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CONSERVATION AND ECOLOGY OF THE RED-BILLED CHOUGH

Pyrrhocorax pyrrhocorax

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Presented in candidature for the degree of Doctor of Philosophy
in the Faculty of Science, University of Glasgow

Department of Zoology
University of Glasgow
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VOLUME I

Declaration

I declare that the work described in this thesis is entirely my own, except where stated otherwise, and that it is my own composition. No part of this work has been submitted for any other degree.

[redacted]

Clive R. McKay

February 1996

DEDICATION

This thesis is dedicated to the memory of my late father,
who had an instinctive interest in, and self-taught knowledge of
the wildlife which shared his world as a young man in western Ireland,
at a time when there was no need for conservation research on
Choughs, Corncrakes and Greenland White-fronted Geese

Altogether, the Chough is a fine fellow.
Long years to him in his last strongholds
on the stupendous wind-torn precipices of the west.

John Walpole-Bond

The Chough is one of the most charming...
but also the most mysterious of our hill birds

Derek Ratcliffe

TABLE OF CONTENTS

SUMMARY i

ACKNOWLEDGEMENTS iv

Chapter 1 INTRODUCTION 1

1.1 World range 1

1.2 Sub-speciation 2

1.3 Habits 2

1.4 Status 3

1.5 Aims 5

Chapter 2 STUDY AREAS AND GENERAL METHODS 7

2.1 Study areas 7

2.2 Classification of age and sex 10

2.3 Classification of seasons 10

2.4 Classification of habitats 10

2.5 Data collection and analyses 11

Chapter 3 THE HISTORY AND DISTRIBUTION OF THE CHOUGH IN SCOTLAND, SINCE 1750 12

3.1 Introduction 12

3.2 Methods 13

- 3.2.1 Record collation, literature review and museum search 13
- 3.2.2 Record verification 14
- 3.2.3 Classification of status 15
- 3.2.4 Map referencing of records 16
- 3.2.5 Distribution mapping 16
- 3.2.6 Population trends 16

3.3 Results 17

- 3.3.1 Record collation 17
- 3.3.2 Distribution since 1750 18
- 3.3.3 Population trends 20

3.4 Discussion 21

Chapter 4 A REVIEW OF POTENTIALLY LIMITING FACTORS INFLUENCING THE STATUS OF THE CHOUGH IN SCOTLAND, PAST AND PRESENT 27

4.1 Introduction 27

4.2 Methods 28

4.2.1 Record collation 28
4.2.2 Persecution 28
4.2.3 The effect of natal site insularity on Chough dispersal 29
4.2.4 Nest-site competition 30
4.2.5 Winter severity 31

4.3 Results 32

4.3.1 Record collation 32
4.3.2 Persecution 32
4.3.3 The effect of natal site insularity on Chough dispersal 32
4.3.4 Nest-site competition 33
4.3.5 Winter severity 34

4.4 Discussion 34

4.4.1 Persecution 34
4.4.2 Niche overlap 36
4.4.3 Isolation and In-breeding 37
4.4.4 Predation 39
4.4.5 Nest-site competition 40
4.4.6 Disease and Toxic Chemicals 41
4.4.7 Parasites 42
4.4.8 Winter severity 44
4.4.9 Nest-site availability 45
4.4.10 Land-use 45
4.4.11 Discussion summary 45

Chapter 5 THE DISTRIBUTION OF THE CHOUGH IN GREAT BRITAIN IN RELATION TO CLIMATIC FACTORS 47

5.1 Introduction 47

5.2 Methods 50

5.2.1 Bioclimatic analysis - Scotland 52
5.2.2 Bioclimatic analysis - England and Wales 52
5.2.3 Weights of roosting Choughs 58
5.2.4 Growth of *Tipula paludosa* larvae on Islay 60
5.2.5 Cold-hardiness of *T.paludosa* larvae in relation to body size 61

5.3 Results 62

5.3.1 Bioclimatic analysis - Scotland 62
5.3.2 Bioclimatic analysis - England & Wales 63
5.3.3 Weights of roosting Choughs 68
5.3.4 Growth of *Tipula paludosa* larvae on Islay 69
5.3.5 Cold-hardiness of *T. paludosa* larvae in relation to size 71

5.4 Discussion 72

5.4.1 The *Potential Climatic Range* of the Chough in Scotland 73
5.4.2 The *Potential Climatic Range* of the Chough in England and Wales 74
5.4.3 A simple climatic model 78
5.4.5 Biology of *Tipula paludosa* 83
5.4.6 Summary 90

CHAPTER 6 THE INFLUENCE OF NEST-SITE AVAILABILITY ON CHOUGH BREEDING DISTRIBUTION 91

6.1 Introduction 91

6.2 Methods 92

6.2.1 Calculation of nest-territory index 92
6.2.2 Climatic control areas 94

6.3 Results 95

6.3.1 Areas climatically identical to Islay 95
6.3.2 Areas not climatically identical to Islay but with some history of Chough occupancy 96

6.4 Discussion 98

6.4.1 Nest-site availability in areas climatically identical to Islay 100
6.4.2 Nest-site availability in areas not climatically identical to Islay 102
6.4.3 Summary 103

CHAPTER 7 HABITAT SELECTION BY CHOUGHS AND THE INFLUENCE OF LAND-USE 106

7.1 Introduction 106

7.2 Methods 107

7.2.1 Rhinns transect 107
7.2.2 Study pairs 114
7.2.3 Land-use on the Rhinns of Islay and the Rhinns of Galloway 117

7.3 Results 119

7.3.1 Habitat use and habitat selection on the Rhinns 119
7.3.2 Vegetation height at feeding sites on the Rhinns 133
7.3.3 Habitat use and habitat selection by study pairs 134
7.3.4 Land-use on the Rhinns of Islay and the Rhinns of Galloway 146

7.4 Discussion 147

7.4.1 Seasonal habitat use on the Rhinns 148
7.4.2 Seasonal Patch use on the Rhinns 150
7.4.3 Study pairs 153
7.4.4 Habitat structure 156
7.4.5 Land-use 158
7.4.6 General discussion 165

Chapter 8 DIET, FEEDING BEHAVIOUR & FOOD AVAILABILITY 172

8.1 Introduction 172

8.2 Methods 174

8.2.1. Diet 174
8.2.2 Comparison of composition of faeces and pellets 177
8.2.3 Feeding behaviour 177
8.2.4 Food availability and feeding site sampling 178

8.3 Results 180

8.3.1 Faecal analysis 180
8.3.2 Comparison of composition of faeces and pellets 183
8.3.3 Feeding behaviour 184
8.3.4 Field sampling and Feeding-site sampling 184

8.4 Discussion 185

8.4.1 Diet 185
8.4.2 Feeding behaviour and feeding sites 189
8.4.3 General discussion 195

Chapter 9 GENERAL DISCUSSION 198

9.1 The Chough in the British Isles 198

9.2 Constraints on the Chough's range in Britain 199

9.3 Habitat use and management on Islay and in relation to other areas 201

9.4 Diet on Islay 202

9.5 Causes of the recent decline of the Chough in Britain 203

9.6 Opportunities for conservation management 204

9.7 Future threats 207

9.8 Future research 209

REFERENCES 210

Appendix 1 Historical records of the Chough in Scotland.

Appendix 2 Pearson Correlation matrix of climatic variables used in Discriminant Function Analyses.

Appendix 3a Maximum invertebrate biomass in field samples, Islay 1988-89.

Appendix 3b Maximum invertebrate biomass in Chough feeding-site samples, Islay 1988-89.

Appendix 4 The influence of habitat on nest-site occupancy by Red-billed Choughs *Pyrrhocorax pyrrhocorax*. Paper submitted to *Biological Conservation*.

SUMMARY

1. The Red-billed Chough *Pyrrhocorax pyrrhocorax* has a population of approximately 1000 breeding pairs in the British Isles, and is afforded special protection under Annex 1 of the EC Directive on Wild Birds. Its British range has contracted over the last 200 years, and it is now restricted to the western coasts of Ireland, Wales and Scotland, and to the Islae of Man.

2. The main aims of the study were: 1) to identify the factors which currently limit the distribution of the Chough, and which may have caused its recent decline, and 2) to describe habitat use and habitat selection by Choughs, particularly in relation to land use practises, to identify measures which could be taken to conserve the species in Scotland and/or to re-establish it in its former range.

3. This study was carried out on the Inner Hebridean island of Islay, which held approximately 90% of the Scottish Chough population at the time of the study (*c*.105 pairs). The island supports a wide range of habitats and land-uses. Particular attention was focussed on the possible threat to Choughs posed by the afforestation of part of the Rhinns of Islay in the early 1980s.

4. The Chough's decline in Scotland has been protracted, with archaeological remains from outwith the recent range suggesting that it was even more widespread prior to 1750 when literary recording began. This suggests the involvement of a long-term climatic relationship in the decline. However, the Chough's distribution since 1750 in Scotland shares the same climatic characteristics as currently occupied areas, suggesting that climate change in this period was probably not the cause of the recent range contraction. It is more likely that the recent decline was accelerated by high levels of persecution/collecting at the turn of the century, and by agricultural intensification in the 20th century. The recent historical range in Scotland was shown not to have been as extensive as suggested in the literature, and no evidence was found to confirm the suggestion that birds formerly bred far inland.

5. The Chough's distribution in Britain shows a close correlation with areas which have both extremely mild winters and warm summers. Based on these climatic characteristics, the Chough's "Potential Climatic Range" was identified. It was concluded that the Mull of Galloway (Scotland) and Cornwall (England and Wales) are currently the most climatically favourable areas for Choughs in the respective countries, despite the species' recent extinction in these areas. This paradoxical situation may be a result of the most favourable climatic conditions for Choughs also favouring detrimental agricultural intensification.

6. Nest-site availability was shown to limit abundance within the potential climatic range. Absences from Coll and Tiree are explained by lack of nest-sites, as is the small population size on Colonsay. Provision of artificial nest-sites in areas of low availability of natural nest-sites which also contain suitable feeding habitats (see below) is recommended.

7. The main habitats used by feeding Choughs on Islay were grazed improved and unimproved pastures, grazed mature dune systems, grazed heath/acid grassland mosaics, rock outcrops and field boundaries. Within these habitats herbivore dung (especially cow dung) and carcases provided important supplementary feeding opportunities. There are marked seasonal changes in habitat use, suggesting that a range of habitats is required in a small area to support Choughs. An age-related difference in dung-feeding was demonstrated. Short vegetation structure and a high component of bare ground were the preferred characteristics of improved pasture fields used for feeding. These characteristics may over-ride simple prey abundance in determining feeding site preferences. This suggests that Choughs may use visual clues such as invertebrate burrow entrances to locate sub-surface prey items.

8. Permanent grazing, high grazing pressure, and a mixture of small and large grazing herbivores all contribute to the maintenance of the right habitat structure and in the provision of a range of feeding opportunities for Choughs. Large herbivores remove rank vegetation and their dung supports proportionally more dung invertebrates than that of small herbivores, whilst grazing by smaller herbivores produces the shortest swards.

9. Choughs on Islay feed primarily on inactive soil-, dung- or carcase-dwelling invertebrates, with some cereal grain taken in the late autumn/early winter. Invertebrates were dominant in the diet throughout the year. 76% (by fresh weight) of prey items taken were soft-bodied invertebrates, mostly larval forms. Faecal and pellet analysis may under-estimate the proportion of soft-bodied prey in the diet, and over-estimate the proportion of vegetable matter, particularly if samples are collected from roost sites. There is a clear need for feeding experiments with captive birds to calibrate findings from faecal analysis.

10. The relationship between climate and the Chough's range in Britain is probably brought about through the effects of climate on the productivity, growth and mortality of the invertebrate populations which make up its diet. Experimental and comparative studies showed that the fecundity, growth and survival of Tipulid larvae was greater within the Chough's range compared to areas with colder winters.

11. The Chough's specialised insectivorous diet in Britain contrasts with that of other races throughout the Eurasian range whose diet is more catholic. It is proposed that inter-specific feeding competition with other corvids, particularly the Rook *Corvus frugilegus*, may have been responsible for the evolution of the Chough's specialised feeding habits and small body size within Britain.

12. A range of favourable and detrimental land uses was identified. The most important land use to Choughs was considered to be the maintenance of year-round high grazing pressure by both large (e.g. cows) and small (e.g. sheep) herbivores. Research into provision of feeding sites by carcase burying and the provision of linear habitat "islands" within fields is recommended.

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Chapter 1

INTRODUCTION

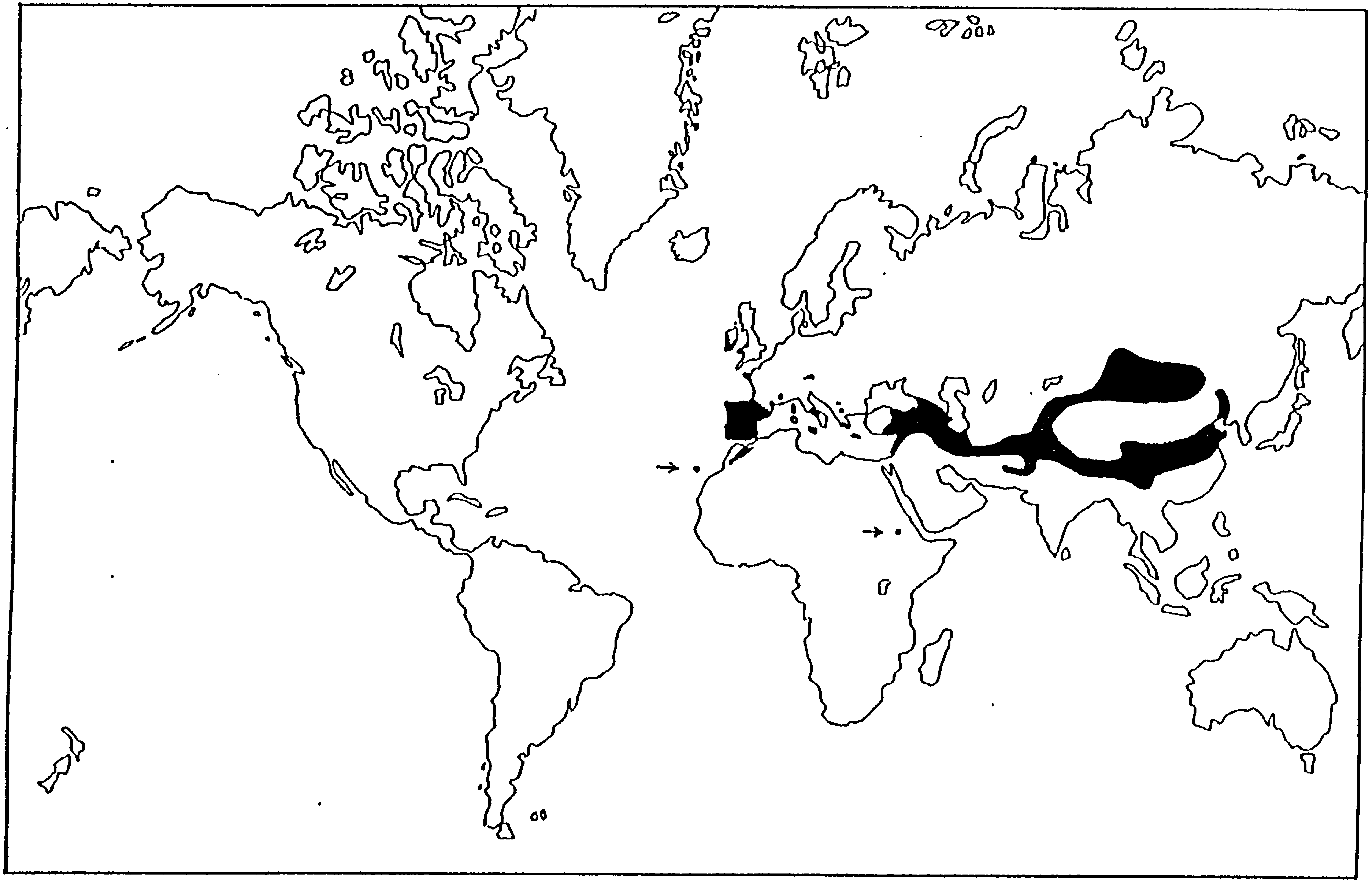
1.1 World Range

The Red-billed Chough *Pyrrhocorax pyrrhocorax* is a medium-sized member of the crow family (Corvidae), one of only two species in the genus (the other being the Alpine or Yellow-billed Chough *Pyrrhocorax graculus*). It is a bird of mountain ranges, steppes and rocky coastlines, occurring where suitable pastoral and rocky feeding habitats juxtapose precipitous cliffs which provide the large crevices or caves needed for nesting and roosting. In some areas buildings may also be used for nesting, from monasteries and dzongs in Himalayan and Mongolian villages, to derelict crofts, mine-buildings and lighthouses in Scotland, the Isle of Man and Ireland (Ali & Ripley 1987, Ralfe 1905, Cabot 1965). Non-natural cliffs and caves, provided by mineshafts and quarries are also used, particularly in Wales (Rolfe 1966).

Unlike the Alpine Chough, which is found exclusively in mountains, the Red-billed Chough breeds over a remarkably wide altitudinal range, from sea-level to 6,000m (Ali & Ripley 1987). Its range mostly comprises mountain ranges (see Figure 1.1), from the Chinese ranges and the Himalayas in the east through to the Pyrenees and Atlas Mountains in the west. Extensions into steppe biotopes occur in central China, Mongolia and on the Iberian Peninsula. Coastal cliffs are used on the western sea-boards of the British Isles, Brittany and Portugal.

Outlying populations are found in the Ethiopian Highlands (1500 miles from the next nearest population in the Atlas Mountains), on the island of La Palma in the Canary Islands, and in the British Isles/Brittany. These disjunct populations presumably result from a formerly wider historical distribution, perhaps during the Würm glaciation, when birds forced to lower altitudes could have occupied the steppes which would have covered central Europe and North Africa at that time. Red-billed Choughs may have simultaneously "discovered" a suitable niche in coastal areas of Western Europe and the Canary Islands (Guillou 1981). The subsequent retreat of the ice, afforestation of central Europe and desertification of North

Figure 1.1 World range of the Red-billed Chough *Pyrrhocorax pyrrhocorax* (after Coombs 1978).



Africa presumably led to the isolation of the discrete populations that remain to this day; the analogous distributions of the Rock/Water Pipit *Anthus spinoletta spp.* and Twite *Carduelis flavirostris* have been explained in the same way (Guillou 1981).

1.2 Sub-speciation

This evolutionary history has resulted in the development of eight recognised sub-species (Vaurie 1959), of which the British and Irish race is the nominate (reflecting the fact that the Chough was first described in Britain, rather than evolutionary antecedence of this sub-species). Interestingly, Vaurie (1954) considered the nearby population in Brittany to belong to a separate race *P. p. erythrorhamphus*, allied to other continental European populations, although Witherby *et al.* (1940) assigned it to the British race. The British race is the smallest in body size (see Vaurie 1954), but otherwise it is typical of Red-billed Choughs: it has glossy black plumage, and coral red bill and legs. The wings are broad, and the primaries strongly emarginated, producing fingered wings used to great effect when soaring and gliding, which are the preferred modes of flight. When forced to employ flapping flight by calm conditions or lack of thermals, the Chough's lack of buoyancy is evident, and at these times they are easily out-flown by Jackdaws *Corvus monedula* and Rooks *Corvus frugilegus*.

1.3 Habits

Choughs feed almost entirely on the ground. The slender bill is down-curved, pointed and laterally compressed, differing from the more generalised bill-shapes of other corvids. It may be used for the delicate extraction of invertebrates from their burrows, or energetically for hacking apart dung, loose soil and ant hills, or in tearing up sub-surface root structures, or in turning over stones and other surface debris (including sea-weed in Britain) to reveal prey. In the British Isles the chough has a specialised invertebrate diet, which contrasts with the omnivorous diets of most other British corvids (Holyoak 1968).

