
London W4 5AL,
England.

5. COLONIZATION BY INVERTEBRATES

Occ. Pub. Ir. Biogeog. Soc. No. 1.

USE OF INVERTEBRATES, AS EXEMPLIFIED BY CERTAIN INSECT GROUPS, IN CONSIDERING HYPOTHESES ABOUT THE HISTORY OF THE IRISH POSTGLACIAL FAUNA

Martin C.D. Speight

Biogeographical patterns: present & past

A comparison of the present Irish species lists of selected (see Appendix 1) taxonomic groups (number of Irish species involved = 475, i.e. approximately 4% of the total Irish fauna) with the present British and continental European species lists for the same taxonomic groups (total number of species involved 1000) demonstrates that the Irish fauna is essentially an extension of the fauna occurring in Western seaboard countries from Denmark round to N. France (only 4% of the Irish fauna is arguably of other origins) and that the Irish fauna has arrived via Great Britain.

It is less easy to decide when during the postglacial the present fauna arrived in Ireland and whether its constitution has altered markedly from time to time during the postglacial. However, the lack of extant endemic taxa among those surveyed and the great similarity between Irish and British species lists provide no support for any notion that the species present today in Ireland have been isolated there for any significant length of time. Indeed, it would seem very doubtful whether any significant fraction of the present Irish fauna arrived in Ireland prior to the last 'cold snap' beginning at 10,500 B.P. (see Table 2). This view is supported by ecological data; no more than perhaps 5% of the present fauna could be expected to survive such a 'cold snap' *in situ* in Ireland.

It is apparent that present, natural, immigration rates among the invertebrates surveyed (calculated as equivalent to one species establishing itself sucessfully in each 100 year period of the last 10,000 years, for each taxonomic group now represented in Ireland by 100 species) would be quite adequate to account for the arrival over 10,000 years of the estimated total Irish fauna of 12-14,000 species. Also, up to the time that man's activities substantially reduced both the range and size of populations of animal species in Great Britain the rate of faunal immigration to Ireland must have been considerably higher (probably by as much as a factor of x 10) than it is now. So there seems to be no need to invoke the existence of a landbridge between Ireland and Great Britain early in the postglacial to explain the existence of the present Irish fauna. Further, the make-up of the present invertebrate fauna provides no more support for the notion that there was a landbridge than it does for the notion that there was no landbridge. Neither does the consitution of the invertebrate fauna suggest that import by human agency has played a major role in establishing species in Ireland.

Some Hypotheses

If this scenario of events is accepted, it is not the similarities between the Irish, British and continental faunas which have the greatest interest, but the differences between them. Using the same selected taxonomic groups to explore these differences and considering the ecology and trophic groups of the species concerned, oak-woodland detritivores are highlighted as a faunal group surprisingly poorly represented in Ireland. The most plausible explanation for under-representation in this component of the fauna is that prior to virtual eradication of native Irish oak forest by man during the historic period and commercialisation (incorporating removal of over-mature trees and 'cleaning' of the forest floor) of the surviving remnant, many of the missing animal species were present in Ireland but are now extinct there. The characteristically relict status of woodland detritivores extant in Ireland may be cited in support of this hypothesis. Oak forest is believed to have been the dominant natural vegetation type in Ireland. So such a drastic influence upon the Irish forest fauna by man would represent a major influence upon the Irish fauna as a whole. Thus, to attempt to divine the character of pre-historic postglacial faunas of Ireland from the constitution of the present day fauna, without first being able to either substantiate or dismiss hypotheses which suggest that major changes have occured in the constitution of the fauna during the historic period, could evidently lead to very misleading results. In order to test the significance of such hypotheses more investigation is needed of the faunal remains preserved in deposits from all times during the post-glacial in Ireland, and in particular of the fauna of deposits dating from the early historic period, prior to the last major phase of forest clearance.

Consideration of the Irish fauna of these various invertebrate groups has brought to light a range of features peculiar to individual taxonomic groups. Thus, one predominantly freshwater wetland group, the horse-flies (Diptera: Tabanidae) is inexplicably under-represented in Ireland (10 species in Ireland, 29 in Great Britain). In other groups considered (eg. Coleoptera; Carabidae; Diptera; Sciomyzidae; Syrphidae) the freshwater wetland component of the fauna is the most complete element in Ireland. It is tempting to erect hypotheses based upon such anomalies as the under-representation of tabanids. Was it, for example, an absence of herds of grazing mammals in Ireland, prior to livestock introductions by man, that accounts for the minimal horse-fly fauna, also demonstrating an inability on the part of horse-flies, at least, to cross the Irish Sea once grazing mammals were available? Development of such hypotheses based on small groups of species is undeniably a useful tool for gaining insights into the possible history of the species groups concerned. But it is less acceptable to extrapolate from the particular to the general in such a way that, in order to explain the presence in (or absence from) Ireland of the species of some small taxonomic group, a hypothesis is erected which is not compatible with the make-up of most of the Irish fauna. Thus, to explain the absence of tabanids from Ireland as due to their inability to cross the Irish Sea and cite this as evidence that the Irish Sea represents a zoogeographical barrier which animal species in general are unable to pass would not be justified in the light of the data available about the other 465 Irish invertebrate species considered here.

Such a criticism could also be made of hypotheses put forward to explain other 'odd-ball' features of the Irish fauna. Thus, is it reasonable to invoke the existence of a landbridge to explain the presence in Ireland today of certain mammal species, when the rest of the fauna (especially when the significance of absentee species, is considered) provides no obvious support for such a notion? Equally, it is reasonable to construct an offshore glacial refugium hypothesis to explain the presence in Ireland of that 1% (or less) of the fauna known elsewhere in W. Europe only from Iberia or the Mediterranean basin? Where such questions are engendered by some small group of present day Irish species, rather than by some major part of the island's flora and fauna, it would seem reasonable that explanations should be sought which would affect only the 'odd-ball' species themselves, rather than all of the island's biota. Perhaps we would be wisest to accept that at present many such 'odd ball' features of the Irish fauna remain inexplicable, biogeographically, rather than seeking to explain them at whatever cost to credibility and logic? Such a course would certainly seem prudent where early postglacial events are involved, since it appears doubtful that analysis of the presentday fauna (or flora) could provide answers to questions such as whether or no there was a landbridge linking Ireland and Great Britain earlier in the postglacial, due to problems of interpretation introduced by subsequent immigration and extinction events. In any case, recent work reviewed during this conference demonstrates there is a good chance that geomorphological/geological research will provide a much clearer picture of the postglacial history of the seabed round the Irish coast than faunal and floral investigation ever could. However, if the Irish floral and faunal history of the last 5,000 years is to be understood, biogeographical analyses of the present species complement backed by work on floral and faunal remains preserved in relevant (eg. archaeological) deposits would seem the tools most appropriate to the task.