In other respects the Chough is a typical corvid (see Coombs 1978, Goodwin 1986). The sexes are alike, though males are slightly larger than females. Populations are divided into territorial monogamous breeding pairs and non-territorial flocks of sub-adults (see Still 1989). Pairs remain together throughout the year, and from year to year until one of the partners dies. Observations of colour-ringed birds on Islay have shown that when a member of a pair disappears, it is usually replaced within a month ($n=3$; *pers. obs.*). Threesomes have been recorded at some nest-sites (Cowdy (in Coombs 1976), Warnes 1983, Roberts 1985 & *pers. obs.*) but little is known of the relationships of these birds. Choughs build their own nests, composed of sticks and twigs lined with wool and hair. The clutch of 3-6 eggs is laid from mid-late April, and is incubated by the female alone, the male feeding her at or near the nest. Incubation usually begins with the third egg (*pers. obs.*) and lasts c.18 days; later laid eggs hatch asynchronously. Both members of the pair feed the chicks; the food is carried in a sublingual pouch, and the pair commute to and from feeding areas together. This results in the chicks being left unattended at the nest for long periods of time, which may dictate the need for nest-sites which are inaccessible to predators. The chicks fledge after c.38 days, the longest fledging period relative to body size of all British corvids.

The fledglings remain dependent on the adults for 1-2 months before they join sub-adult flocks in the early autumn. These flocks are usually centred on communal roost-sites on cliffs which contain abundant roosting ledges and crevices (see Still 1989). Mortality on Islay is 71-74% in the first 2 years of life (Bignal *et al.* 1987b), but is thought to be much lower thereafter. Most females first breed at 2-3 years and males at 3-4 (Bignal *et al.* 1987b) but some birds spend up to 7 years in sub-adult flocks before breeding (*pers. obs.* & see Still 1989). Birds usually enter the breeding population singly, by joining up with unpaired birds in possession of a nest-site, or sometimes by evicting or even killing the incumbents (*pers. obs.*).

Choughs are sedentary, though in mountain ranges there is an altitudinal migration in winter (Ali and Ripley 1987). However, dispersal of young birds can lead to movements of up to 600 km (see Chapter 4). There is a males bias in natal philopatry (Bignal *et al.* 1989). The species may be quite long-lived: Roberts (1985) recorded a male Chough surviving in the wild for a minimum of 17 years.

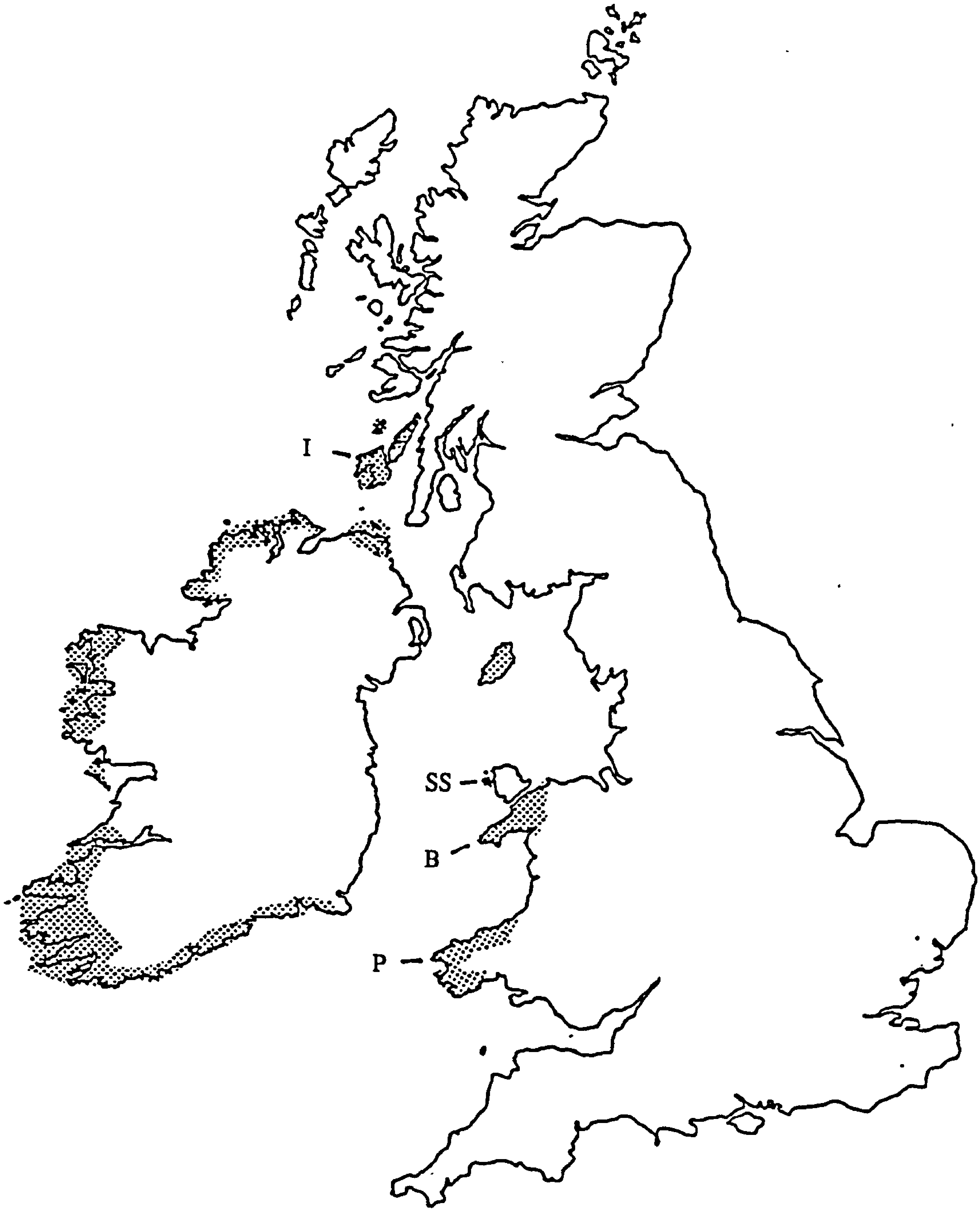
1.4 Status

The Chough is the rarest corvid in the British Isles with an estimated breeding population of 1246 breeding pairs in 1992 (RSPB 1994). It is found along the western seaboards of Ireland, Wales and south-west Scotland, and on the Isle of Man (see Figure 1.2). Here it occupies a unique ecological position at the north-western fringe of the species' world range and racially distinct from its conspecifics in continental Europe. It differs from its conspecifics in having a specialised, primarily insectivorous feeding niche (see Cramp & Perrins 1994).

Throughout Britain and other parts of Europe, the Chough has undergone a marked reduction in range and abundance over at least the last 150 years (Goodwin 1986). In Britain, the most notable reductions occurred in Scotland and southern and south-west England (Coombs 1978). It is now extinct in England, a grave situation considering that the species was formerly known as the "Cornish Chough". In Wales, losses were recorded from some inland areas, but the overall number of pairs has probably remained relatively stable over the last century; 177 breeding pairs were recorded in 1992 (RSPB 1994). In the 19th century, a marked range contraction in Scotland was reported in the literature, with Choughs apparently disappearing from north western, south western and eastern parts of the country (see Baxter & Rintoul 1953, Thom 1986). In 1986, just prior to this study, breeding pairs were present at 105 nest-sites in Scotland, of which 90% were found on Islay (Monaghan *et al.* 1989a). Numbers appear to have remained fairly stable in Eire, which has always been the species' British stronghold (904 pairs in 1992), but fears have been expressed that E.C. grant-aided agricultural intensification might lead to the loss of grazing on the coastal strip through improved fencing, as well as reseeding of semi-natural coastal habitats (Whilde 1989). Similar concerns have been expressed in Northern Ireland (Greer 1989) where there is a continuing decline (9-10 pairs in 1982, 2 pairs 1992).

Due to the Chough's scarcity throughout Europe it was placed on Annex 1 of EC Directive 79/409/EEC. Under this directive member states have an obligation to provide special conservation measures for the bird and its habitat. In addition it is on Schedule 1 of the United Kingdom's Wildlife and Countryside Act, 1981, which confers special protection on the bird and its nest. The Chough is also on the Red Data list of British birds (Batten et al. 1990).

Figure 1.2 Distribution of the Chough in the British Isles (after Sharrock 1976).



Localities of previous Chough studies (see text):

I = Islay
SS = South Stack
B = Bardsey
P = Pembrokeshire

1.5 Aims

The first aim of this project is to attempt to identify the factors which currently limit the Chough's range in Scotland, particularly in relation to the dramatic range contraction which has taken place over the last 100 years. If these limiting factors and the causes of the decline can be determined, it may be possible to take appropriate steps to encourage natural recolonisation of deserted areas. The second major aim is to describe the foraging and feeding ecology of the Chough on Islay in order to provide management prescriptions for Chough conservation on Islay and elsewhere in Scotland.

In Chapter 3 I review the historical literature and describe the historical distribution and the timing and nature of the species' decline in Scotland. Possible causes of this decline are reviewed and assessed in Chapter 4. Climate, nest-site availability and land-use change were identified as either potentially limiting factors, or as factors which may have been implicated in the decline. There is little objective analysis of these subjects in the literature, so this has been attempted in subsequent chapters of this study. In Chapter 5 I determine the climatic characteristics of the Chough's current range in Scotland and in England & Wales, and use the null hypothesis that if the climate of historically occupied areas in which the Chough subsequently became extinct is the same as that of currently occupied areas, then climate cannot be implicated as the cause of the species' decline. In Chapter 6 and Appendix 4 the role of nest-site availability in limiting the species range and nesting density is examined, focussing on the potential use of artificial nest-sites to increase the breeding population in appropriate areas.

The above analyses serve to put the current study of Chough foraging and feeding ecology on Islay into a broader perspective. The results of fieldwork carried out on Islay during 1988-89 are presented in Chapters 7 & 8 and Appendix 4. In Chapter 7 habitat selection and the influence of landuse are examined. Firstly seasonal differences in habitat use, habitat selection and patch use are examined in a large (39 km^2) study area on the south Rhinns of Islay. This area supported a large breeding population of Choughs at the time of the study (*c.* 30 pairs), as well as a wide range of habitats, ideal for the analysis of habitat selection. Particular attention was focussed on the possible impact of the afforestation of approximately 1100 ha of ground within this area during the early 1980s. Secondly intensive observations were made on 5 study pairs nesting in areas of contrasting habitat and land-use. The influence of habitat availability and land-use on the foraging behaviour of individual pairs under the dual demands of having to feed young and having to return to the nest-site is examined.

The results from these habitat and land-use analyses are interpreted in relation to a comparison of historical changes in habitat and land-use in two contrasting areas: the parish of Kilchoman (on Islay) which has always supported a large breeding population of Choughs, and the parish of Portpatrick on the Rhinns of Galloway, Wigtonshire, where the Chough was formerly common but became extinct during this century.

Chough diet and feeding behaviour on Islay are examined in Chapter 8. Three questions are addressed: 1) Particular attention is paid to the possible biases involved in faecal and pellet sampling by comparing the results obtained using these methods with direct observations of feeding birds. 2) Conversion factors were devised to allow fresh weight of prey ingested to be calculated from the results of faecal analysis. 3) Seasonal variations in diet are also examined.

An analysis of nest-site occupancy in relation to habitat distribution is presented in Appendix 4. Choughs have specific nesting requirements thus the influence of nest site availability on the distribution of nesting pairs is also considered.

In Chapter 9 a synthesis of the general conclusions of this study are presented including consideration of the constraints on the Choughs' British range, types of habitat and land-use that are appropriate to Chough feeding ecology, causes of the range contraction in Britain and opportunities for conservation measures and future research.

Chapter 2

STUDY AREA AND GENERAL METHODS

2.1 Study area

The study was carried out on the island of Islay, an Inner Hebridean island off the west coast of Scotland (longitude 6°15'W, 55°45'N) (see Figures 2.1 & 2.2). The island is approximately 30 km wide and 40 km long, covering an area of 610 km^2. The geology of the island is complex (Newton 1988), the main rock types being 1) Lewisian Gneiss in the south Rhinns; 2) Torridonian grits, shales and sandstones in the north Rhinns and around Bridgend; 3) Dalradian slates and phyllites around the Oa and Ardtalla; 4) bands of Dalradian limestone running from the Oa, north through the Ballygrant valley to Rubha Bholsa in the north, and 5) Dalradian quartzite forming most of the uplands, including the island's highest hill Beinn Bheigeir (406m) and the spectacular sea-cliffs below Beinn Mhor on the Oa.

The island's geomorphology and habitats are also diverse. There are several areas of upland character in the north and east and on the Oa, but in contrast to most other Inner Hebridean islands (except Coll and Tiree) approximately 30% of the island is low-lying (altitude <50 m), comprising agricultural land, heath and, in poorly drained areas, bog. Most of the coastline is rocky, with sea cliffs up to 170m high (on the Mull of Oa), providing an abundance of potential Chough nest-sites (see Chapter 6). These cliffs are frequently located above raised beaches (the island is still undergoing a phase of isostatic recovery following the melting of the Rannoch Moor Ice sheet) which probably benefits nesting Choughs, since nests located in caves at the base of these cliffs are less prone to being washed out on stormy days. The low-lying coasts support several dune systems, notably those at Kilchoman, Ardnave, Killinallan and Laggan Bay.

This range of habitats makes Islay an excellent location for a comprehensive study of habitat use and habitat selection by Choughs. Previous studies on small islands such as South Stack and Bardsey in North Wales have inevitably had less scope in this respect due to the limited range of habitats available (eg. Bullock 1980, Roberts 1983). Concomitant with the range of habitats is the variety of land uses on the island. The impoverished uplands support deer forest, most of it heavily grazed. Some areas of heath and bog have recently been affor-

Figure 2.1 South-west Scotland showing main islands

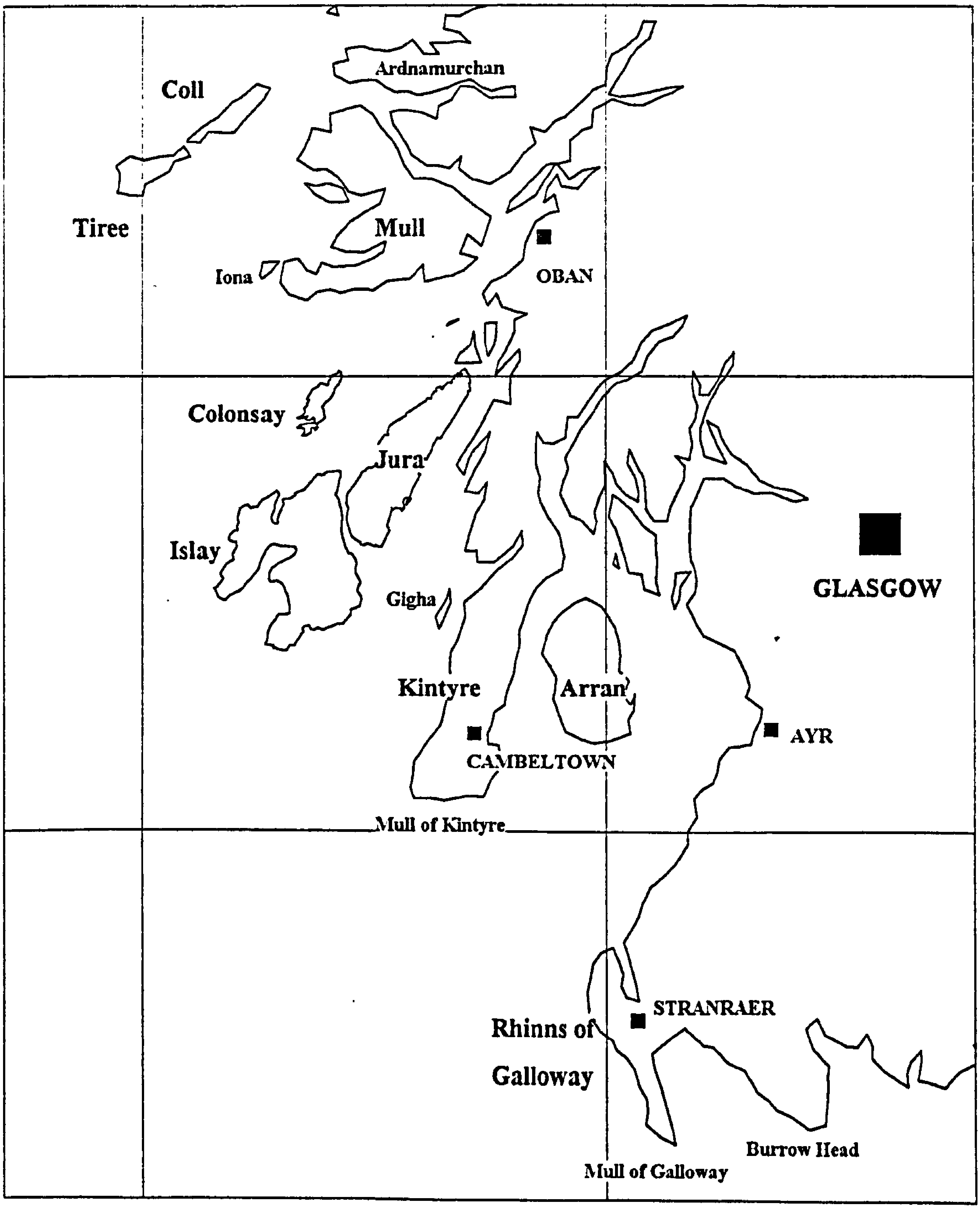
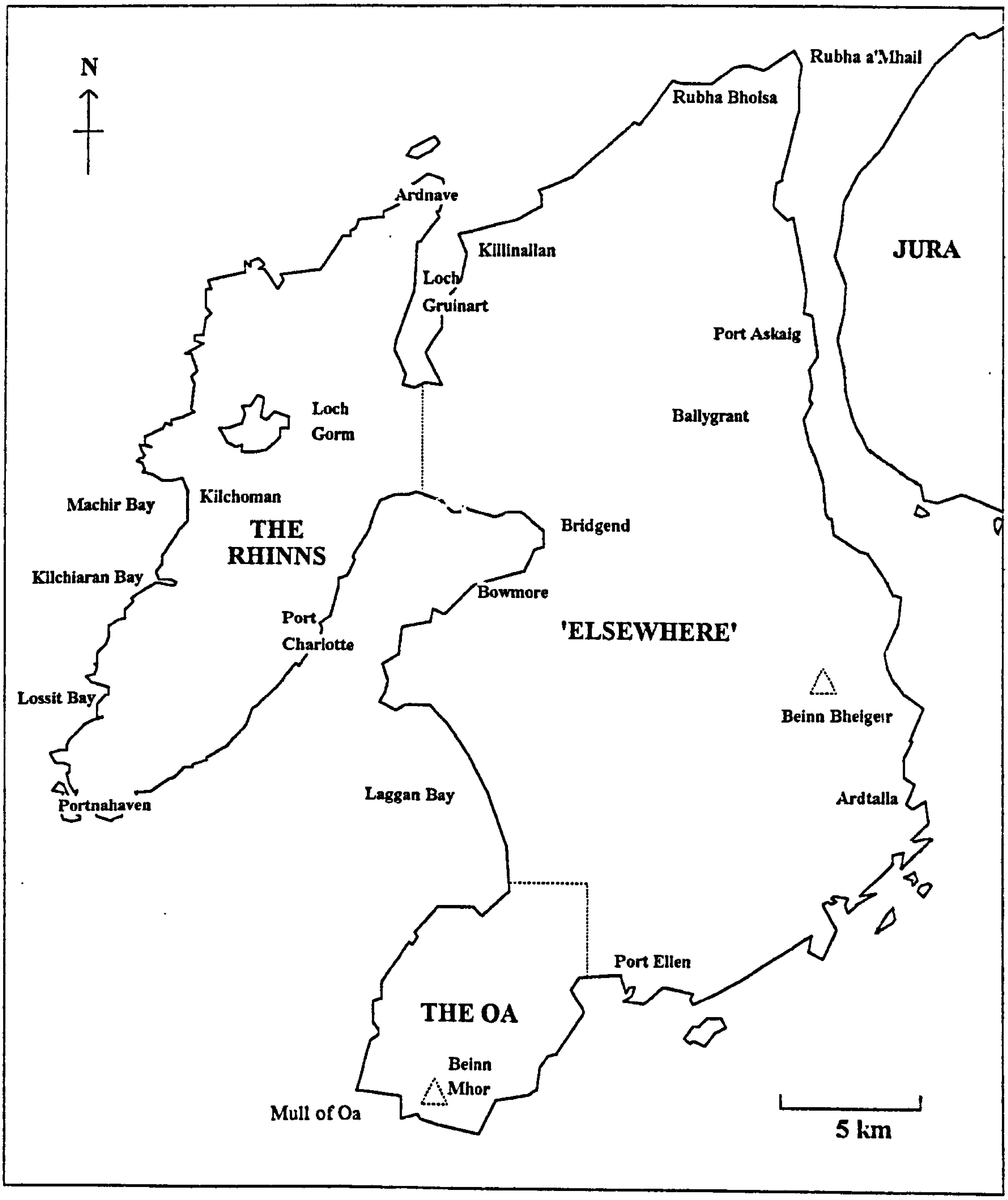


Figure 2.2 Islay, showing regions and localities mentioned in text



ested, notably on the Rhinns (see Chapter 1). Agriculturally, the island is primarily pastoral, with relatively small areas of cereal-growing. The presence of Dalradian limestone, particularly in the Ballygrant/Bridgend valley, has given Islay an "agricultural potential greater than [that of] the other Hebridean Islands" (Newton 1988). Pastoral agriculture ranges from high intensity dairy farming and store beef production, through less intensive store lamb production to low intensity crofting. The degree of agricultural intensification (fertiliser use, regularity of pasture reseeding, investment in farm machinery etc.) depends very much on the quality of the land on which the farm is situated. The presence of several large estates results in some areas being less heavily improved agriculturally than would be the case if they were owner-occupied. The island has its own dairy and its own slaughterhouse, providing valuable outlets for local farm produce. However, most calves and lambs are exported to the mainland where they are fattened further prior to slaughter. Stocking densities are as high now as they have ever been, mostly as a result of the Hill Livestock Compensatory Allowance (Evans & Felton 1987).