It can be concluded that the efforts of Quaternary biologist and biogeographer might be better rewarded from now on if they were focused more upon understanding the recent faunal and floral history of Ireland than on issues like 'the landbridge question'. The alternative would be to risk that we repeatedly obtain inconclusive results. Medawar's definition of science as "the art of the soluble" bears consideration in this context!

*Footnote: Participants were informed that the Cork Conference would not result in published proceedings, so that they could draw upon material not yet ready for publication. Faced subsequently with the invidious choice of presenting either a heap of semi-digested data or conclusions drawn from largely unpublished data, the present author has chosen the latter course.

Appendix 1: Taxonomic groups used

TAXONOMIC GROUP	NO.IRISH SPECIES	NO.GB SPECIES	NO.TEMP.W.EUR.SPECIES
Coleoptera			
Carabidae	200 (Speight et al, 1983)	360	c.450 (Bonadona, 1971; Turin, 1981)
Cerambycidae	18 (Speight, in prep.)	56	c.100
Diptera			
Asilidae	3 (Chandler, 1975)	26	c.50
Sciomyzidae	50 (Speight, 1979b;)	63	c.80
Stratiomyiidae	31 (Chandler, 1975; Speight, 1981b; Speight et al, 1979)	47	c.60
Syrphidae	170 (Speight, 1978a,b; 1979a; 1980a,b; 1981a; 1982; Speight et al, 1979)	256 (Stubbs, 1983)	c.350
Tabanidae	10 (Chandler, 1975; Irwin, 1977)	29	c.50 c.50 (Chvala et al, 1972)
Estimated total	c.12,000	c.20,000	c.100,000

invertebrate

fauna

GB = Great Britain

TEMP.W.EUR. = Atlantic seaboard states from Denmark round to N. France (inclusive)

The information sources used in arriving at figures for the number of Irish species in the taxonomic groups used are given above. the figure for Great Britain are (except for the Syrphidae) derived from the various parts of Kloet, S. and Hincks W.D. A Check List of British Insects (second edition), Royal Entomological Society, London. The figures for the total Temperate Western European fauna are, except where stated otherwise in the table, derived from unpublished lists compiled by the author, using diverse sources.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

References

Bonadona, P. (1971) Catalogue de Coleopteres Carabiques de France Novelle Rev. d'Entomologie, Suppl., Toulouse, 1-177.

Chandler, P.J. (1975) An account of the Irish species of two-winged flies (Diptera) belonging to the families of larger Brachycera (Tabanoidea and Asiloidea). Proc. R. Ir. Acad. 75 B(2): 81-100.

Chvala, M., Lynwborg, L. & Moucha, J. (1972) The Horse-flies of Europe (Diptera, Tabanidae). Entomological Society of Copenhagen. 499pp., 8pl.

Irwin, A.G. (1977) Chrysops sepulchralis F. (Dipt., Tabanidae) new to Ireland. Entomologist's mon. Mag. 112: 172.

Speight, M.C.D. (1978a) A check list of Irish Syrphidae (Diptera). Bull. Ir. Biogeog. Soc. 2, 1977-8: 26-31.

Speight, M.C.D. (1978b) Cheilosia laskai sp.n. (Diptera: Syrphidae) from Western Ireland. Ir. Nat. J. 19: 217-22.

Speight, M.C.D. (1979a) Eumerus tuberculatus, Geomyza majuscula and Pteromicra leuopeza: insects new to Ireland, including a key to British Isles Eumerus species. Ir. Nat. J. 19: 397-9.

Speight, M.C.D. (1979b) A check list of the Irish Sciomyzidae (Diptera). Bull. Ir. Biogeog. Soc. 3: 27-29.

Speight, M.C.D. (1980a) Brachypalpus laphriformis (Diptera: Syrphidae) in Ireland and its probable demise. Ir. Nat. J. 20: 70-2.

Speight, M.C.D. (1980b) Chiloxanthus pilosus, Palloptera modesta and Pipizella heringi confirmed as Irish species. Ir. Nat. J. 20: 72-3.

Speight, M.C.D. (1981a) The Irish Anasimyia species, including a key and first records of A. contracta (Diptera: Syrphidae). Ir. Nat. J. 20: 229-34.

Speight, M.C.D. (1981b) Chorisops nagatomii, an insect new to Ireland and its segregation from C. tibialis (Diptera: Stratiomyiidae). Ir. Nat. J. 20: 327-9.

Speight, M.C.D. (1982) Acrocera globulus, Limnia paludicola and Sphaerophoria loewi: insects new to Ireland. Ir. Nat. J. 20: 369-72.

Speight, M.C.D. (in prep) An annotated list of the Irish Cerambycidae (Coleoptera).

Speight, M.C.D., Anderson, R. and Luff, M.L. (1983) An annotated list of the Irish ground beetles (Col., Carabidae + Cicindelidae). Bull. Ir. Biogeog. Soc. (6), 1982: 25-53.

Speight, M.C.D., Williams, M. de C. and Withers, P. (1979) *Pachygaster minutissima*, *Psacadina zernyi* and *Xylota tarda*: insects new to Ireland. Ir. Nat. J., 19: 354-5.

Stubbs, A.E. (1983) British Hoverflies. British entomological and natural history society, London. 253 p., 12pl.

Turin, H. (1981) Provisional checklist of the European Ground-beetles (Coleoptera, Cicindelidae & Carabidae). Nederlands entomologische Vereniging, Monograph 9, Amsterdam, 249pp.

Author's Address

Research Branch,
Forest & Wildlife Service,
Department of Fisheries and Forestry,
Bray,
Co. Wicklow,
Ireland.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

BIOGEOGRAPHICAL ASPECTS OF IRELAND'S INVERTEBRATE FAUNA

T.K. McCarthy

Introduction

Questions relating to the origin and history of the island's flora and fauna have held a particular attraction for Irish naturalists. There has been much speculation and argument since the publication of Forbe's (1846) essay on the subject. Much of the earlier work has been reviewed by Charlesworth (1930), Praeger (1932) and Beirne (1952). Opinion has remained divided as to whether the entire flora and fauna was obliterated by the Pleistocene glaciations (see Woodman, Watts, Stuart, this volume) or if some elements represent relict populations which survived from interstadial, interglacial or even Tertiary times, in southern or maritime refugia. Palaeoceological studies on the Irish invertebrate fauna are of a very limited nature. This is particularly true of the insects which form the vast majority of the species but also of the, more easily studied, molluscs. This is unfortunate in view of the considerable impact such investigations have had on our knowledge of British and North European faunas generally. The present account deals largely with a biogeographical evaluation of the present day fauna. Even such an approach must be regarded as a preliminary study because much work remains to be done in recording the distribution of invertebrates in Ireland and the rest of Europe. In recent years much effort has been devoted to such work as part of the European Invertebrate Survey.

Biogeographical Patterns: Methodology and Analysis

Most of Ireland's invertebrates are species which occur in Britain's fauna which is in turn largely composed of species common in northwestern Europe. For the purposes of this paper a comparison was made between Ireland and Britain in respect of selected groups of insects and other invertebrate taxa occurring in terrestrial and freshwater habitats. The insects, being mostly winged, might be regarded as having greater powers of active dispersal than other taxa. The groups dealt with are reasonably well studied and are hopefully typical of the island's non marine invertebrates. (Percentages quoted refer to the size of the Irish species list, N, relative to the number in Britain).

The combined Irish species lists for the groups investigated includes 2131 species which represents about 65% of the equivalent number 3297 for Britain. The freshwater insects involved (N = 790) represent about 73% of the equivalent section of Britain's fauna. Individual groups of them differ in their percentage occurrence in Ireland: stoneflies, Plecoptera (N = 19, 61%) mayflies, Ephemeroptera (N = 31, 66%), dragonflies etc. Odonata, (N = 24, 62%), waterbugs, Heterotera (N = 50, 85%), caddisflies, Trichoptera (N = 143, 73%), water beetles, Coleoptera (N = 126, 66%), Chironomid midges, Diptera (N = 347, 75%) and snail-killing flies, Diptera: Sciomyzidae (N = 50, 79%). Further Irish records can be anticipated in respect of several of these groups (Southwood and Leston, 1959; Illies, 1978; Heath, 1978; O'Connor, 1978; McCarthy and Walton, 1980; Walton, 1981; Cotton, 1982; Murray and Ashe, 1984; Costello et al., 1984 and Speight, in this volume). The non-insect freshwater groups investigated (N = 281, 78%) seem to be generally better represented in the Irish fauna, with the unexplained absence of many copepods: freshwater sponges, Spongillidae, (N = 5, 120% Hydrozoa (N = 5, 71%), planarian worms, Tricladida (N = 10, 91%), leeches, Hirudinea (N = 13, 81%), molluscs (N = 56, 71%), Copepoda (N = 32, 51%), Cladocera (N = 135, 91%) and macro-crustaceans (N = 25, 78%) (McCarthy, 1973, 1975; Kerney, 1976; Illies, 1978 and T. Burke, pers. comm.). The combined lists of freshwater insects and other invertebrates (N = 1071) represents 74% of the equivalent elements in the British fauna. A rather similar proportion of terrestrial invertebrates other than insects seems to occur in Ireland. The groups included in this study (N = 189, 77%) were: earthworms, Lumbricidae (N = 22, 85%) land snails (N = 86, 80%), harvestmen, Opiliones (N = 14, 64%), centipedes, Chilopoda (N = 39, 76%) and woodlice (excluding synanthropic forms) Isopoda (N = 28, 74%). (Sankey & Savory, 1974; Kerney, 1976; Cotton, 1978; Mothersill, 1978; Ross, 1979; Dooge and Harding, 1982 and D. Dooge, pers. comm.). The terrestrial insect groups studied (N = 766) represented only 55% of the equivalent components in the British fauna. There is considerable variation in the extent to which particular groups occur in Ireland: Grasshoppers etc., Orthoptera (N = 10, 36%), booklice, Psocoptera (N = 40, 46%), butterflies, Lepidoptera (N = 31, 50%), hoverflies, Diptera: Syrphidae (N = 170, 68%) fungus gnats, Diptera:

gnats, Diptera: Mycetophilidae (N = 205, 45%) ground beetles, Coleoptera: Carabidae (N = 200, 55%), some rove beetle sub-families, Coleoptera: Staphylinidae (N = 67, 80%) ants, Hymenoptera: Formicidae (N = 17, 40 %) and bumble and cuckoo bees (Bombinae) and social wasps (Vespinae) (N = 26, 81%). The absence of many British terrestrial insects is a particularly interesting feature of Ireland's invertebrate fauna. This is especially true of such well known groups as ants and butterflies (Cotton, 1982b; Fahy, 1970; Higgins and Riley, 1970; Chandler, 1977; Smithers, 1978; Hammond, 1980; Speight, in press and J. Breen pers. comm.). Some parasitic invertebrate groups were also included in the analysis: ticks, Acari: Metastigmata, (N = 13, 62%) fleas, Siphonaptera (N = 37, 67%) some parasitic flies, Diptera: Gastrophilidae and Oestridae (N = 8, 73%) and metazoan parasites of freshwater fishes (N = 47, 37%). The overall lower than average occurrence of these parasites (N = 105, 50%) in Ireland reflects the depauperate parasitofauna of the host groups which are themselves very poorly represented in the country (George, 1974; Sleeman, 1980; Conneely and McCarthy, 1984 and T.C. Kelly pers. comm.).

The relationship between species number(s) and the area of islands (A) is generally described by the simple equation $S = CA^z$ which in its log form gives the linear equation $\text{Log } S = \text{Log } C + z \text{ Log } A$. The value of the constant C depends on the taxonomic group involved and geographical region etc. but values of z seem remarkably constant (between 0.20 and 0.35) (MacArthur and Wilson, 1967). Using this approach it is possible to estimate that for the ratios of the values S for Ireland (32,000 sq. miles) and Britain (89,000 sq. miles) should lie between 0.71 and 0.81 (McCarthy, 1975). This approach assumes an equilibrium situation with immigration rates balancing the effects of local extinctions. It can be seen that many of the percentage occurrences in Ireland of the groups dealt with above, such as freshwater forms and non-insect terrestrial groups, are at the equilibrium levels predicted. However, as noted above there are also many groups which clearly are not at such levels and the overall level (67%) remains outside the range predicted. The extent to which this reflects genuine impoverishment of the fauna as opposed to inadequate faunistic data is debatable.