Islay has long been recognised as the Chough's Scottish stronghold (see Chapter 3); a survey of Choughs in Scotland in 1986 found 95 breeding pairs (Monaghan *et. al.* 1989a), approximately 10% of the total British and Irish breeding population as estimated in the 1982 survey (Bullock *et. al.* 1983). Fieldwork for the current project commenced in 1987; the 1986 Scottish survey results provided a valuable baseline of the Chough's distribution on Islay for this study, which also benefited from the on-going Chough colour-ringing scheme on Islay, initiated by Warnes in 1981 and continued by the Scottish Chough Study Group. Most birds were ringed as nestlings, which meant that the age and the natal site of most ringed birds was known.

The south Rhinns of Islay was chosen as the main study area as it supported a large breeding population of Choughs (*c.*30 pairs at the time of the study), and was within the foraging range of non-breeding birds from a communal roost at the edge of the study area. This area also supports a wide range of habitats and land-uses (see Chapter 7), including a large area of recently afforested ground (see above). Additional intensive observations were made on a sample of study pairs outwith the Rhinns study area. To preserve the confidentiality of these sites, no figures of the feeding ranges of individual pairs have been presented. Study pairs were selected to represent different habitats and land uses, and on the basis of at least one of the pair being ringed.

The fieldwork for this study was carried out at a time when the relationship between the local human population and conservationists had been soured, through both the adverse publicity surrounding the extraction of peat from Duich Moss, and also as a result of the Rhinns of Islay Site of Special Scientific Interest being designated (in April 1987, my first field season) without any pre-notification. As the only "conservationist" on Islay at the time who was dependent on the good-will of the community, I had to recognise their concerns. Due to these concerns access was restricted in some areas, difficulties were experienced in obtaining permission to carry out invertebrate sampling, and plans to carry out radio-tracking as part of the study had to be cancelled.

At the end of the first year of the study the possibility of re-locating the study to the Isle of Man was considered. However, it was decided that it was best to continue the study on Islay, primarily because it would have taken too much time to establish a colour-ringed population of birds in a new locality. The work plan and methods of the study had to be substantially modified at this stage, and the fieldwork was restricted to 1988 and early 1989. Fieldwork methods were designed to be as low-key as possible. By the end of the study, there was a much better understanding of the nature of this study in the local community. It would have been a better time to start than finish!

The severity of the weather in the study area in autumn and winter also hampered fieldwork to some extent. As a result of my absence from the island visiting university and attending a Chough workshop for parts of the months of September and November, and due to bad weather during the remainder of these months, no data for the Rhinns transect were gathered in these months (see Chapter 7). In both cases however, observations were made at the beginning of the following months, and it is hoped that these data would have differed little from those of the preceding month.

2.2 Classification of age and sex

I have followed Still's (1989) classification of age-groups. She first recorded newly fledged Choughs at communal roost sites on 1st July, and used this date in her classification of age-classes: birds were classed as first years until 1st July of the year after hatching. It is not possible to age Choughs in the field unless they are carrying colour-rings. With practice, members of pairs can be sexed in the field (the male being larger and longer legged than the female). It is impossible to sex Choughs in large groups.

2.3 Classification of seasons

The yearly cycle was divided into four three-month long seasons: spring, summer, autumn and winter. The spring "season" was determined by the Chough's breeding season. Eggs are laid in April, and young fledge in June, so the 3 month period April-June was classed as "spring". The remaining seasons followed on from this. This classification seemed biologically meaningful in terms of the species ecology.] Summer (July - September) includes the period when juvenile Choughs become independent and join sub-adult flocks, whilst the adults complete their wing and body moult. Autumn was later (October - December) than the conventional autumn period, but in the mild winters experienced on Islay, the extension of autumn into December was appropriate. Winter (January - March) includes the coldest month on Islay (February). There were significant differences in habitat use by Choughs based on these seasonal divisions (see Chapter 7), which suggests that the adopted classification was biologically meaningful.

2.4 Classification of habitats

It was considered important in this study to use a standard habitat classification for the categorisation of habitat use by Choughs. Comparison of the results of some previous Chough studies is hindered by the non-standardisation of their habitat categories. It was also important that the habitat classification be familiar and easily interpretable, particularly if the results are to be used by regional staff of bodies such as Scottish Natural Heritage or the Royal Society for the Protection of Birds to implement Chough conservation measures.

For these reasons I used the Phase I habitat classification of the Nature Conservancy Council/Royal Society for Nature Conservation (NCC/RSNC 1984). This classification has been used throughout Britain for habitat mapping, and can be converted to National Vegetation Classification categories. At the time of this study NCC were engaged in mapping the Rhinns of Islay using the Phase I classification, and the results of this survey were made available for this study.

The Phase I classification was adequate for description of habitats on a wide scale, but not so for the description of the fine scale habitats used by foraging Choughs. To provide the necessary resolution a 4-level hierarchical structure for habitat description was devised. Habitats at the first level are the same as those used in the Phase I classification, followed by sub-habitats at the 2nd level, patches at the 3rd level and "dung-patches" at the 4th level (see Chapter 7). This ensured compatability with Phase I without loss of detail.

2.5 Data collection and statistical analyses

Field observations were made using 10x40 Zeiss Dialyt binoculars and a tripod-mounted Optolyth 18-60x60 zoom telescope. Field data were entered into notebooks or dictated into a personal tape recorder. Statistical testing was carried out using *SPSS/PC V2.0 and SPSS/PC+ Advanced Statistics V2.0* (see Norusis 1986, 1988).

Chapter 3

THE HISTORY AND DISTRIBUTION OF THE CHOUGH IN SCOTLAND SINCE 1750

3.1 INTRODUCTION

Over the last 200 years the Chough has undergone a marked range contraction in Britain; by the second half of this century it had become extinct as a breeding bird in England, and was all but lost from the Scottish mainland (Baxter & Rintoul 1953, Rolfe 1966, Warnes 1983, Bullock *et al.* 1983 and Thom 1986). Choughs were apparently (but see below) much more widespread in Scotland in the past; for example, in the literature of the 1800's Choughs were recorded in Sutherland, the Outer Hebrides, Troup Head (Banffshire), St. Abb's Head (Berwickshire), and at several inland sites in Perthshire, Stirlingshire and Fife (see summary in Baxter & Rintoul 1953). There were records of breeding on the Kintyre peninsula, along the rocky coasts of Ayrshire, Wigtownshire and Kircudbrightshire, and they were said to have been more widespread in the Inner Hebrides, including Skye, Mull, Iona, Gigha and Arran. By 1986 the Scottish Chough population was restricted to three Inner Hebridean islands: Islay, Jura and Colonsay, comprising 105 probable or definite breeding pairs, plus 115-120 non-breeding individuals (Monaghan *et al.* 1989a). Ninety percent of all birds were found on Islay.

It is considered important to quantify the extent and the nature of this dramatic decline in order to 1) provide a historical background to the current study, and 2) to provide data for an objective assessment of the causes of the decline in Chapter 4. In particular, it is important to identify whether the decline was as dramatic as suggested in the literature, and if so, whether the factors which brought about the decline are reversible by appropriate conservation action.

In this chapter I describe the Chough's Scottish distribution in each 50 year period since 1750 (when the first records appear in the literature), to present a clearer picture of the timing and the nature of the species' decline. It soon became apparent that there are many inconsistencies and misleading statements in the literature, so particular attention was paid to assessing the validity of each statement by referring to other sources. Attempts were made to estimate the extent of the species' range whilst allowing for differences in recording effort between the different periods.

3.2 METHODS

3.2.1 Record collation, literature review and museum search

A complete review of the current and historical Chough literature relevant to Scotland was undertaken, with a view to 1) collating references on the Chough's status at the time of the reference (both presence and absence) and 2) checking the authenticity of historical records. The term "record" is used here to represent one statement on the Chough's status per date and locality. Thus a statement "Choughs were present on Islay and Jura in 1902" represents two records, whereas "90 pairs of Choughs bred on Islay in 1985" represents one record. Three separate references stating that "Choughs were present on Islay in 1925" would represent 3 records. This approach was taken to allow for the great differences in recording effort and accuracy that inevitably result from an analysis spanning a 230 year period.

Literature searches (manual and computerised) were conducted at Glasgow University Library and in the Alexander Library, Edward Grey Institute, University of Oxford. All references in accounts concerning the Chough's Scottish distribution (particularly Buchanan (1882), Baxter & Rintoul (1953), Rolfe (1966) and Bullock *et al.* (1983), were checked against the original reference where possible. The indices of most relevant journals were consulted: *British Birds, Ibis, Scottish Birds, The Scottish Naturalist, The Glasgow Naturalist, The Western Naturalist, Proceedings of the Glasgow Natural History Society, Proceedings of the Royal Physical Society of Edinburgh*, and *The Annals of Scottish Natural History.* County avifaunas and local bird reports were also checked, along with the annual *Scottish Bird Reports* published by the Scottish Ornithologist's Club since 1970. Local bird recorders were consulted in areas where Choughs have occurred regularly, and requests for information on Scottish records of Choughs were placed in the newsletters of the British Trust for Ornithology and the Scottish Ornithologists Club. Several hundred references were collated and assessed, and over 150 were used, producing 423 individual records. Each record was 1) verified 2) classified according to its status 3) indexed by region and year, and 4) referenced by locality on the national grid to the nearest 1 km square where possible (see below for details). The Scottish regions used in this analysis (which correspond to counties or islands) are illustrated in Figure 3.1.

In addition the egg and skin collections of 44 museums were consulted, including the Royal Scottish Museum (Edinburgh) and the British Museum (Natural History, Tring), producing many previously unpublished records. Questionnaires were sent to all museums in the British Isles with large skin and/or egg collections, as listed in *The Birdwatcher's Yearbook, 1981* (John E. Pemberton (ed.) 1980, Buckingham Press). Most Scottish museums were also contacted. The main collections were visited in person (including those in the Royal Scottish Museum (Edinburgh) and the British Museum (Natural History), Tring. The questionnaire asked for details of date and site of collection of the specimen, plus any other interesting circumstances - eg. whether bird shot, clutch size, etc. The museum search generated a further 58 records, over 50% of which came from museums outwith Scotland.

3.2.2 Record verification

References were generally taken at face value, but careful attention was paid to the exact wording and implications of the original reference wherever possible. There were several instances where originals were misquoted or embellished. For example, referring to the Chough in Dunbartonshire, Lumsden (1876) originally stated that "the Chough has been *obtained* near Bowling", but in a later publication (Lumsden & Brown 1895) this became "this species at one time bred near Bowling", but with no evidence supporting this apparent change in status. The latter statement was subsequently quoted by B & R (1953). In such instances the record always assumes the status of the original reference (in this case "A" - extra-limital record, see "category descriptions" below).

Loosely worded statements were double-checked against other relevant references where possible. For example, referring to several Hebridean islands Gray (1871) stated that Choughs "are no longer present" implying, but with no supporting evidence, that they once were. In such cases, where there are no other/earlier references to birds having been present at the site in question, the later references are categorised as "questionable". In some cases it was possible to cross-reference conflicting reports: eg. from Eigg, Harvie-Brown and Buck-

Legend for Figure 3.1

AB	Aberdeen
AN	Angus
AA	Arran
AR	Argyll (mainland, excluding Kintyre peninsula)
AK	Argyll (Kintyre peninsula)
AY	Ayr
BA	Banff
BE	Berwick
BU	Bute
CA	Caithness
DF	Dumfries
DB	Dunbarton
FF	Fife, Clackmannan & Kinross
IV	Inverness
KC	Kincardine
KK	Kircudbright
LA	Lanark
LO	Lothians (East, Mid & West)
MO	Moray
NA	Nairn
OR	Orkney
PB	Peebles
PR	Perth
RF	Renfrew
RO	Ross and Cromarty
RX	Roxburgh
SE	Selkirk
SH	Shetland (not shown, 90 km NE of Orkney)
SI	Fair Isle (not shown, 60 km NE of Orkney)
ST	Stirling
SU	Sutherland
WI	Wigtown

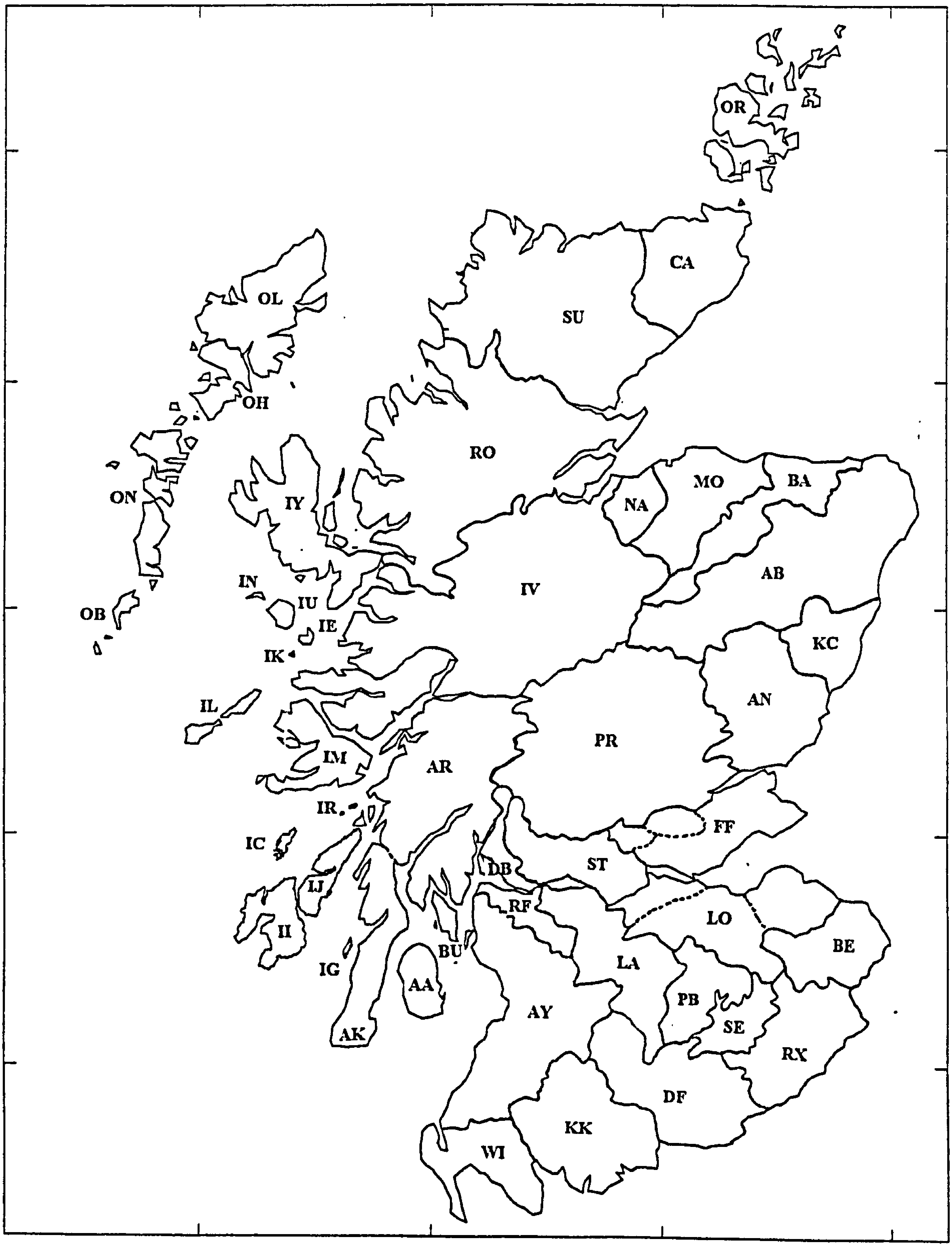
INNER HEBRIDES

IC	Colonsay & Oronsay
IE	Eigg
IG	Gigha & Carra
II	Islay
IJ	Jura
IK	Muck
IL	Coll & Tiree
IM	Mull & Iona
IN	Canna
IR	The Garvellachs
IU	Rhum
IY	Skye & Raasay

OUTER HEBRIDES

OB	Barra
OH	Harris
OL	Lewis
ON	North Uist, South Uist & Benbecula

Figure 3.1 Scottish regions as used in collation of Chough records.



See facing page for legend.

ley (1892) were told by a crofter that in c.1886 "four pairs nested on the northern cliffs", but Evans (1885) writing about the birds of Eigg during 1879-84 didn't record a single Chough. In such cases, a published reference is given precedence over a word-of-mouth reference. In some instances there was a specific reason for questioning the authenticity of a record (see Harvie-Brown 1911).

3.2.3 Classification of status

Each record (*n*=481) was assessed and placed in one of six hierarchical categories, the last three of which correspond closely with those used in the British breeding bird atlases (Sharrock 1976, Gibbons *et al.* 1993) (but see note below); the categories are listed in order of increasing likelihood of breeding having taken place:

Category	Description
.	No information available.
P	"Pre-historic" record from archaeological source (*n*=3).
0	Negative record - no reference to the Chough in an otherwise exhaustive species list (*n*=159).
?	Questionable record - records of questionable authenticity (see 3.2.2 above), whatever their implied breeding status (*n*=25).
A	Extra-limital visitor - records of less than two birds, or of two birds outwith the breeding season (*n*=50).
1	Possible breeding - pair present in the breeding season (*n*=65).
2	Probable breeding - more than two birds present at any time of year, or (museum records only) two specimens collected from the same locality within five years of each other (*n*=80).
3	Definite breeding - any reference which mentions "breeding, nesting, eggs or nestlings". Includes clutches/nestlings/juveniles in museum collections (*n*=99).

NB. Category "1" is not as strict as Sharrock's, as it does not require that the birds be in "suitable habitat"; obviously this is impossible to determine from the older references. The same applies to category "2", which in this classification also includes flocks (ie. more than 2 birds) seen outwith the breeding season as "probably breeding"; this is considered justifiable on the basis that out of a total of 246 10 km squares in which flocks (in this case more than 4 birds) of Choughs were recorded in the *Winter Atlas* (Lack 1986), only 3 were more than one 10 km square distant from the nearest square in which breeding was recorded in the *Breeding Atlas* (Sharrock 1976).

3.2.4 Map referencing of records

Each discrete record was given a map reference on the national grid whose accuracy depended on the details given in the source reference. This necessitated the use of three categories of map reference:

X - Accurate grid reference (n=157): A four-figure grid reference where the exact place name is known (eg. "present at the Kirk of Mochrum"), accurate to the nearest 1 km grid square.

C - Approximate grid reference (n=100): A four-figure grid reference whose location was estimated from the available information eg. "one pair near Portpatrick". Probably accurate to within two 10 km squares.

G - General grid reference (n=224): Records for which it was not possible to assign a grid reference e.g. "present at an undisclosed locality in Lanarkshire".

3.2.5 Distribution mapping

A distribution map of Chough range was produced on a 10 km square basis by using geographically accurate (**Type X** and **Type C**) references only. The distribution map thus utilises only records which are thought to be accurate to within two 10 km squares. **Type G** records were not used in the production of this map due to the inaccuracy of the records. It should be noted that 104 (46.4%) of the 224 **Type G** records were negative records, describing only Chough absence, and that the remaining positive records all came from regions where more accurate **Type X** and **Type C** records were available. Thus the inclusion of the general records would have added very little extra detail to the 10 km square distribution map. The maximum recorded breeding status during 1750-1988 was plotted on a 10 km square basis.

3.2.6 Population trends

The number of "occupied" regions in each of the 16 recording periods (see below) since 1750 was used as a measure of the Chough's range. There is an obvious bias in this approach, since the number of records will be influenced by recording effort: the greater the recording effort, the greater the chance of finding small sub-populations, outlying pairs or wandering individuals, thereby increasing the implied range. To overcome this problem I first regressed range on recording effort, and then used the residual values from this regression as a measure of the Chough's range after removing the effect of recording effort.

a) Occurrence of Choughs by region

The number of separate regions (as used in Appendix 1) with Chough records was totalled by decade, except where there were less than 10 records, in which case records were aggregated over a longer recording period until a minimum sample size of 10 records was achieved. Conversely, the large number of records for the 1980s (n=62) enabled this decade to be split into two 4-year periods. This produced a total of 16 recording periods representing the years 1750-1988. Chough "records" were limited to the three breeding categories - possible, probable and definite breeding. It would have been preferable to use only records of the highest status (probable and definite breeding), but this would probably have biassed the results in favour of more recent periods, for which references are generally more detailed. The inclusion of the "possible" breeding category provides a degree of leeway for the less precise data available for earlier recording periods.

b) Assessment of recording effort

Records in the following five status categories were used to asses recording effort (see section 3.2.3 for further details): negative and extra-limital records and possible, probable and definite breeding. Questionable and pre-historic records were excluded. It is assumed that summing these records for each decade gives a reasonable estimate of recording effort. Negative records were included as they also contribute to the assessment of recording effort.

3.3 RESULTS

3.3.1 Record collation

The literature and museum searches produced a total of 481 records, of which 322 (67.0%) were positive records, and 159 (33.1%) negative records. Fifty eight (12.1%) of these were records from the museum search, comprising 60 skins/mounts and 15 clutches. A breakdown of the numbers of records falling into each of the 7 status categories is given in Table 3.1.

Table 3.1 *The number of records of Choughs in Scotland and their status, collated from literature and museum searches.*

RECORD TYPE	STATUS	RECORDS (*n*)
Negative	0	159
Questionable	?	25
Pre-historic	P	3
Extra-limital	A	50
Possible breeding	1	65
Probable breeding	2	80
Definite breeding	3	99
TOTAL		481

Details of each individual record or museum specimen, its original source/reference (quoted verbatim) and the status that I have accorded each record are given in Appendix 1. Records are indexed by region (see Figure 3.1) and year, along with a grid reference to the nearest 1 km square where possible (see section 3.2.4).

3.3.2 Distribution since 1750

Period 1750-1849 (including pre-historic records). Records of Chough remains found at archaeological digs come from North Uist, Lewis and Orkney. Two pre-1750 records relate to breeding Choughs at St. Abb's, Berwickshire in 1578, and to possible breeding at Mochrum, 3 km inland of the Wigtownshire coast on the Burrow Head peninsula, in 1684. Available information for the period 1750-99 is very limited, vague references making status determination difficult. Choughs definitely bred in Argyll on the islands of Colonsay and Lismore, and at St. Abb's Head/Fast Castle in Berwickshire.

There are few records for the period 1800-49, but Choughs probably bred in the Inner Hebrides and Argyll, and definitely bred at St. Abb's and on the coasts of Wigtownshire and Kircudbrightshire. Birds were also recorded in Sutherland and Barra, but there was no evidence of breeding.

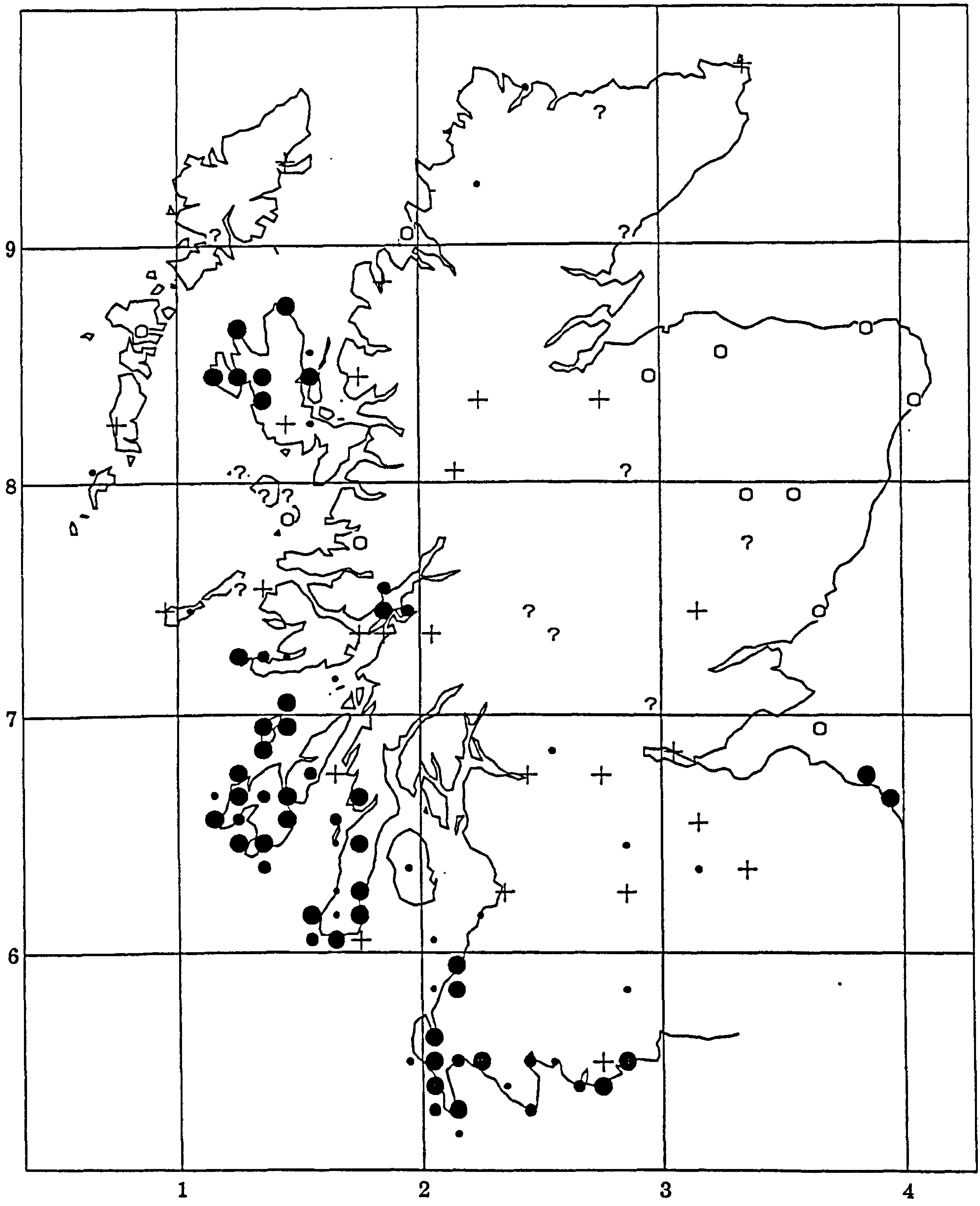
Period 1850-99 The recorded range is greater than for the previous period, but this is probably due to much better recording during the Victorian era. Probable and/or definite breeding was recorded from Kircudbrightshire, Wigtownshire, Ayrshire, the Kintyre peninsula and the Inner Hebridean islands of Islay, Jura, Colonsay, Mull, Iona and Skye. However, breeding probably ceased at St. Abb's before this period. Though there were reports of birds at several inland sites on the mainland, there is no evidence that breeding took place. Despite the wide extent of records, the first references to the species' decline were made during this period, primarily in Berwickshire, Kircudbrightshire and Wigtownshire, and it seems likely that the range was less extensive than in the previous 100 year period.

Period 1900-49. The breeding range was very similar to the previous period, but references indicate that numbers were much reduced within the range. By 1900 the Chough was definitely extinct in Berwickshire and Kircudbrightshire, and probably from Colonsay and Mull. Much smaller numbers were noted in Wigtownshire, Ayrshire and Skye shortly after the turn of the century, and it appears that these birds also disappeared soon afterwards. However, against this trend, single pairs were seen inland in Lanarkshire and Peebleshire (though there was no evidence that these birds were breeding), and extra-limitals occurred in the Outer Hebrides, Orkney and Berwickshire.

Period 1950-88. During 1950-79 there was a further contraction of range, culminating in extinctions in Skye and Mull (though see below). A small population was present intermittently at the Mull of Kintyre but, with only occasional breeding records, this population appears not to have been self-maintaining. Islay remained the species' stronghold (eg. 78 pairs of probable or confirmed breeders in 1986) with a few pairs breeding on nearby Jura and Colonsay. There was a small range re-expansion in the 1980s: single pairs attempted to breed in Wigtownshire from 1988 onwards, and on the Isle of Mull from 1989 onwards. There was a wide scatter of sightings of extra-limital birds throughout the period, with records from Shetland, Orkney, Caithness, the Outer Hebrides, Ayrshire and Kircudbrightshire.

Maximum breeding status 1750-1988 (Figure 3.2) This map summarises the maximum breeding status by 10 km square since regular recording began. All breeding records relate to the west coast, from Skye in the north to Kircudbrightshire and Wigtownshire in the south,

Figure 3.2 Maximum breeding status of Choughs in Scotland, 1750-1988 by 10 km square. The grid overlay represents the national 100 km grid.



Key:

Large filled circles = definite breeding
Medium filled circles = probable breeding
Small filled circles = possible breeding
Open circles = no records
+ = accidental
? = status unclear due to questionable records

NB. Orkney and Shetland: maximum status = accidental apart from the isolated records from St. Abb's/Fast Castle in Berwickshire prior to 1850. Apart from the St Abb's records, the entire east coast of Scotland is devoid of breeding records of any kind. Likewise there are no confirmed records of breeding at any sites more than 10 km inland on the mainland.

3.3.3 Population trends

a) Occupancy of regions

The frequency distribution of occupied regions is shown in Figure 3.3. The peak periods were 1840-59, 1870-99 and 1985-88. However, one cannot take these figures at face value due to the possible influence of recording effort.

b) Recording effort

The frequency distribution of Chough records (n=481) collated from the literature and museum searches for each decade since 1750 is shown in Figure 3.4. There has been much variation in recording effort since 1750. There are very few records during 1750-1849. A sharp increase in recording from 1850-1900 coincides with the main Victorian "collecting" era (see Chapter 4). Recording effort declined throughout the 20th century, but rose sharply from 1970 onwards. The regression of Chough range on recording effort gave a significant positive correlation (r=.635, P<.01, n=16) (Figure 3.5), indicating that the number of regions with Chough records is influenced by recording effort. This would have the effect of exaggerating the extent of the Chough's range during periods of high recording effort because there is a greater likelihood of wandering birds outwith the normal range being detected. This is shown clearly for the period 1950-88, when recording effort was at its highest (see Figure 3.4) but when the Chough's breeding range was extremely limited. During this period extra-limital birds were recorded from a larger number of regions than in any other period, from Shetland and Orkney in the north to Kircudbrightshire in the south (see section 3.3.2).

c) Population trends

By using the standardised residuals from the above regression a corrected estimate for the extent of the Chough's range was obtained, one which allows for variation in recording effort between periods. The standardised regression residuals are plotted against the 16 recording periods in Figure 3.6. A standardised residual value of 0 indicates that the number of occu-

Figure 3.3 Number of regions in Scotland occupied by Choughs, 1750-1988 (status categories - possible, probable and definite breeding).

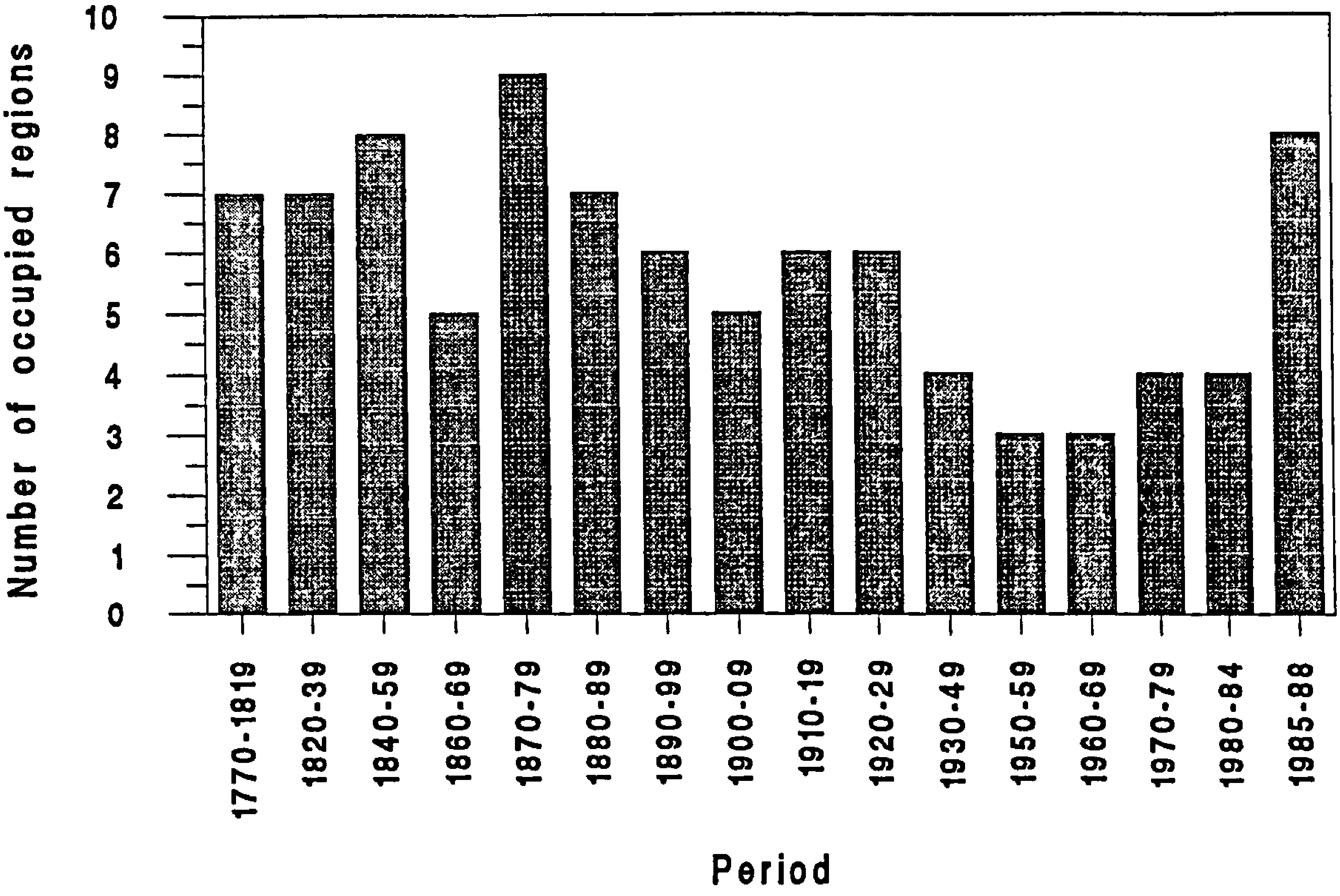
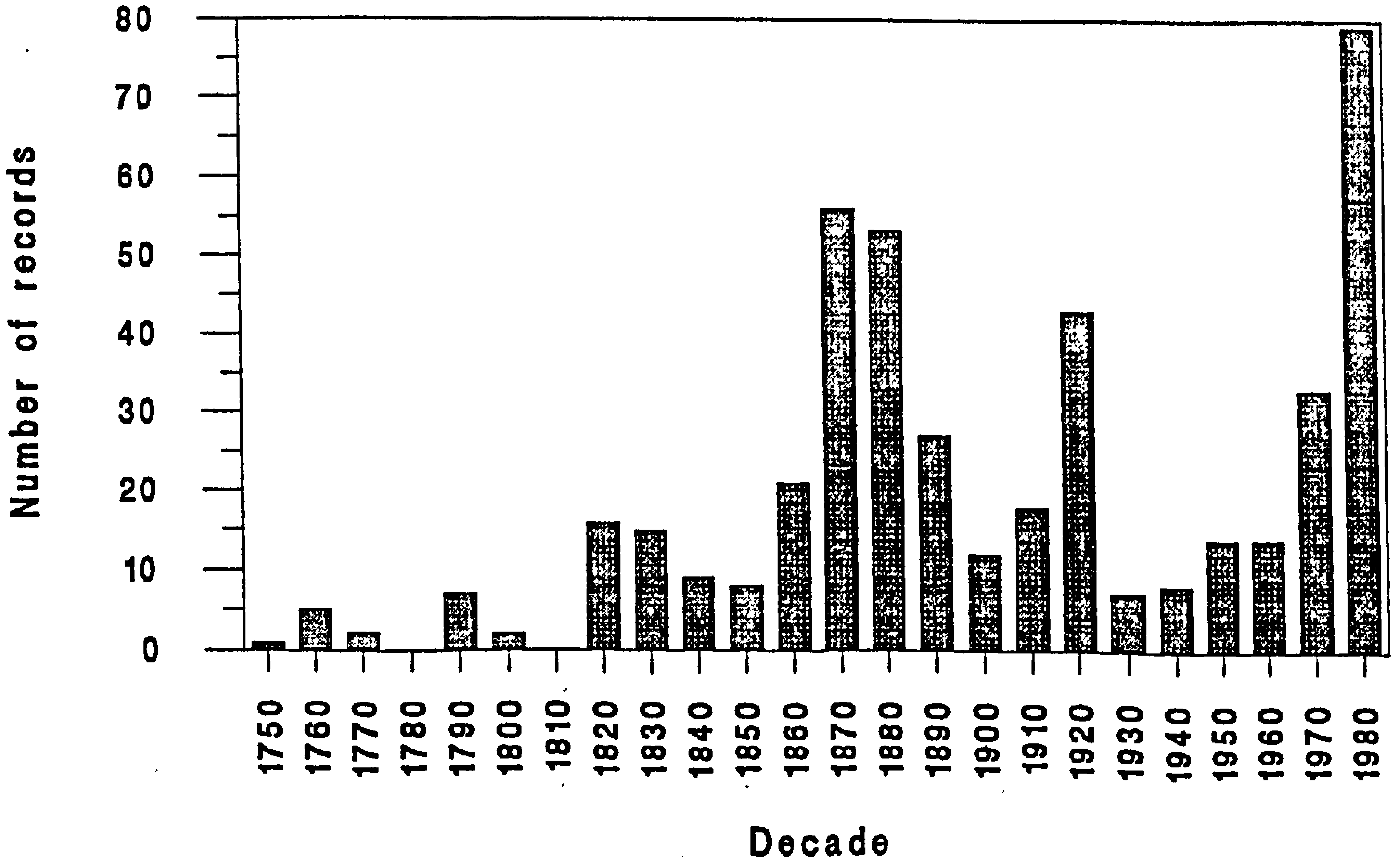


Figure 3.4 Frequency distribution of Chough records (see text) for each decade, 1750-1988 (n=481).



pied regions is as expected from the regression of occupied regions on recording effort, a positive value represents more occupied regions than expected, and a negative value represents less occupied regions than expected.