Similar 'species-area' curves describe the patterns of species diversity in the case of non-isolated sections of mainland but values of z are lower and generally range from 0.12 to 0.17 (MacArthur and Wilson, 1967). Data such as the checklists of freshwater animals given by Illies (1978) can form the basis for such analyses. However, attempts to base curves on widely separated parts of Europe generally did not indicate statistically significant relationships. The distributional patterns were complicated by strong latitudinal gradients in diversity and high levels of endemicity in the faunas of southern geographical zones. To overcome these difficulties curves, for various taxa, were based on combinations of France with adjacent zones (zones 4, 8, 9, 13 and 14 in Illies account) to gain thirteen sets of points. This approach proved more satisfactory with the values of z ranging from 0.17 to 0.21 for the groups studied. The curve for a combined group of invertebrates :sponges, Hydrozoa, triclads, leeches, snails, Bryozoa, waterbugs and mayflies is typical and is given by the equation: $\text{Log } S = 1.92 + 0.19 \text{ Log } A$. Such curves can be regarded as saturation curves and should allow predictions to be made regarding the number of species that could be expected to occur in Britain or Ireland if the isolation effects of the marine biogeographical were absent. Not surprisingly the actual diversity of many groups is less than the predicted level for both Britain and Ireland, providing evidence of the varying extent to which isolation has affected different taxa. There are some groups, such as the waterbugs, which are apparently at saturation levels in both countries. However, it must be pointed out that this analysis was greatly restricted by the wide confidence limits that applied to most predicted values of Log S. It should be possible to investigate the relationship in a much more satisfactory manner using the atlases of species distribution which are being published as a result of the European Invertebrate Survey. In the context of the British Isles z values of 0.17 to 0.21 suggest that in the absence of the marine barriers Ireland's fauna would be of the order of 79% to 84% as diverse as the equivalent groups in Britain. Even lower values of z, would indicate higher percentage occurrences in Ireland, such as 88% when z = 0.12. The biota of Ireland and perhaps even more so Britain show impoverishment relative to small ecologically less diverse countries like Denmark and Belgium (Webb, 1983). However, this does not necessarily imply that missing species did not reach the British Isles since lower S values on islands are the result of the interacting influences of both lower immigration rates and higher extinction rates than in corresponding units of mainland (MacArthur and Wilson, 1967). That taxonomic groups should differ in the extent to which they approach saturation levels in Britain and Ireland may reflect differing dispersal abilities. Freshwater habitats such as ponds are transitional isolated units and the problems of passing from one catchment basin to another may be every bit as significant as trans-marine dispersal. Clearly animals of apparently low vagility have managed to become widely dispersed among the isolated freshwater habitats and disperal mechanisms are essential to their continued survival as species. Culver *et al*. (1963) concluded in the case of animals living in limestone caves in West Virginia that the aquatic forms had higher powers of dispersal that the terrestrial ones.

Dispersal Mechanisms

Studies on current immigration rates and modes of dispersal employed by invertebrates are of limited value in attempting to reconstruct the postglacial history of Ireland's fauna. There is naturally a bias in favour of observations on dispersal involving human agency and extensions of range by other natural active or passive mechanism largely go unnoticed. Variations in the nature of imports, their origin and mode of transport means that present day observations cannot be used to calculate what past rates of colonization by such mechanisms would have been. A wide variety of exotic insects and other invertebrates have been reported in recent years (see for example O'Connor and Nash, 1979, 1981, 1982, 1983). An early study by O'Rourke (1950) showed the potential of air traffic in this regard. The risk to agriculture from immigrant pests can be considerable (Elton, 1958). That accidental importations have occurred frequently in the past is evident from the number and distribution of synanthropic woodlice, myriopods, molluscs etc. in Ireland and insects including species such as, the formerly widespread, domestic cricket *Acheta domesticus* (L.) and cockroaches (Cotton, 1982b). Other examples in the country's terrestrial habitats include the Australian land nemertean *Argonemertes dendyi* (Dakin) and land planarian *Geoplana sanquinea* (Moseley)(Anderson, 1980; O'Connor *et al*., 1983). There are also a number of freshwater invertebrate immigrant species in Ireland which were introduced deliberately or accidentally by man. The oligochaete Branchiura sowerbyi Beddard is known only from two Irish localities, the Botanic Gardens in Dublin and Blarney lake in Cork where it may have been introduced at a time when imported medicinal leeches were stored there (McCarthy, 1974). The Canadian amphipod Crangonyx pseudogracilis Bousfield, an outstandingly successful colonist in Britain but unknown in mainland Europe (Macan, 1974), has recently been obtained in ponds near Dublin Zoo (Holmes, 1975). The North American amphipod Gammarus tigrinus Sexton is spreading through the northern part of Ireland as is the European Gammarus pulex (L.), introduced as fish food from Britain, which is apparently competitively displacing the native Gammarus duebeni Lilljeborg and and which may entirely replace the glacial relict form Gammarus lacustris Sars (Strange and Glass, 1979). The canal network greatly facilitated the spread of some freshwater immigrants, including the gammarids mentioned above and snails such as Bithynia leachi (Sheppard) and Planorbarius corneus (L.). The railway network has also facilitated the spread of some species. The woodlouse Eluma purpurescens Budde-Lund is in Ireland associated with railway lines and may have been dispersed by man in ballast (Dooge and Harding, 1982).

Natural colonization must have played the major role in establishing the present patterns of Ireland's animal communities. However, there are relatively few direct observations, though migrations of insects such as dragonflies, butterflies and moths are regularly recorded (e.g. Haynes and Hillis, 1981; Myers, 1981). The role of birds as agents of dispersal for freshwater organisms seems to be of some importance (Thienemann, 1950; Loffler, 1963; Maguire, 1963). Many authors, most recently Walton (1981) in the case of Microvelia pygmaea (Dufour), have discussed birds potential role for introducing new invertebrates to Ireland. Wind blown insects and other arthropods are frequently taken in samples of marine neuston off the west coast of Ireland giving an indication of the composition of the aeroplankton on such occasions (unpublished data). Insects themselves may also play a role in in dispersing smaller forms.

Local Extinctions

Evidence of local extinction of invertebrates is difficult to obtain and such events are generally not recorded. In recent times the relict psam--mophilic beetle Bembedion argentiolum Ahrens which formerly occurred round Lough Neagh appears to have become extinct in Ireland (Anderson, 1979) due perhaps to lake level changes and eutrophication. Clearence of the woodland at Powerscourt deerpark, County Wicklow, appears to have resulted in the disappearance of the hoverfly Brachypalpus laphriformis Macquart and other species from Ireland (Speight, 1980). The decline of woodland insects in Britain and the rest of Europe due to forest destruction is well documented (Hammond, 1974). O'Connor (1979) reported the occurrence of the beetle Blaps lethifera Marsham from medieval excavations in Dublin yet the species no longer occurs in Ireland. The medicinal leech Hirudo medicinalis L., which was originally an imported element in the Irish freshwater fauna, seems to have become extinct in the past century (McCarthy, 1974). Examples such as these serve to illustrate the fact that local extinctions occur periodically in the case of Irish invertebrates though the rate of such occurrences is unknown. The limited palaeocological evidence regarding Ireland's postglacial molluscan fauna provides further evidence of species decline (Kerney, 1976). The snail Vertigo alpestris Alder which occurred as a Flandrian sub-fossil in Ireland and the south of England now is restricted to northern western parts of England and Wales and is absent from Ireland. Yet the related form Vertigo geyeri Lindholm has become extinct in Britain but survives in Ireland (Norris and Pickrell, 1973).