The standardised residuals in Figure 3.6 can be compared with the uncorrected totals of occupied regions in Figure 3.3. Both show a similar pattern of overall decline in the Chough's range over the last 200 years, but the corrected estimates emphasise that the Chough's range was at its greatest extent prior to 1850 (when records were relatively scarce) and that it contracted to its minimum extent during 1950-79. Whilst the number of regions recorded as occupied in the 1980s is only one less than the maximum recorded for any period, correcting for recording effort suggests that the 1980s range was similar in extent to that at the turn of the century, which in turn represented a contraction from its pre-1850 extent.

3.4 DISCUSSION

Archaeological evidence suggests that Choughs were more widespread before regular bird recording began, with archaeological remains being found in both the Outer Hebrides (Baxter & Rintoul 1953) and the Orkneys (Booth & Reynolds 1984). One can only assume that Choughs once bred in these areas, and that they were hunted for food. Since 1750 Choughs have only been recorded as accidentals in these islands.

Analysis of post-1750 records shows that the Chough's range has contracted almost continuously over the last 240 years. That it was even more widespread before 1750 suggests that the recent decline may merely be a continuation of a much longer term range contraction. A similar conclusion was reached by Burton (1995) who considered it probable that the Chough "has been declining in Europe ever since the end of the very warm Little Climatic Optimum". The latter warm period extended from *c.*AD 750 to *c.*AD 1250, and was marked by a northward and westward expansion of the ranges of many Mediterranean and Lusitanian species (Burton 1995).

Poor documentation for the period 1750-1849 does not enable a precise determination of status over that period to be made, but the limited data available suggest that the range was more extensive then than at any time subsequently. Whilst there are few explicit breeding records it is clear that Choughs occurred (and probably bred) along the coast of south-west

Figure 3.5 Regression of Chough range extent on recording effort (see text) for records of definite, probable or possible breeding for the 16 recording periods from 1750-1988 (n=15).

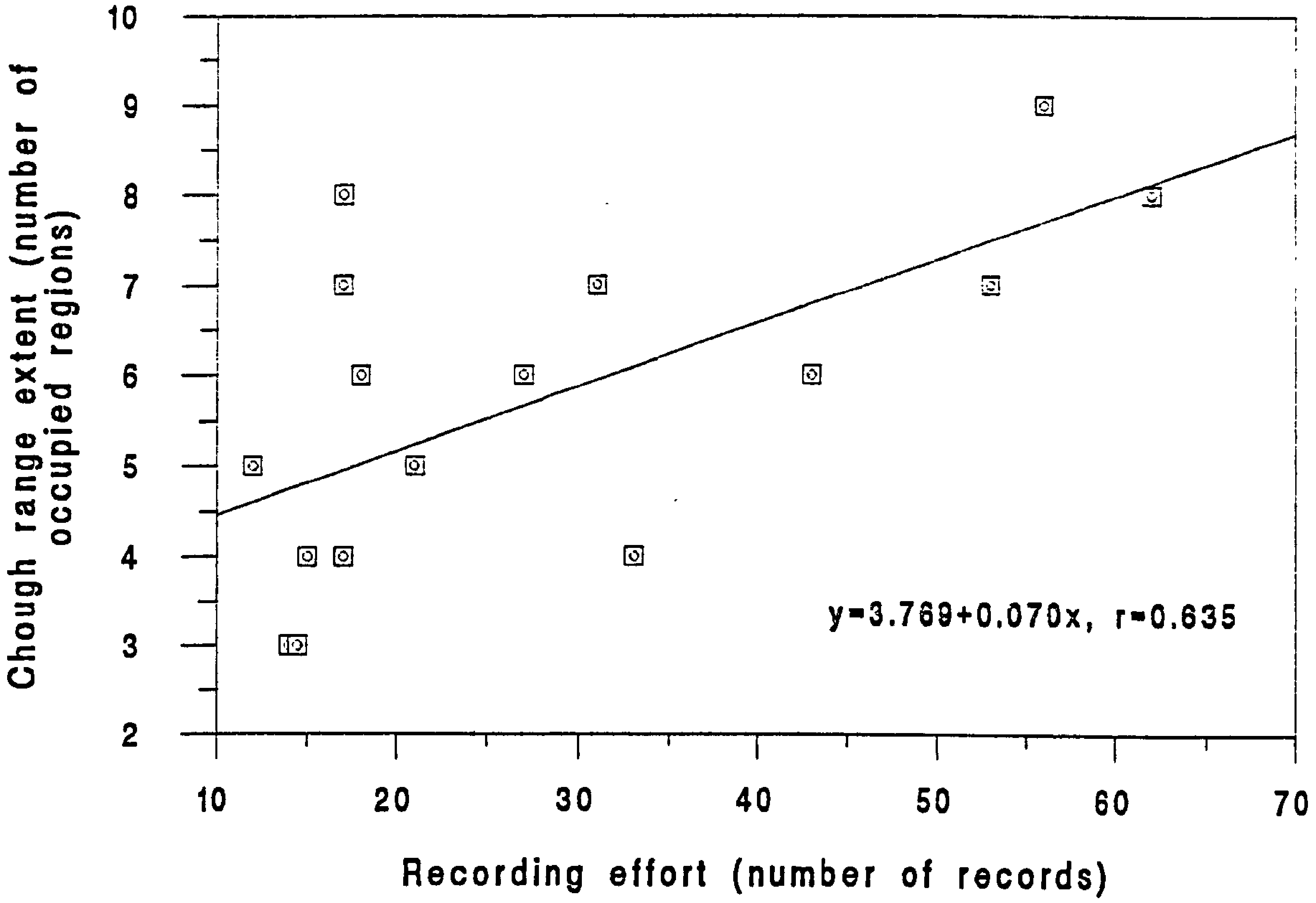
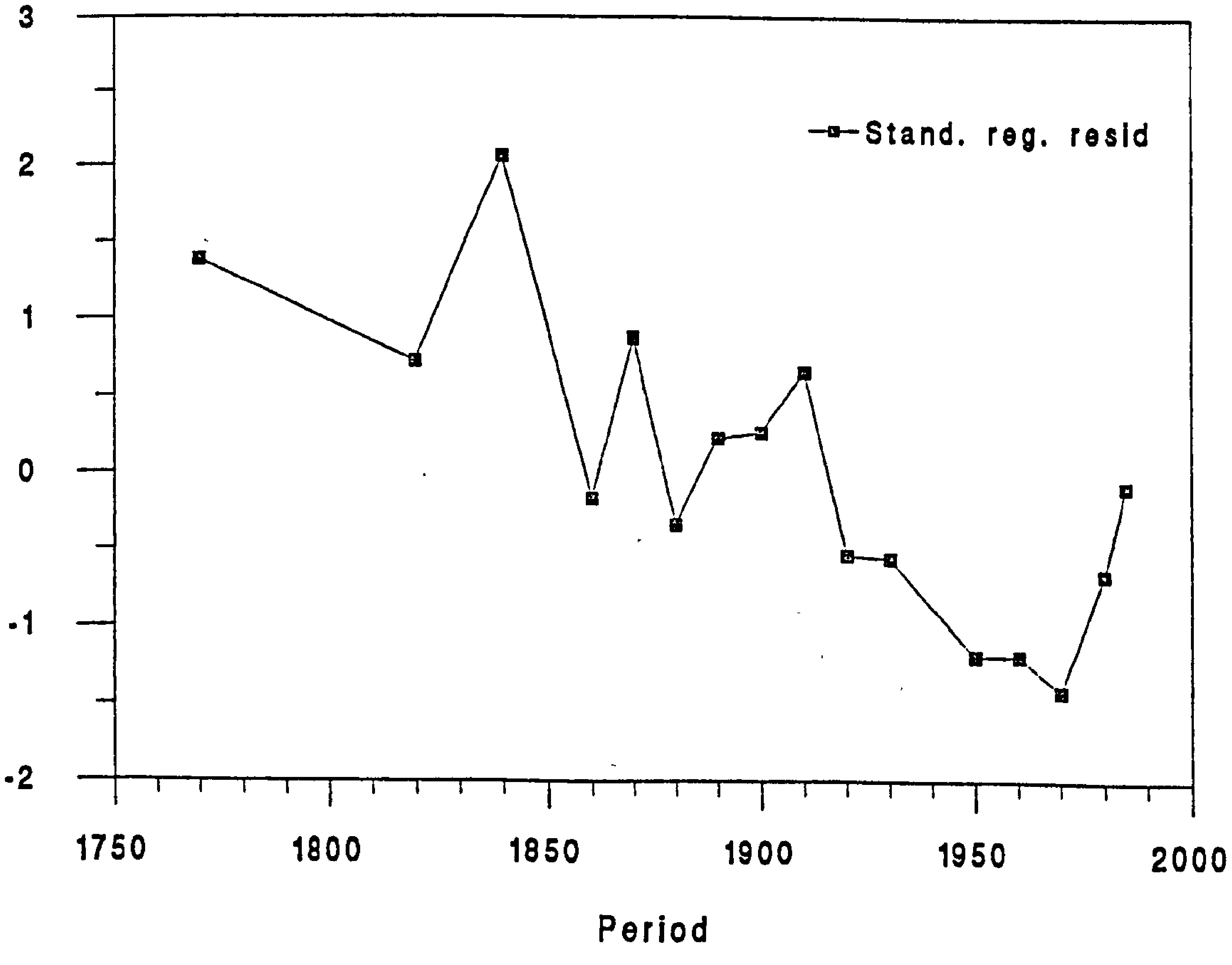


Figure 3.6 Plot of standardised regression residuals from regression of Chough range on recording effort for the 16 recording periods from 1750-1988.



Scotland from Kircudbrightshire to Ayrshire, on Kintyre and possibly Arran, and on Islay, Colonsay, Mull and probably Skye. Breeding probably occurred at two sites (Lismore Island, Argyll, and St. Abb's, Berwickshire) from which there were no subsequent records. A probable Chough was seen "chattering like a Jackdaw" in Assynt, Sutherland in 1768, and in 1848 St. John records seeing a "few" Choughs at Durness on the north Sutherland coast. In the *Old Statistical Account* "pairs" were noted at two inland localities in central Scotland (Campsie, Stirlingshire and the Corra Linn, Lanarkshire). None of the latter records specifically state that the birds were breeding, but their mere presence at such a wide range of sites during a period of limited recording effort suggests that the Chough must have been more abundant then than it was to become in the late 1800s.

However, the Chough's Scottish range during the early 1800s may have been exaggerated by some late 19th century authors, particularly Robert Gray (1871). His implications that it bred at several inland sites, on most of the Inner Hebridean and some of the Outer Hebridean islands, and at some east coast sites, are not supported by any other references in the literature (see below). These unsubstantiated reports have not been included in the current assessment of the Chough's status.

Nevertheless, by the late 1800s several authors had noted that the species was in decline (Gray 1871, Buchanan 1882, Service 1885). It had become extinct at St. Abb's by 1850, followed by Kircudbrightshire in 1885, and had become much rarer in Ayrshire, Wigtownshire, Mull and Iona. Choughs maintained a foot-hold in the Inner Hebrides, Skye and on the Wigtownshire/Ayrshire coast at the turn of the century, and there may even have been a slight increase in some of these areas. This coincides with a period of climatic amelioration which occurred between 1850 and 1950 (see Burton 1995).

From 1900 onwards extinctions occurred in Skye (c.1910) and Colonsay (c.1910). There was a marked decline from 1920 onwards, with extinctions in Ayrshire (c.1940), Gigha (c.1940) and Wigtownshire (c.1940). The period 1950-79 represented the minimum extent of the Chough's range in Scotland in recorded history, when it occurred only on Islay, and possibly on Jura and Colonsay, with intermittent breeding records from the Kintyre peninsula.

The Chough appeared to be heading towards extinction in Scotland at this time, but fortunately there was a reversal of the downward trend. Choughs "returned" to Colonsay in 1967, and to Mull and Wigtownshire in the late 1980s. By the late 1980s the population on Islay was at a high level, with 95 pairs present at nest sites (Monaghan *et al.* 1989), representing over 30% of the UK population at that time. This expansion has been facilitated by the recently adopted trait of using derelict buildings for nesting (Warnes 1983). Approximately 26% of the breeding population used such sites in 1986 (Monaghan *et al.* 1989), enabling breeding pairs to exploit inland areas where natural nest-sites are scarce.

Interestingly, despite a contracting range in the 20th century, Choughs continued to occur at a wide range of inland sites as extra-limitals, and as far afield as Caithness, Orkney and Shetland, indicating an ability to disperse up to 600 km (the distance from Islay to Shetland). Ringing recoveries show that Choughs reared at mainland sites tend to disperse further than those from islands (see Chapter 4). Perhaps then the suspicions that the Chough bred at inland sites in the 19th and early 20th century resulted from more regular occurrences of Choughs as they dispersed widely from mainland populations which existed at that time in coastal Ayrshire, Wigtownshire and Kircudbrightshire. Such wandering birds would have become less frequent in later years when the bulk of the Scottish population became restricted to an island site - Islay. The small breeding population at St. Abb's before 1850 may have owed its existence to the proximity of breeding populations across the Southern Uplands in Kircudbrightshire and Wigtownshire: following the demise of the latter populations, there have been no records of Choughs from Berwickshire.

Despite the species' obvious ability to disperse over long distances, there are some localities which are notable for their lack of Chough records. In particular it is curious that there is no evidence that Choughs have ever bred on the Inner Hebridean islands of Coll and Tiree, nor on the coasts of Ardnamurchan, Moidart and Knoydart. There are only questionable breeding records from Rhum, Eigg, Muck and Canna, and Choughs have apparently only occurred as vagrants in the Outer Hebrides since 1750. Possible reasons for these absences are discussed in subsequent chapters.

This analysis of historical records has produced some results which differ considerably from previous accounts of the Chough's status in Scotland. For example, I can find no evidence to support Baxter & Rintoul's claim (1953) that "the old records show beyond a doubt that the Chough in Scotland was a bird of the inland as well as of the sea-cliffs" nor that "it was abundant on almost all the rocky headlands in Scotland in 1835, but had vanished nearly everywhere [by] 1865". They suggested that this was the main period of a "rapid decline". The current findings suggest that the Chough's decline in Scotland has been quite protracted: local extinctions have occurred from the early 1800's (Lismore Island) through to the present (Mull of Kintyre), and we know that some time before 1750 it disappeared from Orkney and the Outer Hebrides.

The main source of divergence between my results and the statements made by Baxter & Rintoul derive from the treatment of Robert Gray's (1871) account of the Chough in *The Birds of the West of Scotland.* He paints a picture of a "deplorable decrease" having overtaken the Chough in Scotland in the 30 year period leading up to his publication, and Baxter & Rintoul have obviously taken his statement at face value. However, many of Gray's statements are not supported by other references of the time. Within his account one can detect two types of records: firstly, many highly credible accounts where he obviously had first-hand knowledge or contacts, backed up by accurate and elegant descriptions of the birds, their haunts, and behaviour; secondly, he lists a series of negative records such as "no longer known in Tiree, Coll, Rhum or Canna" without supplying supporting references or accounts. It appears that Gray may have commented on these areas for "completeness' sake" when in fact he had no data on which to base his conclusions. This latter group of unsubstantiated records have, in my opinion, misled many subsequent authors who, naturally enough, have quoted Gray's statements, eg. Buchanan (1882), Baxter & Rintoul (1953) and Warnes (1983).

There may have been other sources of inaccuracies in the literature. Harvie-Brown (1906) suggested that some questionable records (such as those of Choughs seen at inland sites in Perth and Angus by Pennant (1771) and Donn (c.1870) respectively) may have resulted from confusion between the Scots word *sheugh* (meaning literally a ditch or furrow), often applied to small glens/gullies, and the English word *Chough.* Whether or not this was the case, it is worth noting that Harvie-Brown, one of the most eminent Scottish natural historians of the Victorian era, should have his doubts about the authenticity of some of the published Chough records of his time.

Another possible source of confusion comes from the fact that in Gaelic-speaking areas the word *Cadhag* is frequently used for both the Chough and the Jackdaw, even to this day (eg. on Islay *pers. obs.*). (Similar ambiguities have confounded analysis of the Chough's historical distribution and abundance in England where the name "Chough" pronounced "Chow" as in cow, was used for both Choughs and Jackdaws (see Meyer 1991)). The crofter who told Harvie-Brown about the nest of a "Caag" in a chimney on Skye in 1886 (Harvie-Brown & Buckley 1904) may have been referring to Jackdaws rather than Choughs (though in the current analysis I have taken the record at face value). Indeed, if Loder (1935) is correct in stating that *Chramhaich* is the Chough's true Gaelic name, then many of the older records of "Caags" or "Cadhags" may have related specifically to Jackdaws. Unfortunately, the Chough does not feature in Gaelic folk-lore or place-names: in a thorough map-search of the coasts of the Inner Hebrides and Argyll, I found no cliffs or caves with the suffix "Chramhaich" or "Cadhag"; Loder (1935) describes one such cave on Colonsay, but this does not feature on recent OS maps.

In recent times the Chough's Scottish breeding range, appears to have comprised six sub-populations, if we define a sub-population as being discrete when it is separated from the nearest other sub-population by 20 km of sea or unoccupied land. These are 1) Skye 2) Mull, Iona and Lismore Island, 3) Islay, Jura and Colonsay, 4) the Kintyre peninsula, Gigha, Davaar Island and Arran, 5) the mainland coasts of Ayrshire, Wigtownshire and Kircudbrightshire and 6) St. Abb's and Fast Castle Heads in Berwickshire. All these areas supported Choughs during 1750-1850, but by 1950-70 only 1 sub-population was extant - the Islay/Colonsay/Jura group. A recent increase in numbers means that the Chough has returned to two further areas - the Mull group and the Wigtownshire coast. With only one pair in each area, it is too early yet to consider these sub-populations as being re-established. Despite attempting to breed every year between 1989 and 1995, the Mull pair have yet to breed successfully (*Scottish Bird Reports*). The Wigtownshire pair have successfully reared young each year between 1990 and 1995, but none of the young have been seen in the vicinity subsequently, and the female of the breeding pair disappeared later in 1995 (C. Rolley *pers. comm.*)

It is interesting to note the possible affinities between these sub-populations. The Mull sub-population clearly owes its current existence to the Islay sub-population, and in turn the extinct sub-population on Skye would almost certainly be dependent on the presence of a productive population on Mull for its re-establishment. Observations on the intermittent population which existed on the Kintyre peninsula in the late 1970s/early 1980s suggest that these birds originated from Northern Ireland, and may even have commuted to and from Ireland across the Irish Sea on a regular basis (B. Zonfrillo *pers. comm.*). It is only 20 km to Northern Ireland across the North Channel of the Irish Sea from Kintyre, whereas it is 35 km "as the crow flies" to the Oa on Islay, or 45 km to Islay via the Kintyre peninsula and Gigha. Thus, in the short term at least, the presence of Choughs on Kintyre may depend upon the health of the Ulster Chough population; this hypothesis is supported by the current absence of Choughs on Kintyre at a time of population decline on the adjacent coast of Northern Ireland (*Irish Bird Reports*). The nearest population of Choughs to the Wigtownshire/Kircudbrightshire/Ayrshire sub-population is on the Isle of Man (30 km from Burrow Head in Wigtownshire); it is almost certain that the pair which have nested on the Wigtownshire coast since 1988 originated from the Isle of Man, as this pair have been observed feeding along the tideline in winter (*pers. obs.*), a common habit amongst Manx birds but rarely recorded on Islay (see Chapter 7).

If these hypotheses are correct, then we should not consider the Scottish Chough population as being a closed population, but rather a grouping of several sub-populations, two of which have closer affinities to populations outwith Scotland than to others in Scotland. It appears that only one of the current Scottish sub-populations is a productive or "source" population (*sensu* Newton 1991, see Chapter 5) - that on Islay and Colonsay (Jura supported only three breeding pairs in 1986, none of which bred successfully (*pers. obs.*, see also Appendix 4)).

Maintenance of the Wigtownshire and Mull sub-populations will be dependent on recruitment from the Isle of Man and Islay/Colonsay respectively. The presence of these isolated pairs represents a good opportunity to consolidate populations outwith the core Scottish area of Islay/Colonsay. Their presence also indicates the importance of maintaining and if possible enhancing, the Chough populations on Islay and in the Isle of Man.

Chapter 4

A REVIEW OF POTENTIALLY LIMITING FACTORS INFLUENCING THE STATUS OF THE CHOUGH IN SCOTLAND, PAST AND PRESENT.

4.1 INTRODUCTION

In Chapter 3 I described how the Chough's range in Scotland has contracted since 1750; many former breeding areas have been deserted, including Skye, Gigha, the Mull of Kintyre, Ayrshire, Kircudbrightshire and Berwickshire. A similar decline occurred simultaneously in England, where the species is now extinct as a breeding bird, having once been quite widely distributed along the south coast from Cornwall to Sussex (Owen 1989). Some areas of Wales have also been deserted eg. Glamorgan and Anglesey (Owen 1989), though the decline appears not to have been so pronounced in this country (see Bullock *et al.* 1985). The species now has a very restricted and unique range in the British Isles, being found mostly on the western seaboards of Ireland, Scotland and Wales.

In this chapter I review the various factors which have been suggested in the literature as having produced this restricted range, or as having been causes of past contractions of the range. The aims of this review are to attempt an objective assessment of these factors, particularly those which are likely to be limiting Chough populations at the current time. Wherever possible I have attempted to quantify the proposed relationships, rather than making subjective assessments. It is hoped that this overview will help to identify areas worthy of research, eliminate spurious relationships, and provide a useful background to the current study.

Several authors have made similar reviews, most with particular reference to the possible causes of the Chough's past decline: Baxter & Rintoul (1953), Rolfe (1966), Warnes (1983), Bullock *et al.* (1983, 1985), Owen (1989) and Meyer (1991). My intention is to approach the question with specific regard to Scotland, making use of the data on past distribution and timing of the decline obtained in Chapter 3. Several "new" possible causes of the decline have been proposed and examined. Potential limiting factors are summarised below, with a brief description.

Persecution: shooting, egg-collecting, skin-collecting, trapping etc.

Niche overlap: with other corvids.

Isolation and in-breeding: due to restricted distribution in Britain.

Predation: primarily from the Peregrine Falcon.

Nest-site competition: competition from other species of birds.

Disease and Toxic Chemicals.

Parasites: Infection by the nematode parasite *Syngamus trachea.*

Winter severity: the impact of severe winters on survival.

Nest-site availability: limits to population size posed by nest-site availability.

Land-use change: trends away from pastoral agriculture.

4.2 METHODS

Suggested causes of the Chough's decline and potentially limiting factors were assessed by reviewing the relevant Chough literature as described in Chapter 3. Observations made during the course of this study were used where relevant. The results of the review are presented in the Discussion (section 4.4). Where new analyses were carried out, the methods are described below. Only those analyses which involved reanalysis of data or statistical analyses are presented in the Results section.

4.2.1 Record collation

Historical records of Choughs (date, locality and status) were collated from the relevant literature and from a questionnaire sent to British and Irish museums, as described in section 3.2.1. The historical references (presented verbatim in Appendix 1) were specifically checked for statements made by the authors on the possible causes of the Chough's decline, and on the incidence and type of persecution etc.

4.2.2 Persecution

The collection of Chough skins and/or clutches is a form of persecution whose chronology, unlike most others, can be traced through the resulting specimens found in museum collections. From the museum search described in section 3.2.1, accurate data on year of collection for 161 skins/mounts (hereafter referred to only as "skins") and 336 clutches collected in the

British Isles were obtained. Collection dates were aggregated by decade. Only "collected" specimens were included in the analysis, i.e. excluding birds simply found dead.

To determine whether levels of persecution within Scotland reduced population size, or merely reflected it, the index of Chough range extent (see section 3.2.6) was correlated with persecution (the number of specimens collected in each decade). As some decades had to be aggregated to obtain the index of Chough range, persecution was aggregated over the same periods, necessitating the calculation of the mean number of specimens collected per decade.

If range extent is positively correlated with persecution in the same decade (decade *x*), this suggests that persecution merely reflects range extent. If persecution is causing a contraction in range, then one would expect a negative correlation between persecution in the previous decade (decade *x-1*) and range in decade *x*.

4.2.3 The effect of natal site insularity on Chough dispersal

Ring recoveries from the British Trust for Ornithology ringing scheme were analysed to assess the influence of natal site insularity (ie. island *vs.* mainland nest-sites) on subsequent dispersal. Seventy recoveries of Choughs ringed as nestlings have been generated by the BTO ringing scheme. This analysis was restricted to birds ringed as nestlings since these were the only birds whose natal site was definitely known. Recoveries of birds less than 3 months old were excluded from the analysis (reducing the number of cases to 38) as these probably represented birds that had died at the nest, or very soon after fledging. The Isle of Man and Islay were categorised as island sites (distance to nearest mainland 30 km and 23 km respectively). All other birds were ringed at mainland sites, except for those ringed at Bardsey Island, which has been included as a "mainland" site since it lies only 2 km from the Lleyn peninsula, and it is known that there are daily movements of Choughs to and from the mainland at certain times of year (Roberts 1983). Distance of recoveries of birds up to 1 year old was compared with that of birds older than 1 year in an attempt to determine the age at which dispersal occurs.

4.2.4 Nest-site competition

Many authors have cited nest-site competition with Jackdaws as a possible cause of the Chough's historical decline (see section 4.1), but none have attempted to quantify this. Moreover, some other potential nest competitors (Kestrel, Rock Dove, Barn Owl) have not been mentioned at all in the literature. The effect of nest-site competition was assessed by looking at the number of nest-site desertions and their apparent causes at a sample of 62 nests checked annually during 1987-89. Nest-site abandonment is used here to mean instances where birds failed to appear during the breeding season at a previously used nest-site. This should not be confused with nest desertion where birds are present at a site and attempt to breed but where the breeding attempt is later aborted. Choughs are very site faithful and use the same site year after year (see Chapter 6) so if a site is deserted it strongly suggests that it has become unsuitable in some way. It is possible that such desertions might be caused by predation of both members of the breeding pair. However, the density of breeding Choughs on Islay is high (Monaghan *et al.* 1989) and there is a large non-breeding population (Still 1989) so one would expect any such vacant nest-sites to be rapidly filled. Some sites are only occupied irregularly, presumably because of poor feeding conditions in their vicinity, so this analysis was restricted to sites that were known to have been regularly used prior to or during the study period.

Data on occupation of sites were collated from BTO nest record cards, the 1986 census of Choughs in Scotland (Monaghan *et al.* 1989) and from personal observations during 1987-89. Nests were not visited during the breeding season (except for some in 1987) unless it was clear that the site had been abandoned. Sites were checked after it became obvious that no birds were present that year. Sometimes the cause of nest-site desertion was obvious, e.g. the nest-site entrance having been blocked during renovation work to a building. Where the cause was less clear, the site was checked for signs of the presence of other species of birds, and the nest checked to see, for example, whether it had been washed out during a storm. These "after the event" assessments can only provide circumstantial evidence of the cause of site abandonment, but similar methods have been used by other workers e.g. for Sparrowhawks *Accipiter nisus* (Newton 1986). It could be argued that a site is more likely to become occupied by a Barn Owl after it has been abandoned by Choughs, and that the current analysis would incorrectly conclude that the Barn Owl had been the cause of the abandonment. However, Choughs are very reluctant to abandon regularly used nest sites. Breeding pairs on Islay have continued to use nest sites which have been subject to building work, farming operations and Barn Owls roosting within 2m of the nest.

Bearing this in mind, it seems fair to accept the interpretations of causes of nest abandonment made here, which are based on several years' field experience. Despite some potential biases, this quantified approach is preferable to the subjective observations which have been used to support assertions made in the literature to date. Moreover, the approach taken here is conservative in that I only looked at sites which had previously been regularly used. The chances of making the type of spurious correlations described above would have been much greater had irregularly used sites also been included.

4.2.5 Winter severity

assess the possible relationship between fluctuations in winter severity and the extent of the Chough's Scottish range, an index of the latter (see section 3.2.6) was correlated with the number of days each year with Westerly winds (between WSW and WNW) over the British Isles (10-year means, data from Lamb 1977). The variable "number of days with westerly winds" was chosen as an indicator of winter mildness (ie. negatively correlated with winter severity) as Lamb (1977) has shown that in Britain over the last 300 years this variable has correlated closely with general trends in air temperature in the northern hemisphere, and is thus one of the few data sets with a long enough run to be appropriate for this analysis. The estimate of range extent in each decade was calculated in such a way as to allow for variations in recording effort between periods (see section 3.2.6). The analysis was restricted to the period 1860-1970, these being the decades for which climatic data were available. To allow for a possible lag between the effect of winter severity on population size, a second analysis of range in decade x correlated with westerly winds in decade $x-1$ was carried out. The two decades covering 1930-49 were aggregated into one period due to the small number of records in each decade; this gave 11 periods for the first analysis and 10 periods for the lag analysis.

4.3 RESULTS

4.3.1 Record collation

Statements in the historical literature concerning factors influencing the Chough's decline are quoted verbatim in Appendix 1 under the appropriate region.

4.3.2 Persecution

The frequency distribution of year of collection of 55 skins and 11 clutches from Scotland is shown in Figure 4.1, and for 161 skins and 336 clutches from the rest of the British Isles (excluding Scotland) in Figure 4.2. The frequency distributions of year of collection are close to normal, with the mean for Scotland (1880.0) being 25 years earlier than for the rest of the British Isles (1905.0) (*ANOVA*, $F_{1,495} = 33.224$, $P < 0.001$).

Skins collected in Scotland represent a high proportion (34.2%) of the British and Irish total, whereas fewer clutches were collected in Scotland (3.3% of the total). If the median dates of collection of clutches and skins are considered separately for both Scotland and the rest of the British Isles (median dates are used due to some positively skewed distributions when the data are separated into skins and clutches), the median dates for Scotland remain earlier, though the difference is only significant for skins: *skins*: Scotland 1880, rest of British Isles 1897 ($U = 1707.5$; $z = -4.31$; *2-tailed* $P < 0.001$), *clutches*: Scotland 1887, rest of British Isles 1906 ($U = 1270.0$; $z = -1.63$; *2-tailed* P .102, Mann-Whitney U-test).

There was no significant correlation between range extent and persecution in period x ($r=0.11$, $n=16$, NS.), nor in period $x-1$ ($r=.07$, $n=15$, NS.). This suggests that levels of persecution did not simply reflect population size, nor adversely affect it.

4.3.3 The effect of natal site insularity on Chough dispersal

The distance moved by Choughs greater than three months old from their natal site is strongly positively skewed (Figure 4.3), with a median distance of 6.0 km. Of the 40 recoveries, 22 (55.0%) came from within 10 km of the natal site, whilst 13 (32.5%) exceeded 20 km; the maximum movement was 143 km.

There was no significant difference between the median distance moved by birds

Figure 4.1 Year of collection of 55 skins and 11 clutches from Scotland currently held in British and Irish museum collections.

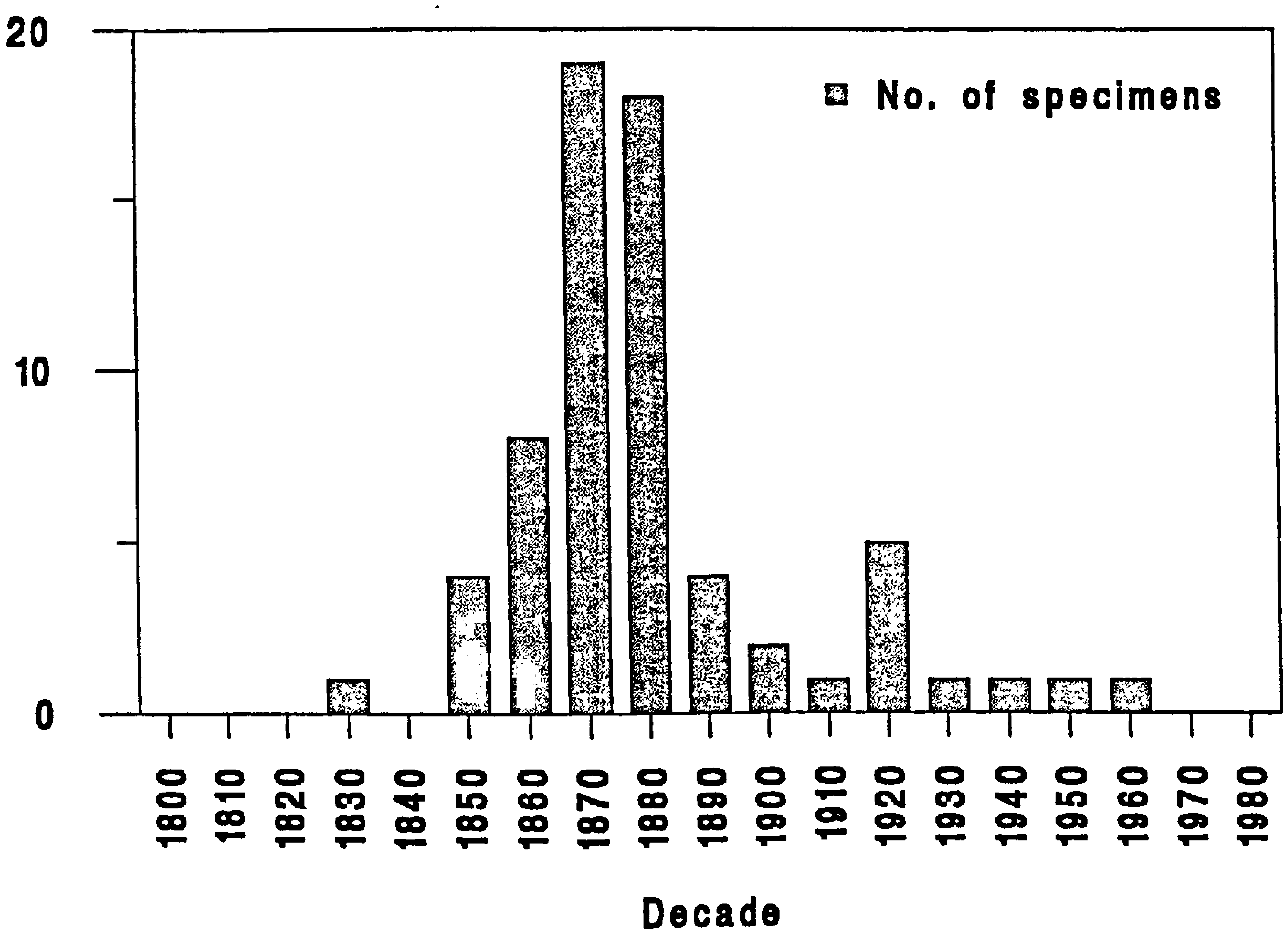


Figure 4.2 Year of collection of 161 skins and 336 clutches from the British Isles (excluding Scotland) currently held in British and Irish museum collections.