The woodlouse Acaeroplastes melanurus (Budde-Lund) which formerly occurred at Howth, County Dublin, and was regarded as a Lusitanian species, also appears to have become extinct in Ireland (Dooge and Harding, 1982) and the small mountain ringlet butterfly Erebia epiphron, Knoch has not been recorded since 1901 (Baynes, 1964).

Special Faunal Categories

No account of Irelands fauna and flora would be complete without reference to three special biogeographic groupings: the American species, the Lusitanian species and the glacial relicts. One species, the sponge Heteromyenia ryderi (Potts), is regarded as representing an animal equivalent of the small grouping of plants recorded as American or amphi-Atlantic (Praeger, 1932). However, this sponge occurs in the

Faroes and its resistant stages, gemmules, whilst perhaps enabling it to survive cold periglacial conditions could also have been dispersed by birds. The evidence in favour of its being a survivor from pre-glacial times is thus debatable. The invertebrate species comprising the Lusitanian group includes the well known examples of the Kerry spotted slug Geomalacus maculasus Allman, and others absent from Britain such as the earthworm Lumbricus friendi Cognetti, the woodlice Oritoniscus flavus (Budde-Lund) and Acaeroplastes melanurus (Budde-Lund) . However , a variety of other species with a predominantly south westerly distribution in Britain, like the snail Theba pisiana (Muller) and the woodlice Metoponorthus cingendus (Kinahan) and Halophiloscia couchi (Kin), have been included at one time or another. The continental distributions of the species differ significantly with some occurring generally along Atlantic coasts of Europe and others extending into the Mediterranean. They do not form the discrete assemblage that the name Lusitanian suggests and they could be regarded now as a mixture of categories (Webb, 1983). In view of the role man has played in the dispersal of woodlice, earthworms etc. attempts to generalize regarding Ireland's fauna on the basis of the so-called Lusitanian species must be treated with caution (Corbet, 1962).

A wide variety of Ireland's invertebrates are regarded as glacial relicts in one sense or another. One category, called marine relicts, includes the crustacean Mysis relicta Loven. This is thought to have evolved in a large Siberian proglacial lake, along with other glacial relicts of marine origin, during the penultimate glaciation. It is considered to be derived from the marine form Mysis oculata Fabricius , of which some authorities regard it to be a sub-species. Having retained a tolerance to salinity it, and the other marine relicts, apparently spread along the margins of the ice caps during the last glaciation and repeatedly adapted to freshwater and brackish conditions (Segerstrale, 1966). Gammarus lacustris may have had a similar history and the present day distribution and physiology of Gammarus duebeni, which in the absence of competition colonized most inland waterways of Ireland, illustrate the potential that some brackish water animals have in this respect (Sutcliffe, 1971). It is curious that the copepod Limnocalanus macrurus Sars, a marine relict, which often occurs with M. relicta and which has been reported from Britain (Pennington, 1959), has not been found in Ireland.

Mysis relicta in Ireland frequently occurs in systems containing fish such as char, Salvelinus alpinus and Pollan, Coregonus pollan which can also be regarded as marine relicts of a sort.

Arctic and boreo-alpine representatives of many insect orders are known to occur in Ireland. It has been estimated that 15% of the chironomid midges in the Killarney area belong to these categories (D. Murray pers. comm.). Well known examples from other orders include the stonefly Capnia atra Morton, the caddisfly Apatania auricula (Forssland), the waterbugs Glaenocorisa propinqua (Fieber) and Sigara fallenoidea (Hungerford) and the water beetles Dytiscus lapponicus Gyllenhal and Agabus arcticus (Paykull) (Walton, 1967; O'Connor, 1978b, 1981; Costello et al., 1984). These animals are, in Ireland, generally considered to be represented by relict populations which were more widespread in the past when climatic conditions were more severe. Whether it is correct to regard them all as being survivors from the lateglacial is debatable. Studies on fossil Coleoptera have indicated a much more greater degree of flux in the fauna of the British Isles than was traditionally supposed (Coope, 1965). The small mountain ringlet butterfly, which appears to have recently become extinct in Ireland could have been included in this category of relicts (Baynes, 1964). The stenothermal, and generally spring dwelling, rheophilic flatworms which have been used in attempts to date the separation of Britain from mainland Europe, Crenobia alpina (Dana) and Polycelis felina, (Muller) could also be included as might the planarian Bdellocephala punctata (Pallas) whose only Irish station is at Lough Gur, County Limerick. (O'Rourke, 1946; McCarthy, 1973). Some sandy shore dwelling beetles known only from Lough Neagh in the British Isles are also regarded as relict species (Anderson, 1979).

Conclusions

From the foregoing account it can be seen that a great deal remains to be learned concerning the history of the Irish fauna. Further distributional surveys and particularly study of subfossil remains will obviously be of value. However, the focusing of attention on the ecological rather than historical aspects of the problem would seem to provide the best opportunities, at least in the short term, for a better understanding the composition of present day and past biotas. Webb

(1983) was able to conclude that about half the British species of flowering plants absent from Ireland were excluded by virtue of their ecological requirements rather than simply being unable to cross the Irish Sea. The restricted diversity of habitat and climatic conditions that animals and plants have available to them in Ireland is clearly of importance. The history of the flora has important implications for the insects associated with them (Southwood, 1961) and as Lack (1969) pointed out ecological factors appear to be of great importance in restricting Ireland's avifauna. However, the Irish fauna does clearly show signs of the havoc wrought by the glaciations in respect of certain taxonomic groups, the general lack of endemic species and the virtual absence of ecological groups, with special dispersal problems like cave-dwelling animals.

References

Anderson, R. (1979) The Coleoptera of a Lough Neagh sandy shoreline with recent records of Stenus palposus Zetterstedt (Staphylinidae) and Dyschirus obscurus Gyllenhal (Carabidae). Ir. Nat. J. 19: 297-302.

Anderson, R. (1980) The status of the land nemertine Argonemertes dendyi (Dakin) in Ireland. Ir. Nat. J. 20: 153-156.

Baynes, E.S.A. (1964) A revised catalogue of the Irish Macrolepidoptera (butterflies and moths). Classey. Middlesex.

Beirne, B.P. (1952) The origin and history of the British fauna. Methuen, London.

Chandler, P.J. (1977) New records of Irish fungus gnats (Diptera: Mycetophilidae). Ir. Nat. J. 19: 12-16.

Charlesworth, J.K. (1930) Some geological observations on the origin of the Irish fauna and flora. Proc. R. Ir. Acad. 39(B): 358-390.

Conneely J.J. and McCarthy, T.K. (1984) The metazoan parasites of freshwater fishes in the Corrib catchment area. J. Fish Biol. 24: 363-375.

Coope, G.R. (1965) Fossil insect faunas from late quaternary deposits in Britain. Adv. Sci. March 1965: 564-575.

Corbet, G.B. (1962) The "Lusitanian" element in the British fauna. Sci. Progr. 50: 177-191.

Costello, M.J., McCarthy, T.K. and O'Farrell, M.M. (1984) The stoneflies (Plecoptera) of the Corrib catchment area, Ireland. Annls. Limnol. 20: 25-34

Cotton, D.C.F. (1978) A revision of the Irish earthworms (Oligochaeta: Lumbricidae) with the addition of two species. Ir. Nat. J. 19: 257-260

Cotton, D.C.F., (1982a) Coenagrion lunulatum (Charpentier) (Odonata: Coenagrionidae) new to the British Isles. Entomologist's Gaz, 33: 213-214

Cotton, D.C.F. (1982b) A synopsis of the Irish Orthoptera. Entomologist's Gaz, 33: 243-254

Culver, D., Holsinger, J.R. and Baroody, D. (1963) Towards a predictive biogeography: the Green Briar Valley as a case study. Evolution, 27: 689-695.

Dooge, D. and Harding, P.T. (1982) Distribution atlas of woodlice in Ireland. An Foras Forbartha, Dublin.

Elton, C.S. (1958) The ecology of invasions by animals and plants. Chapman and Hall, London.

Fahy, E.D. (1970) The distribution of the Irish Psocoptera. Proc. R. Ir. Acad. 69(B): 139-163.

Forbes, E. (1846) On the connection between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area, especially during the epoch of the northern drift. Mem. Geol. Surv. Brit. 1: 336-432.

George, R.S. (ed.), (1974) Provisional atlas of the insects of the British Isles. Part 4. Siphonaptera, Fleas. Biological Records Centre, Huntingdon.

Hammond, P.M. (1974) Changes in the British coleopterous fauna. pp 323-369, in Hawksworth, D.L. (ed.), The changing flora and fauna of Britain. Academic Press, London.

Hammond, P.M. (1980) Staphylinidae (Coleoptera) in Ireland 1: Micropeplinae, Proteininae, Omaliinae and Piestinae. Ir. Nat. J. 20: 133-140

Haynes, R.F. and Hillis, J.P. (1981) Report on migrant insects in Ireland for 1980. Ir. Nat. J. 20: 296-299

Heath, J. (1978) Provisional atlas of the insects of the British Isles. Part 7. Odonata. Institute of Terrestrial Ecology. Huntingdon.

Higgins, L.G. and Riley, N.D. (1970) A field guide to the butterflies of Britain and Europe. Collins, London.

Holmes, J.M.C. (1975) Crangonyx pseudogracilis Bousfield a freshwater amphipod new to Ireland. Ir. Nat. J. 18: 225-226

Illies, J. (ed.) (1978) Limnofauna Europaea: a checklist of the animals inhabiting European inland waters with accounts of their distribution and ecology (except Protozoa). Gustav Fischer Verlag, Stuttgart.

Kerney, M.P. (ED.), (1976) Atlas of the non Marine Mollusca of the British Isles. Institute of Terrestrial Ecology, Cambridge.

Lack, D. (1969) The numbers of birds on islands. Bird Study.16: 193-209.

Loffler, R.H. (1963) Bird migration and the spread of Crustacea. Verh. dt. zool. Ges 27: 311-316. Freshwater Biol. Ass., Translation (N.S.) No. 56).

Macan, T.T. (1974) Freshwater invertebrates, pp. 143-145 in Hawksworth, D.L. (ed.), The changing flora and fauna of Britain. Academic Press, London.

Maguire, B. Jr. (1963) The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161-185.

MacArthur, R.H. and Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, Princeton.

McCarthy, T.K. (1973) A note on the occurrence in Ireland of the flatworm Bdellocephala punctata (Pallas) (Tricladida: Dendrocoelidae). Ir. Nat. J. 17: 419-420

McCarthy, T.K. (1974) A note on two interesting freshwater oligochaetes occurring in Ireland Chaetogaster Limnaei von Baer (Naididae) and Branchiura sowerbyi Beddard (Tubificidae). Ir. Nat. J. 18: 46-48

McCarthy, T.K. (1975) Observations on the distribution of the freshwater leeches (Hirudinea) of Ireland. Proc. R. Ir. Acad. 75(B): 401-451

McCarthy, T.K. and Walton G.A.W., (1980) Sigara selecta (Fieb. (Hemiptera/Heteroptera: Corixidae) new to Ireland, with notes on water bugs recorded from the Dingle Peninsula. Ir. Nat. J. 20: 64-66

Mothersill, C. (1978) Progress report on the recording schemes for harvestmen, false-scorpions and centipedes. Bull. Ir. Biogeog. Soc. No.2: 49-54

Murray, D.A. and Ashe, P. (1984) An inventory of the Irish Chironomidae (Diptera). Mem. Am. Ent. Soc. 34: 223-233

Myers, A.A. (1981) Migrant nocturnal Lepidoptera in Co. Cork, 1971-1980: a review. Ir. Nat. J. 20: 301

Norris, A. and Pickrell, D.G. (1973) Notes on the occurrence of Vertigo geryeri Lindholm in Ireland. J. Conch. 27: 411-417.

O'Connor, J.P. (1978a) The stonefly Capnia atra Morton (Plecoptera, Capniidae), confirmed as an Irish species. Entomologist's Gaz, 29: 156-158.

O'Connor, J.P. (1978b) A progress report on studies of Irish Trichoptera. Proceedings of 2nd International Symposium on Trichoptera, 1977, Junk, The Hague. pp. 303-308.