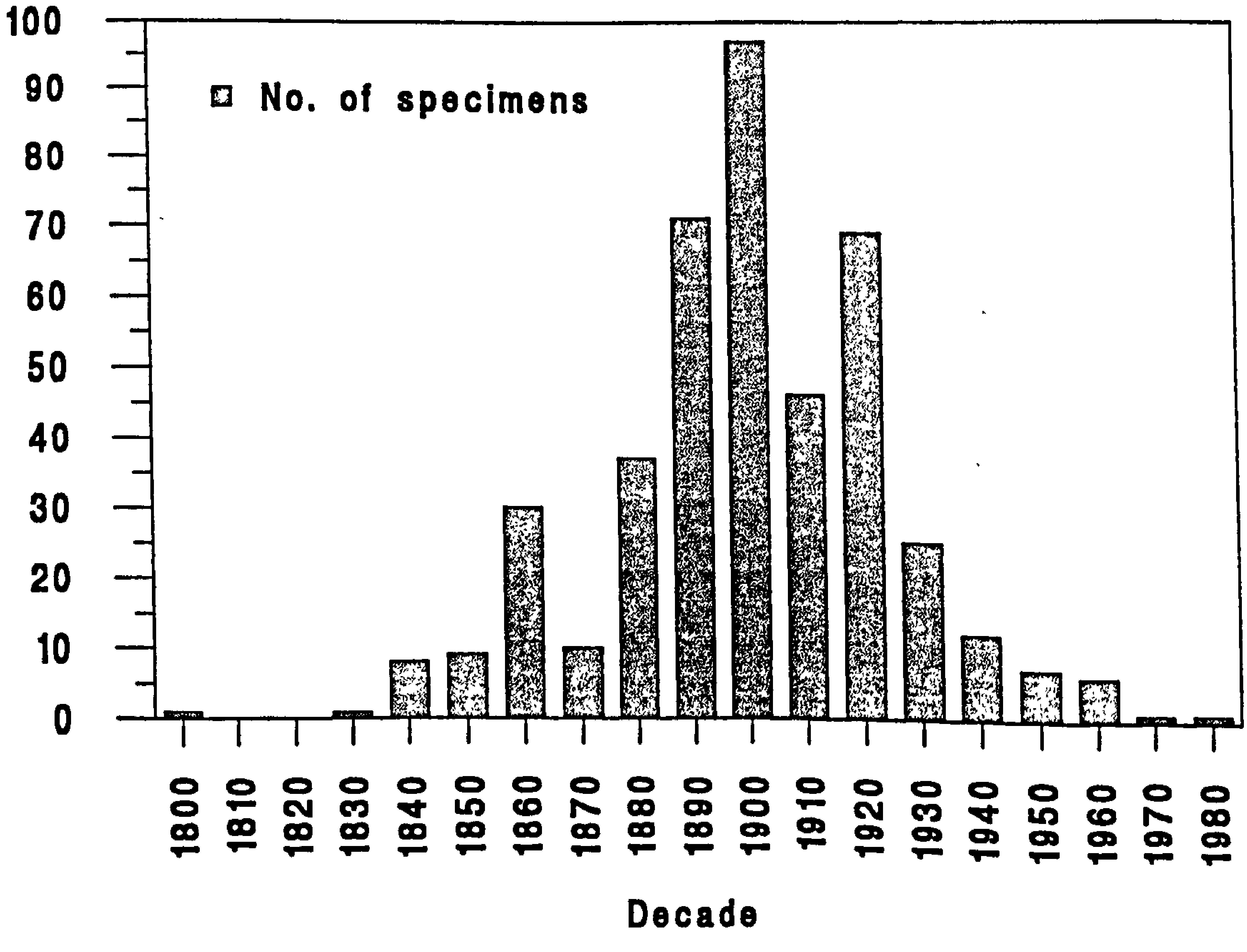
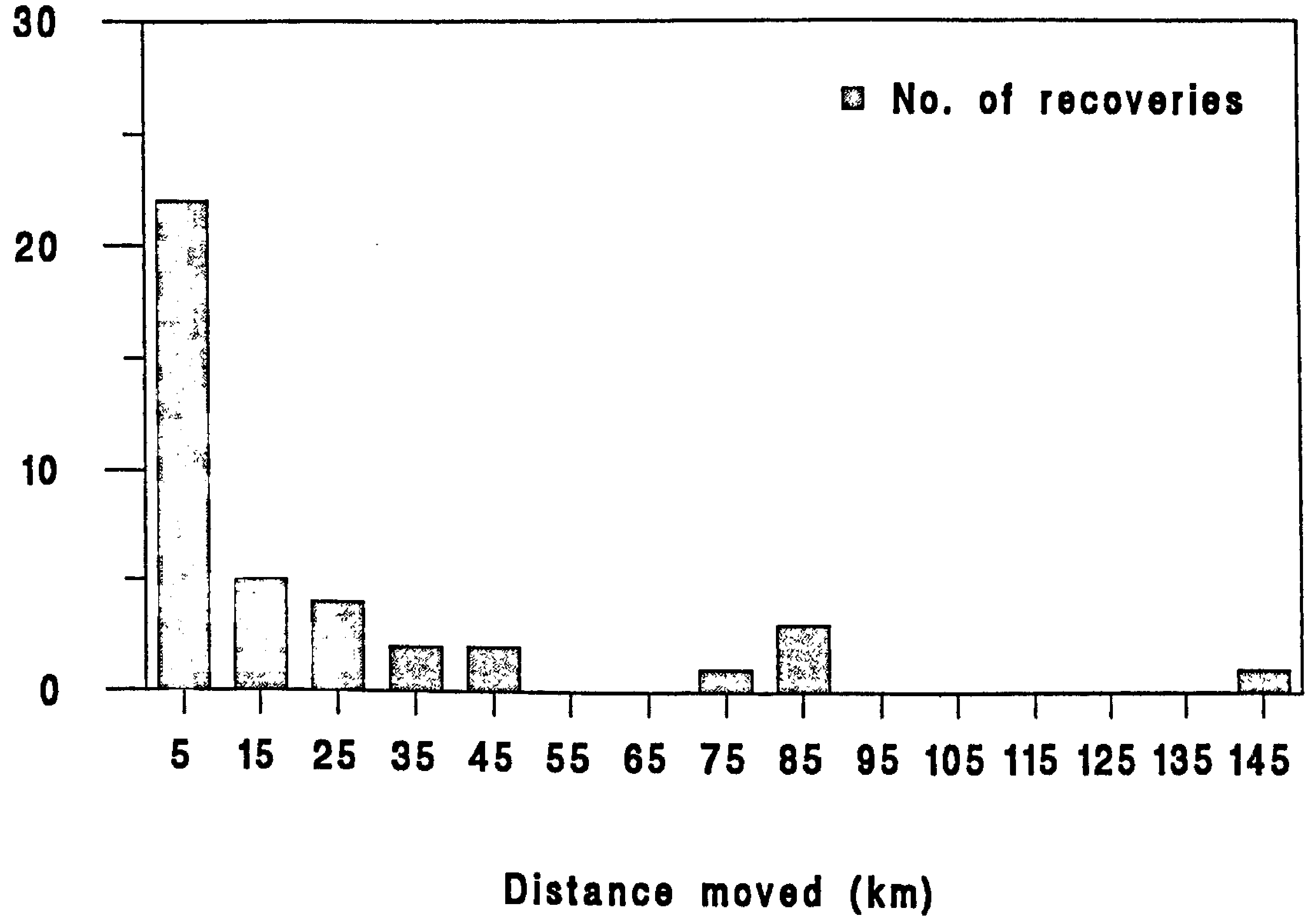


Figure 4.3 Distance moved by Choughs ringed as nestlings in the British Isles and recovered at age >= 3 months (n=40).



ringed as nestlings recovered up to 1 year of age (n=21) compared with that of birds recovered when more than one year old (n=17) (U=17; z= -1.37; NS. Mann-Whitney U-test). This implies that most dispersal occurs in the first year of life since there was no tendency for older birds to be recovered at greater distance from the natal site. This suggests that birds undergo dispersal from their natal sites in their first year, subsequently settling in the areas to which they have dispersed.

When recoveries of birds ringed at *island* as opposed to *mainland* sites were compared, it was found that the median distance moved by 9 *mainland* birds (47.0 km), was significantly greater than that (6.0 km) of 17 *island* birds (U = 18.5; z = -3.14; *2-tailed P* = 0.002, Mann-Whitney U-test).

4.3.4 Nest-site competition

During 1987-89 fifteen nest abandonments were recorded at the 62 previously regularly used nest-sites which were monitored (Table 4.1). Only four of these abandonments were at natural nest-sites, the rest being in buildings. Dereliction of, or improvements to buildings accounted for 66.7% of all abandonments, whilst the two sites where Barn Owls were thought to be the cause of the nest-site abandonment were also in buildings.

Table 4.1 *Causes of nest-site abandonment by Choughs, Islay 1987-89.*

Cause of abandonment	No. of nest-sites	Percent of totally abandoned sites (n=15)
Dereliction of building	6	40.0
Improvement of building	4	26.7
Presence* of Barn Owls	2	13.3
Nest washed out by sea	1	6.7
Cause not known	2	13.3

* Presence means that birds are present in the immediate vicinity of a nest-site, eg. in the same section of a cliff, same cave/cave entrance, building or sea-gully.

4.3.5 Winter severity

There was no correlation between the mean number of days each with westerly winds over the British Isles for the 11 periods covering 1860-1970 (see section 4.2.5) with the estimate of Chough range extent in the same period ($r=.470$, $n=11$, $P=.144$), or in the previous period ($r=.146$, $n=10$, $P=.686$).

4.4 DISCUSSION

The factors which may have influenced the decline of the Chough in Scotland since 1750 are discussed below.

4.4.1 Persecution

There are many different methods by which the Chough has suffered persecution at the hands of man. Records of persecution taken from the Scottish literature (see Appendix 1) are frequent, with examples from all parts of the Scottish range. The Chough was probably particularly susceptible to persecution from indiscriminate shooting, and from shooting for collecting purposes, sport and "control of vermin", since first-year birds are unusually tame (*pers. obs.*), and adults are very bold when defending their nests. Trapping also posed a threat: it seems that Choughs were easier to trap than other corvids (Gray 1871, Matheson 1931), and were often inadvertently caught in gin traps set on cliff slopes for rabbits (Meiklejohn & Stanford 1954, Gordon, unpubl.). Nestlings were also taken to be reared as pets, and it is even said that on Colonsay Choughs were considered to be "very palatable in Chough pie" (Gathorn-Hardy 1914)! A similar catalogue of persecution was recorded from England at the same time (see Owen 1989 and Meyer 1991).

It is difficult to quantify the effects of such persecution on the population as a whole, since most persecution goes unrecorded. The current analysis which uses Chough specimens currently held in museum collections as an index of persecution levels obviously has limitations. However, it is assumed that the timing of collecting *per se* may act as a general index of persecution levels, and that these recorded levels represent only a small proportion of that which occurred but went unrecorded.

The results show that collecting began in earnest in Scotland and in the rest of the

British Isles from 1850 onwards (see Figures 4.1 & 4.2). The onset of collecting coincided with the development of breech-loading and sidelock shotguns in the 1850s and 1860s respectively (Gooders 1983), which improved both their fire-power and their efficiency.

Most specimens collected in Scotland were skins rather than eggs, and the peak collecting period fell between 1870-1889, tailing off rapidly thereafter. This contrasted with the situation in the rest of the British Isles, where collecting continued unabated until c.1920. The median date of collection of skins from Scotland (1880) was significantly earlier than that for the rest of the British Isles (1897). This may suggest that persecution had so reduced numbers in the more accessible parts of Scotland that earlier collecting levels could not be sustained, despite the fact that collecting remained popular in the rest of the British Isles well into the 20th Century.

The decline of the Chough in the late 19th century coincided with the decline and eventual extinction, through persecution, of several species of rapacious birds in Scotland, including the White-tailed Eagle *Haliaeetus albicilla*, Red Kite *Milvus milvus*, Goshawk *Accipiter gentilis* and Osprey *Pandion haliaetus* (see Baxter & Rintoul 1953). This shows how universal and potent was the threat posed by the combined methods of persecution. During this time corvids were high on the list of "vermin", and there can be little doubt that, as a member of the crow family, the Chough suffered persecution, whether deliberate or not. Referring to the Chough's decline in Kircudbrightshire, Service (1885) wrote "I have positive evidence that it was the gun that swept off the few pairs that survived up to a comparatively recent period, when to shoot a Chough from the cliffs was considered a decent sort of a feat". Rolfe (1966) quotes the case of Sir William Jardine, who in 1827 shot 30 Choughs in one morning (in the Isle of Man), and quotes D'Urban and Matthew who in 1896 reported that they knew of "six Choughs having been killed at a single shot when feeding at a manure heap at Braunton [Devon] by a sportsman wishing to discharge his gun before returning home". Both Owen (1989) and Meyer (1991) concluded that persecution was one of the major factors involved in the decline of the Chough in south-west England in the late 19th and early 20th centuries.

References in the literature to persecution of Choughs in Scotland were most frequent from mainland regions, where specific statements were made concerning reduced numbers and/or extinction in Ayr, Wigtown and Kircudbright (Gray 1871, Buchanan 1882, Service 1885, Stewart 1928). It seems likely that their greater accessibility was to the detriment of the Chough in these areas. Nevertheless, the majority of Scottish Chough specimens were in fact taken on Islay, suggesting that even here it was not safe from determined collectors. Scot-Skirving (1876), writing on the Chough on Islay, noted that it was "subjected to much persecution on account of an increasing demand for the skins by dealers in natural history specimens".

4.4.2 Niche overlap

Overlap in diet between Jackdaws and Choughs has been considered by Bullock *et al.* (1983). They considered it unlikely to have been the cause of the Chough's decline on the basis that whilst there is some overlap in diet, differing feeding behaviour separates the species: the Jackdaw is short-billed and primarily a surface-feeder, whilst the Chough is long-billed and digs or probes for its food.

I consider the Rook to be a more likely competitor with the Chough due to similarities in their feeding ecology. The diet and the feeding methods of the Rook are similar to those of the Chough, particularly in the breeding season when both feed in pastures by probing for sub-surface invertebrates (Feare *et al.* 1974, Coombs 1978). At other times of year the Rook has a more catholic diet than the Chough, taking much grain and vegetable matter (Holyoak 1968, Feare *et al.* 1974). Corvids are one of the few groups of birds for which interspecific competition for food has been experimentally demonstrated: Högstedt (1980) showed that Jackdaws experimentally induced to breed within Magpie territories competed for food to such an extent that the breeding success of the Magpies was significantly reduced. The breeding success of the Jackdaws did not suffer from the presence of Magpies. Birkhead (1991) suggests that this result "makes sense because, unlike Magpies, Jackdaws are not tied to a territory and could forage over a wide area.

It is possible that colonially nesting Rooks could compete with territorial Choughs in the same way, with the Rooks assuming the dominant competitive role as a result of their greater numbers and greater size. Personal observations have shown Rooks to be dominant over Choughs in feeding disputes. Moreover, Rooks in Britain breed earlier than Choughs, such that Rooks foraging for their nestlings might deplete food resources needed by the later-breeding Chough.

These hypotheses remain to be tested. However, it is interesting to note that the Rook increased its range and numbers in Scotland during the 19th century (Gray 1871) at a time when the Chough was declining. The British Bird Winter Atlas (Lack 1971) and recent Breeding Bird Atlas (Gibbons *et al.* 1993) show that Rooks are found at low densities within the Chough's current strongholds on Islay and Colonsay, whereas they are abundant on the south west coast of mainland Scotland (Kircudbright to Ayrshire) where Choughs became extinct at the turn of the century. Rooks are also scarce in the Chough's stronghold on the west coast of Ireland.

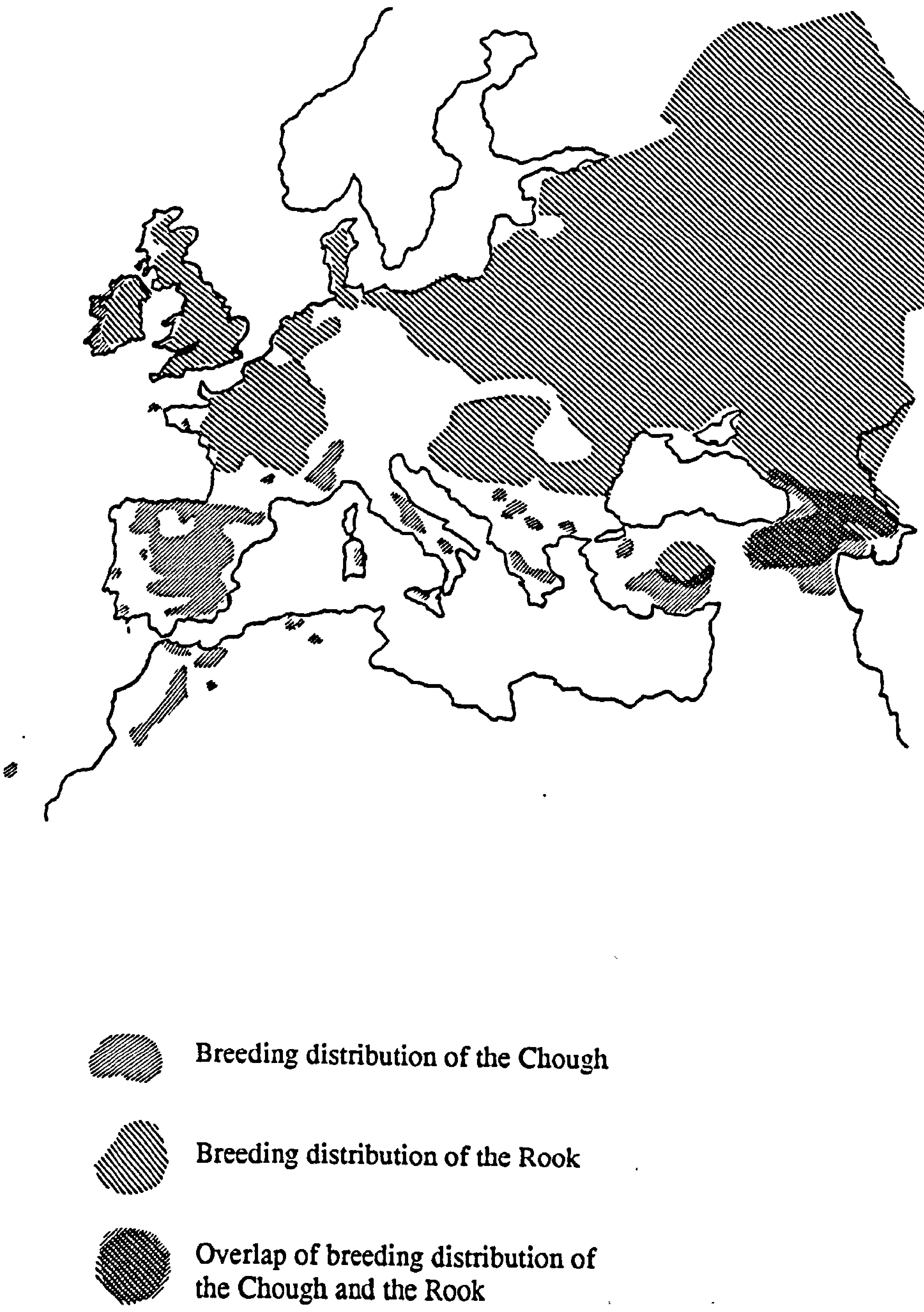
If one looks at the Chough's distribution in the rest of Europe, it is notable that they generally occur where Rooks are absent (Figure 4.4). This is clearly the case in the mountain ranges of the Alps, Pyrenees, Apennines and in the Balkans where one would not expect to find Rooks anyway. However, it is also true in the one "continental" area where Choughs occur away from coastlines or mountain ranges where one might expect to find Rooks: the Iberian peninsula. The only area of considerable overlap between the two species lies to the east of the Black Sea on the borders of Turkey, Iran and the Georgian state of the former USSR. It is possible that there is altitudinal separation between the species in this area which contains several mountain ranges.

Other types of possible inter-specific interactions between Choughs and corvids are discussed below (see **Parasites and Nest-site Competition**).

4.4.3 Isolation and In-breeding

Whilst these two factors could not of themselves have *caused* the Chough's decline in Scotland, they could reduce a population's ability to recolonise formerly occupied areas once its range had become restricted to an island such as Islay - as has been the case in Scotland since c.1950. Monaghan (1989) has shown that the Islay Chough population does not show a reduced level of genetic heterogeneity compared to a large number of bird species, hence in-breeding is probably not a problem on Islay.

Figure 4.4 The breeding distribution of the Red-billed Chough *Pyrrhocorax pyrrhocorax* and the Rook *Corvus frugilegus* in the Western Palearctic (reproduced from Cramp and Perrins 1994).



Still (1989) showed that sub-adult Choughs benefited from feeding in moderate sized flocks (as opposed to small or large flocks) through having to spend less time vigilant and thus increasing their feeding rates. Foraging in flocks may also increase an individual's chance of finding patchily distributed food, as suggested for the Rook (Feare *et al.* 1974, Waite 1981, MacDonald & Whelan 1985). The specialised diet of the Chough (see Holyoak 1968) may mean that such social enhancement is particularly important, and the fact that sub-adult Choughs spend their non-breeding years feeding in flocks and utilising communal roosts (Still 1989) strongly suggests that such flocking behaviour is advantageous. The absence of such flocks in small and/or fragmented populations or in areas where the species has become extinct may slow down population growth or recolonisation. The situation is probably exacerbated by the fact that most dispersal is undertaken by the least experienced age-group - first year birds (see below), which are probably the most dependent on flocking associations.

Analysis of ringing recoveries shows that Choughs may disperse as far as 143 km from their natal site, but also that island populations disperse less far from their natal sites than birds born at mainland sites. This suggests that the sea acts as a barrier to dispersal: so far no birds ringed on Islay or the Isle of Man have been recovered away from their respective islands, whereas birds from Bardsey have moved widely throughout Wales. Assuming that the causes of the Chough's disappearance no longer operate, one would predict that the species' recolonisation of formerly occupied areas would be slower from an island base than from a mainland one. Choughs also exhibit natal site philopatry: Bignal *et al.* (1989) found that the median distance moved between natal site and breeding site on Islay was only 3 km for males and 9 km for females. Walls & Kenward (1995) suggested that such philopatry "may be an important hindrance to avian recolonisation following local extinctions". Isolation of island sites and/or natal site philopatry may explain the slow rate at which Choughs have re-colonised mainland sites not too distant from the relatively large populations on Islay and the Isle of Man. It also emphasises the need for positive conservation measures for any Choughs that do become established at mainland sites, such as the pair that have bred recently on the Galloway coast and on Mull (which is very close to the mainland).

4.4.4 Predation

The Peregrine Falcon *Falco peregrinus* is probably the main natural predator of the Chough, being larger in body size, occurring in similar habitats, and even nesting on the same cliffs. It has been accused of causing local extinctions (eg. on Eigg 1886 (Harvie-Brown & Buckley 1892) and at two sites in inland Wales in the 1980's (Roberts & Hawkins 1990)) or population declines (eg. Islay c.1914 (Baxter & Rintoul 1953)). However, Ratcliffe (1980) showed that the extinction of the Chough in Cornwall this century occurred at a time when the Peregrine was also decreasing. He considered it "extremely doubtful if predation [by the Peregrine] has been a significant factor affecting the status of the Chough anywhere in Britain". Islay currently supports healthy populations of both Choughs and Peregrines, not to mention other avian predators such as Hen Harrier *Circus cyaneus* and Common Buzzard *Buteo buteo*, and it seems quite implausible that predation could have been the ultimate cause of the Chough's historical decline. However, it may play a more important role where populations are small or fragmented.