O'Connor, J.P. (1979) Blaps lethifera Marsham (Coleoptera: Tenebrionidae) a beetle new to Ireland from Viking Dublin. Entomologist's Gaz. 30: 295-297

O'Connor, J.P. (1981) Apatania auricula (Forsslund). Ir. Nat. J. 20: 302.

O'Connor, J.P. and Nash, R. (1979) Records of six insect species (Coleoptera: Orthoptera) recently imported into Ireland. Ir. Nat. J. 19: 433-434

O'Connor, J.P. and Nash, R. (1981) Notes on five species of insects (Hemiptera: Coleoptera) imported into Ireland. Ir. Nat. J. 20: 299-300.

O'Connor, J.P. and Nash, R. (1982) Further records of insects (Dictyoptera Lepidoptera, Coleoptera, Diptera) imported into Ireland. Ir. Nat. J. 20: 393-395

O'Connor, J.P. and Nash, R. (1983) Insects imported into Ireland 5. Records of Orthoptera Hemiptera, Hymenoptera and Coleoptera, Ir. Nat. J. 21: 114-117

O'Connor, M.A., O'Connor, J.P. and Jones H.D. (1983) A second record of the Australian land planarian Geoplana sanguinea (Moseley) var alba Dendy. Ir. Nat. J. 21: 95.

O'Rourke, F.J. (1946) Planarians and prehistory. A review of some zoogeographical evidence as to the date of separation of Britain and the continent. J. R. Soc. Antiq. Ir. 76: 101-3

O'Rourke, F.J. (1950) The dangers of carriage of insects by aircraft and a suggested precautionary measure. Proceedings of the VIIIth International Congress of Entomology, 946-7

Pennington, W. (1959) Relict fauna of Ennerdale Water; a problem of distribution. Nature, London.184: 1421-1422

Praeger, R.L. (1932) Recent views bearing on the problem of the Irish flora and fauna. Proc. R. Ir. Acad. 41(B): 125-145

Ross, H. (1979) A checklist of the Irish land and freshwater Mollusca. Bull. Ir. Biogeog . Soc. No. 3: 37-41

Sankey, J.H.P. and Savory, T.H., (1974) A synopsis of the British harvestmen. Linn. Soc. Lond. Publ., No. 4

Segerstrale, S.G. (1966) Adaptational problems involved in the history of the glacial relicts of Eurasia and North America. Rev. Roumaine Biol. - Ser. Zool., 11: 59-66

Sleeman, D.P. (1980) A checklist and bibliography of Irish Oestridae and Gastrophilidae. Bull. Ir. Biogeog . Soc. No. 4: 28-29

Smithers, C.N. (1978) A new species and new records of Psocoptera (Insecta) from Ireland. Ir. Nat. J. 19: 141-148

Southwood, T.R.E. (1961) The number of species of insect associated with various trees. J. Anim. Ecol. 30: 1-8

Southwood, T.R.E. and Leston, D. (1959) Land and water bugs of the British Isles. Warne, London.

Speight, M.C.D. (1980) Brachypalpus laphriformis (Diptera: Syrphidae) in Ireland and its probable demise. Ir. Nat. J. 20: 70-2

Strange, C.D. and Glass, G.B. (1979) The distribution of freshwater gammarids in Northern Ireland. Proc. R. Ir. Acad. 79(B):145-153

Sutcliffe, D.W. (1971) Regulation of water and some ions in gammarids (Amphipoda). 1. Gammarus duebeni Lilljeborg from brackish water and freshwater. J. Exp. Biol. 55: 325-344

Thienemann, A. (1950) The transport of aquatic animals by birds Binnengewasser, 18: 156-159. Freshwater Biol. Ass., translation (N.S.) No. 57.

Walton, G.A.W. (1967) A site particular zoological interest Doughruagh mountain, Kylemore, Co. Galway. Ir. Nat. J. 15: 309-312.

Walton, G.A.W. (1981) Microvelia pygamaea (Dufour 1833) (Hemiptera: Veliidae), a flightless water bug new to Ireland. Ir. Nat. J. 20: 223-228

Webb, D.A. (1983) The flora of Ireland in its European context. J. Sci. R. Dubl. Soc. 4: 143-160

Author's Address

Department of Zoology,
University College,
Galway,
Ireland.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

THE IMMIGRATION OF NON-MARINE MOLLUSCA INTO LATE GLACIAL IRELAND

G.F. Mitchell

The movement of non-marine mollusca into Ireland during the Woodgrange Interstadial, 15,000 to 10,000 B.P. (Mitchell, 1976), is in urgent need of investigation, as present knowledge presents a curiously irregular pattern.

At some well-investigated sites, eg. Ballybetagh, Co. Dublin (Farrington and Jessen, 1938), no molluscs are reported from the calcareous openwater mud of Woodgrange age. At Knocknacran, Co. Monaghan (Mitchell, 1951) 24 forms, identified by A.W. Stelfox, are recorded. The calcareous mud here was later given a C^{14}age of 11,310 + 720 BP (No. 355), in a very early dating by W.F. Libby (1952). Mapastown, Co. Louth (Mitchell, 1953), 20km east of Knocknacran, had 3 forms. Roddansport, Co. Down (Morrison and Stephens, 1965) with several C^{14}dates of Woodgrange age, had 9 forms. The lateglacial basin at Ratoath, Co. Meath (Mitchell, 1941) had 10 forms; the adjoining basin at Lagore, Co. Meath (Mitchell, 1940) had none.

Lateglacial calcareous muds with Megaloceros giganteus are numerous in Co. Limerick; at Cahercorney (Mitchell, 1951, p. 170) a forelimb, a rib and some other bones of Megaloceros lay horizontally at or just below what was interpreted as the contact between muds of Woodgrange and of Nahanagan age. Abutting against the rib was a rich pocket of seeds and shells; nine molluscan forms were identified; the pocket also contained three small fish vertebrae.

Similar pockets or sheets of apparently current-sorted molluscs have been noted at other glacial sites, for example at Bog of the Ring, Co. Dublin (O 187597) (Mitchell, unpub.).

At the White Bog, Co. Down (Stelfox et al. 1972), there was a very rich molluscan fauna, but the stratigraphy was difficult to interpret and the forms identified are not included in the following list.

Ballyclander, Co. Down (Mitchell and Stelfox, 1971) had Megaloceros and a few molluscs, but again the stratigraphy was not clear.

The mollusc forms identified so far are Lymnaea peregra (Muller), L. truncatula (Muller), Pisidium casertanum (Poli), P. conventus Clessin, P. hibernicum Westerlund, P. lilljeborgii Clessin, P. milium Held, P. nitidum Jenyns, P. obtusale (Lamarck), P. obtusale var. lapponicum (Clessin), P. subtruncatum Malm, Planorbis contortus (L.), P. crista (L.), P. laevis Alder, Pupilla muscorum (L.), Sphaerium corneum (L.), Succinea oblonga Draparnaud, S. pfeiffer (Rossmassler), Valvata cristata Muller, V. piscinalis Muller, Vertigo antivertigo Draparnaud, V. genessi (Gredler), V. lilljeborgii (Westerlund), Vitrina pellucida (Muller).

References

Farrington, A. & Jessen, K. (1938) The Bogs at Ballybetagh near Dublin, with remarks on Lateglacial Conditions in Ireland, Proc. R. Ir. Acad. 44(B): 205-260.

Libby, W.F. (1952) Radiocarbon Dating. Chicago (University of Chicago Press).

Mitchell, G.F. (1940) Studies in Irish Quaternary deposits: some lacustrine deposits near Dunshaughlin, Co. Meath, Proc. R. Ir. Acad. 46(B): 13-17.

Mitchell, G.F. (1941) Some lacustrine deposits near Ratoath, Co. Meath, Proc. R. Ir. Acad. 48(B): 173-182.

Mitchell, G.F. (1951) Studies in Irish Quaternary deposits No. 7, Proc. R. Ir. Acad. 53(B): 111-206.

Mitchell, G.F. (1953) Further identifications of macroscopic plant fossils from Irish Quaternary deposits especially from a late glacial deposit at Mapastown, Co. Louth, Proc. R. Ir. Acad. 55(B): 225-281.

Mitchell, G.F. (1976) The Irish Landscape. Collins, London.

Mitchell, G.F. & Stelfox, A.W. (1971) Late glacial deposits at Ballyclander, near Downpatrick, Co. Down, Ir. Nat. J. 17: 17-19.

Morrison, M.E.S. & Stephens, N. (1965) A submerged late Quaternary deposit at Roddansport on the north east coast of Ireland. Phil. Trans. R. Soc. Lond. (B) 249: 221-55.

Stelfox, A.W., Kuiper, J.G.J., Mc Millan, Nora F., and Mitchell, G.F. (1972) The lateglacial and postglacial mollusca of the White Bog, Co. Down. Proc. R. Ir. Acad. 72(B): 185-207.

Author's Address

School of Botany,
Trinity College,
Dublin,
Ireland.

Occ. Pub. Ir. Biogeog. Soc. No. 1.

CONCLUSIONS

CONCLUSIONS

R.J.N. Devoy, D.P. Sleeman and P.C. Woodman

Islands have served as important models for evolutionary and ecological theory but, as can be seen from the preceding discussion, it is not entirely clear how and when, Ireland became an island. However, the combination of the narrow stretch of water and Ireland's relatively large land mass makes Ireland a particularly interesting case which does not fit easily within established models in biogeography.

It is hardly surprising that the conference did not emerge with a definite statement on the origins of Ireland's life forms. On the other hand, there was a greater appreciation not only of the data base from which we work, and the varying approaches to the problems - geomorphological, historical and ecological. These differences are reflected in the contributions and in the emphasis of the reviews which have so far appeared. (Corbet, 1984; Speight, 1984; Devoy, 1985).

Professor Watts reminded the Conférence of the danger of over-extrapolation from a narrow data base. There is a danger of an over-simplistic approach by those involved in historical sciences: and animal is often considered to have only existed from its earliest occurrence in the archaeological record. On the other hand, there is a certain naivety on the part of those working within a contemporary ecological framework assuming that ecological systems can simply be transported backwards in time to a period of dynamic change, i.e. the early postglacial. In particular, some reviewers coined the phrase the "pygmy shrew syndrome" typifying the use of a very limited body of anomalous data to explain island colonization.'

There was a lack of support for the traditional type of refugia and that, therefore, we must look for explanations based on more recent origins for most of Ireland's biota. It was felt that there were still many imponderables and that areas such as microclimatology, pedology etc., factors which could inhibit colonization, had not received sufficient attention. It was even noted by Dr. Corbet that an environmentally and spatially determined classification instead of the traditional Linnaean approach could in itself provide important insights.

There was a general consensus of the need to identify critical research areas and much of the discussion centered on the best methods and means of developing these aims. The main areas identified were as follows:-

(1) High priority should be given to an organised and inter-disciplinary search for suitable repositories of faunal and floral information of Late Midlandian and postglacial age; such as caves, lake basins, inter-drumlin areas, turloughs and swallow holes. Particular reference should be given to southern areas which have may remained unglaciated during the last cold stage.

(2) Particular attention should be paid to the collection of well established environmental indicators such as Coleoptera and fresh water molluscs. These have been relatively neglected to date in Ireland. Recent work on freshwater molluscs in Ireland (Preece, R. 1984 pers. comm.) would appear to show much less impoverishment than had hitherto been expected.

(3) Further research on introductions and extinctions caused by man through examination of doçumentary and archaeological sources.

(4) The lack of good chronological information necessitates a structured programme of dating, e.g. C^{14} and other radiometric methods, amino acid racemization, Thermoluminescense, Electron Spin Resonance, etc.

(5) An integrated programme of offshore geophysical, bathymetric and stratigraphic data collection relevant to land/sea-level studies. This information is a pre-requisite to any meaningful examination of the question 'Was there a land bridge(s)?'

(6) The "oddball" elements of Ireland's biota need to be assessed within their broader ecological and palaeoecological context, both in Ireland and Atlantic Europe in general. In particular the concept of refugia should undergo fundamental re-examination, in the light of correct knowledge of Quaternary environmental and paleogeographic change.

(7) A directed programme to examine the emergence of genetic differences should be encouraged. Modern techniques such as electrophoresis already applied, particularly to fish, should be extended to other groups both modern and sub fossil.

These research themes, whilst highlighting the need to study aspects of Ireland's apparent uniqueness within the geological, ecological and archaeological framework of Northwest Europe, should not obscure the equal need to look outward to the island's broader relationships .

REFERENCES

Corbet, G.B. (1983) The postglacial colonization of Ireland. The Mammal Society Newsletter No. 57 December 1983.

Devoy, R.J.N. (1985) The postglacial colonization of Ireland: conference review. Quat. Sci. Rev. In Press.

Preece, R. (1984) Personal communication on current research on late and postglacial molluscan sequences in Ireland in the Sub-Dept. of Quaternary Research, University of Cambridge

Speight, M.C.D. (1984) Account of the 'Postglacial Colonization of Ireland' conference, University College Cork. Bull. Ir. Biogeog Soc. 7: 58-59

FODHLA PRINTING