There are few records of Chough nests being lost through predation as they are usually placed in inaccessible and dark situations in caves and cliff crevices. In three years of nest observations I have recorded only one species, the Hooded Crow *Corvus corone cornix*, as a nest predator (taking eggs), and this on only one occasion and not resulting in the complete failure of the breeding attempt. This nest was in an uncharacteristically open site, brought about by the gradual decay of the ruined building in which it was situated, giving easy access to the crows. Most Chough nests are inaccessible to crows, and it may be that the specific nest-site requirements of the species are an adaptation to avoidance of nest-predation by crows, as suggested for other corvid species by Bossema *et al.* (1986).

Barn Owls may nest in close proximity to Choughs (see below). There was no evidence from 10 such sites on Islay that the Barn Owls ever preyed upon nesting birds, their eggs or nestlings (M.A. Ogilvie *pers. comm.*). Cowdy (1962) recorded one instance of Chough nestlings having apparently been dragged from their nesting crevice on Bardsey, probably by a Little Owl *Athene noctua*. There have been no subsequent records of this type of predation from Wales, so it seems unlikely that Little Owls pose a significant threat to the

Chough. The Little Owl is absent from western Scotland.

4.4.5 Nest-site competition

Of 62 nest-sites monitored on Islay outside the breeding season during 1987-89 fifteen were abandoned, a loss of 24.2%. In most cases the pair moved to a nearby but previously unused site, such as another part of a building, so this did not represent a 24.2% decline in the breeding population. Most of the abandonments occurred at nest-sites in buildings, either through natural dereliction or through improvements to buildings made by man. The only bird species implicated in causing nest-site abandonment was the Barn Owl: two sites were involved, one in a building and one in a coastal cave. In both cases Barn Owls nested or roosted close to the Chough's former nest-site, and this presumably proved intolerable. At two sites in buildings, the temporary presence of Barn Owls in the breeding season of 1987 caused nest desertions, but the Choughs returned to these sites in future years after the Barn Owls had disappeared.

The Barn Owl is a scarce species on Islay, with only 10-15 breeding pairs in any one year (Dr. M.A. Ogilvie *pers. comm.*), so their interference at 4 Chough nest-sites suggests a high degree of overlap in the nest-site requirements of the two species. The recent afforestation of parts of Islay has fuelled an increase in the Barn Owl population, and one further Chough site in a building on the Rhinns has been usurped since this study was carried out (Dr. M.A. Ogilvie *pers. comm.*). Most buildings provide sufficient potential nest-sites for the species to nest far enough apart to avoid conflict, but where this is not the case, efforts should be made to provide artificial sites for both (see Chapter 6).

In 1871 Gray suggested that the increase of the Jackdaw *Corvus monedula* (which coincided with the decline of the Chough) "must be looked upon as the cause of the decrease [of the Chough]" through Jackdaws usurping Chough nest-sites. Though this view has often been repeated (eg. Muirhead 1889, Paton & Pyke 1929, Meiklejohn & Stanford 1954, Burton 1995), it is now generally accepted that the nest-site requirements of the two species show little overlap (Ryves 1948, Williamson 1959, Bullock *et al.* 1983) and that nest-site competition between them is unlikely. Jackdaws are common throughout the range of the Chough on Islay, and frequently nest in the same buildings. There was no evidence of Jackdaws having caused any of the 13 nest-site abandonments for which the cause was known, and they were not present at the two sites where the cause of abandonment was unknown. It seems that the Jackdaw's preference for darker and more enclosed nest-sites enables them to coexist with Choughs without conflict.

Rock Doves were present at many Chough nest-sites, including caves and buildings. No instances of Rock Doves interfering with Choughs were recorded, but Choughs were found to be very intolerant of Doves, chasing them away from nest-sites and sometimes pulling out nest contents of nests in the same building. Choughs were also noted interacting aggressively with Kestrels, and one Chough nest-site was usurped for (one breeding season only) by a pair of Kestrels.

It seems unlikely that nest-site competition from any of the above species could have contributed significantly to the Chough's decline in Scotland. However, competition from Barn Owls, and to a lesser extent Kestrels, may limit the number of nest-sites available to Choughs in any one locality, particularly at inland sites.

4.4.6 Disease and Toxic Chemicals

Whilst the Chough is known to suffer from several common avian diseases (Bullock *et al.* 1983), there is no evidence that they are any more susceptible to these than any other species. The pesticides most likely to have been used recently in the western parts of Britain occupied by Choughs are those used for dipping sheep, namely DDT (from 1947 onwards), and dieldrin (HEOD, which replaced DDT from c. 1955 onwards, subsequently banned in 1966) (Ratcliffe 1980). These chemicals were found to be the cause of a substantial decline in the breeding success of Golden Eagles *Aquila chrysaetos* in west Scotland, brought about through ingestion of sheep carrion (Lockie *et al.* 1969). Choughs do not feed directly on carrion (*pers. obs.*), but do feed on blowfly (Diptera:Muscidae) larvae which feed in, and pupate close to carcasses. Choughs feeding on blowfly larvae may have been exposed to pesticides: Harrop (1970) found a dead nestling Chough in a Welsh nest which contained "small amounts of pesticides"; he had earlier seen the adults feeding on maggots at a sheep carcase. Rolfe (1966) also reported low levels of DDT, dieldrin and mercury in three corpses analysed. Clearly, pesticide use occurred too late to account for the 19th century decline of the Chough, but it may have limited numbers during the latter part of the 20th century.

4.4.7 Parasites

Attention has recently been focussed on the role of the Chough as a host of the nematode parasite *Syngamus trachea* (Haycock 1975, Bignal *et al.* 1987a, Meyer & Simpson 1988), commonly known as gapeworm. *S. trachea* is a blood-sucking nematode that infects the trachea of many species of birds. Coughed-up eggs are swallowed and appear in the birds' droppings. The eggs quickly hatch to produce larvae which are ingested by intermediate invertebrate hosts such as earthworms (Lumbricidae). Birds eating the infected invertebrates then become infected themselves.

Bignal *et al.* (1987a) suggested that the relatively small and isolated population of Choughs on Islay might be vulnerable to chronic infestations by this parasite, particularly in wet summers which favour survival of the infective larvae. Meyer & Simpson (1988) suggested that gapeworm may have been the cause of death of an extra-limital Chough which occurred in Cornwall in 1986/87. They concluded that other avian hosts of gapeworm, such as Magpies and Starlings, might "contaminate" the Chough's environment (by spreading *S. trachea* eggs) whilst remaining less susceptible themselves to infection and/or its harmful effects. To this list of "vector species" should be added the Rook, Jackdaw, Carrion/Hooded Crow, and the Pheasant *Phasanius colchicus*, all of which have been identified as frequent hosts of gapeworm in Britain (Campbell 1935).

Despite the above implications that the Chough is highly susceptible to gapeworm infection there is still little quantitative evidence concerning its effects on the Chough population as a whole. Bignal *et al.* (1987a) and Meyer & Simpson (1988) describe instances of individual Choughs dying as a result of gapeworm infection, but these are isolated cases, and it is not clear whether their susceptibility to parasite infection was induced by some other form of stress. Indeed, whilst infection levels of *S.trachea* in hosts may reach high levels, this does not necessarily result in mortality. Holyoak (1971) found that in Rooks the number of infected individuals fell from 100% in nestlings, to 0-7% in adults, whilst there was a parallel reduction with age in the number of worms per infected individual. He suggested that as the birds matured into adults, they lost their worms [probably through age-resistance as recorded in domestic poultry (see Lapage 1968)]. The above references to gapeworm in Choughs may reflect a similar pattern of infection; the infection levels noted by Bignal *et al.* (1987a) are certainly no higher than those noted in the Rook. It is possible that gapeworm infection poses no more of a threat to the Chough than to its other hosts (most of which, it should be noted, are particularly abundant species).

On the other hand, if the Chough is particularly susceptible to gapeworm infection, and if this results in higher levels of mortality than recorded for other hosts, then the distribution and abundance of the parasite, and of its avian vectors, may have a profound effect upon the ecology and distribution of the Chough. Taylor (1935) found that earthworms are the main intermediate host of *S. trachea*, whereas he obtained negative results from other potential intermediate hosts - caterpillars, leatherjackets, millipedes, click beetles, dung beetles, woodlice and Muscid flies. All of the latter groups except woodlice feature in the diet of Choughs and Jackdaws (Roberts 1982 and Chapter 8). This raises the possibility that worms are not taken in order to avoid gapeworm infection. If so, then there may be little exposure to the parasite in the Chough and Jackdaw, which in turn would tend to make them more susceptible to infection.

For the following reasons I would propose that the Rook is the most likely *Syngamus* vector in areas occupied by Choughs: 1) it feeds in similar habitats, 2) it generally occurs in large numbers and 3) juvenile Rooks (the most highly infected age-group) fledge several weeks before nestling Choughs leave the nest, thus there is a period of around 3 weeks during which juvenile Rooks foraging in the same fields as breeding Choughs can contaminate their feeding areas. Infected invertebrates may then be fed to their chicks.

It is worth noting that the four cases of gapeworm infection in nestling Choughs that I have recorded on Islay have all been in areas containing large Rookeries. Current knowledge of the possible interactions between the Chough, Rook and *Syngamus trachea* are still too limited to enable us to conclude whether gapeworm infection has played a part in the decline of the Chough in Scotland, or in limiting its current distribution. This subject may warrant further research, but this was not within the scope of the current study.

4.4.8 Winter severity

It has been suggested that the Chough in the British Isles may be particularly susceptible to severe winters, as its distribution is limited to western coasts and islands which experience very mild winters (Rolfe 1966, Bullock *et al.* 1983, Bullock *in* Lack 1986, and see Chapter 5). In the historical literature, there are few direct references to climate in relation to the Chough. Pennant (1776) wrote that "it is a very tender bird, and unable to bear very severe weather". Service (1904-05) reconsiders his earlier statement (1885) that the gun was the cause of the Chough's decline in Galloway, stating that "later and riper information induces me rather to lean to the opinion that here... we have some climatic reason at work".

In the current analysis, no correlation was found between the extent of the Chough's range in Scotland and long term trends in air temperature in the same or in the previous decade. The lack of correlation may reflect inadequacies in the data on the Chough's range and climate change. It should be noted that in recent times Rolfe (1966) recorded a sharp decrease in the number of breeding pairs in Scotland following the severe winter of 1962-63, and Bullock *et al.* (1983) considered the 1981-82 winter to have caused a reduction in the population of Choughs in Wales, particularly those breeding at inland sites.

Paradoxically, the Chough's Scottish range contracted from 1920 onwards (see Figure 3.3 & 3.6) at a time of climatic amelioration which reached its 20th century optimum in the early 1940s (Lamb 1977). However, this followed a period of high persecution (see above), which may have limited the species' potential to recover during a climatically favourable period. The downward trend in air temperature from 1950 to 1975 was probably the longest period of climatic cooling in Britain since 1700 (Lamb 1977). The Chough's Scottish range simultaneously fell to its minimum recorded extent since (at least) 1750, at a time of limited or no persecution. The subsequent upturn in the Chough's fortunes in the 1980s has occurred during a long run of unusually mild winters. Overall it seems that there is some correlation between winter severity and changes in the Chough's range. In Chapter 5 I make a detailed bioclimatic analysis of the Chough's range in order to identify the current climatic parameters which may be limiting the Chough's range in Britain. If the relationship with winter severity suggested above is correct, it should show up in this analysis.

4.4.9 Nest-site availability

Nest-site availability is a factor which may limit the size of nesting populations within any one area (see Newton 1994). It is unlikely that changes in nest-site availability could be responsible for the past decline of the Chough. Indeed, in recent times the availability of nest-sites may have increased as birds have "learnt" to nest in ruined buildings. However, nest-site availability may limit the distribution of the Chough at both a local and national level. This is investigated in detail in Chapter 6 and in Appendix 4 (*Environmental factors influencing the distribution of nesting Red-billed Choughs* Pyrrhocorax pyrrhocorax).

4.4.10 Land-use

There are no historical references to habitat change or land-use change in relation to the Chough's decline. More recently, several authors have identified grazing by wild and domestic herbivores as an important land-use impinging on the Chough's ecology (Bullock *et al.* 1983, Warnes 1983, Roberts 1983). In Chapter 7 I compare land-use on Islay with that on the Rhinns of Galloway in Wigtownshire, an area in which the Chough became extinct earlier this century.

4.4.11 Discussion summary

Several factors have been discounted as causes of the Chough's decline - predation from Peregrine Falcons, nest-predation, nest-site competition, niche overlap with the Jackdaw, disease, toxic chemicals and inbreeding. Although there was no significant correlation between range extent and persecution, anecdotal evidence suggests that persecution by humans was an important factor in limiting numbers during the period 1860-1930, possibly extending into the 1950s through rabbit-trapping. These factors were probably most marked in the more accessible mainland areas, such as Wigtownshire and Kircudbrightshire. The use of the pesticides DDT and dieldrin in sheep-dips during 1947-1966 may have contaminated Choughs feeding on maggots associated with sheep carrion, with potential negative effects on population size. The potential dangers of anti-parasitic drugs such as Ivermectin are currently being investigated (see McCracken 1992a), but since they have only recently become available, they obviously played no rôle in the historical decline of the Chough.

Once the population had become restricted to Islay, the insularity of the island may have inhibited recolonisation of formerly occupied areas. Since dispersal appears to occur in the first year of life, the absence of sub-adult flocks in formerly occupied areas may further inhibit colonisation by inexperienced first-year colonists.

The feeding niche of the Jackdaw is unlikely to overlap with that of the Chough, but that of the Rook may do so, thus the Rook is considered to be the Chough's most obvious potential inter-specific competitor. Competition for nest-sites came from Barn Owls and Kestrels, but not Jackdaws or Rock Doves. However, the incidence of competition was so low that it was considered unlikely to have had a significant impact on Chough populations.

The role of the nematode parasite *Syngamus trachea* in the feeding ecology of the Chough was considered, particularly in relation to the apparent absence of worms and slugs in its diet. Available evidence suggests that these food items are avoided by Choughs (and Jackdaws); it is possible that this may be in order to avoid infection with *S.trachea*, for which the earthworm is the main intermediate host. In areas of sympatry, Rooks (particularly juveniles), are proposed as the most likely birds to "contaminate" the Chough's environment with infective *S.trachea* larvae.

There was no significant correlation between winter severity and Chough range, but the relationship may have been confounded by a period of high persecution levels coinciding with a period of climatic amelioration. There was evidence to suggest that the range expanded slightly during the climatic amelioration between 1850-1950 (despite high levels of persecution), and that it contracted between 1950-70 during a period of climatic cooling. The effects of climate, nest-site availability and land-use are considered further in Chapters 5, 6 and 7 respectively.

Chapter 5

THE DISTRIBUTION OF THE CHOUGH IN BRITAIN IN RELATION TO CLIMATIC FACTORS

5.1 INTRODUCTION

Environmental factors can limit species' distributional boundaries (Brown & Gibson 1983). The potential effects of "global warming" have focussed attention on the role that climate plays in determining species ranges, especially those of threatened species. Lindenmayer *et al.* (1991) modelled the distribution of a threatened arboreal marsupial, Leadbeater's Possum *Gymnobelidius leadbeateri*, and found that the species' range would contract under the influence of global warming, and that it might even become extinct. For other species, temperature rises may lead to range expansion or range shifts (Beerling 1993). The effects of climatic factors on bird species distributions have rarely been studied due to the difficulty of collecting detailed distributional data over a large enough area to enable general patterns to be identified (see Root 1988). However, using the Audubon Society's "Christmas Bird Count" data Root (1988) was able to analyse the distributions of 148 wintering North American land birds, and found many associations between distributional boundaries and a range of climatic variables such as average minimum January temperature. Turner *et al.* (1988) found that the distributions of small insectivorous birds in Britain in summer and winter correspond with the "species-energy" hypothesis which proposes that the steep decline in the number of species from Tropic to Pole may be explained by the latitudinal decline in the input of solar energy. Using Canonical Correspondence Analysis Hill (1991) showed that the distributions of several British birds had a climatic component, but that a simple spatial south-east/north-west axis was the major axis of variation.

Several authors have suggested that the restricted nature of the Chough's British distribution may have a climatic basis. Bullock *et al.* (1983) noted that the Atlantic coasts inhabited by Choughs in the British Isles experience mild winters which guarantee that the birds' feeding grounds remain relatively free from frost and snow; they speculated that warmer winter soil temperatures may also "sustain greater insect activity, crucial to [the Chough's diet". Cullen and Jennings (1986) identified a close association between the 38°F January mean isotherm and the Chough's British distribution. They suggested that "this is the minimum mean temperature acceptable to the species within the British Isles". For Scotland, Monaghan *et al.* (1989a) identified an association with Birse's (1971) $O_1H_3T_1$ bioclimatic sub-region, which is characterised by mild winters, fairly warm summers and moderate levels of potential water deficit (see section 5.3.1).

It has also been suggested that climatic changes may have been responsible for the contraction of the Chough's British range over the last two hundred years. Rolfe (1966) stated that "the period of cold winters, 1820-1880 synchronises with the Chough's disappearance or decrease in many, if by no means all, parts of the British Isles". However, Bullock *et al.* (1983) and Owen (1989) considered that there was no long-term historical relationship between climatic factors and the decline of the Chough. Similarly, in Chapter 4, no long-term correlation between the extent of the Chough's Scottish range and winter severity was found. Owen (1989) analysed data from the Calf of Man and Bardsey bird observatories from 1953 and 1959 onwards (respectively). He looked at the number of breeding pairs and their breeding success in relation to minimum winter temperature, minimum spring temperature and average spring rainfall. He found only one significant relationship, a positive correlation between spring rainfall and fledging success.

However, short-term declines in Chough numbers following hard winters have been noted: Rolfe (1966) described a marked reduction in the Scottish breeding population following the severe winter of 1962-63, and Bullock *et al.* (1985) found that the number of breeding pairs at inland sites in Wales dropped following the hard winter of 1981-82. The task of identifying climatic factors which may control the population dynamics of the Chough is complicated by the suite of other environmental and biotic factors that might be operating simultaneously (see Hill 1991). For example, Owen (1989) considered that profound changes in land-use at the Calf of Man during the period in which the data he analysed were collected would probably have masked more subtle climatic correlations. Likewise, in the current study (section 4.4.8) it was considered that persecution might have prevented expansion of the Chough's range during a period of climatic amelioration between 1850-1950 (Burton 1995). The impact of severe winters and the correlation between the Chough's range and areas of winter mildness strongly suggest that Choughs in Britain may be dependent upon a restricted set of climatic conditions.

The aim in this chapter is to attempt to determine objectively whether the Chough's British range is correlated with climatic variables, and if so, which ones. An understanding of these relationships and how they might operate will be of great use in understanding the ecology of the species in Britain and in interpreting historical changes in its range. With this knowledge it will be possible to restrict conservation efforts to those areas climatically suitable for Choughs. For example, is there a climatic basis for objecting to the proposed re-introduction of the Chough to Cornwall? Should efforts be made to conserve the single pairs of Choughs in Galloway and Mull, or is the climate in these areas unfavourable? Are there as yet unidentified areas where Chough conservation or re-introdiction programmes should be considered?

As discussed in Chapter 4, it is difficult to obtain accurate historical estimates of population size to enable analyses of long-term climatic correlations between Chough range and climate to be made. My approach here is a more conservative one, in which I attempt to determine the climatic characteristics of areas currently occupied by Choughs using bioclimatic classifications. These characteristics are then used to identify all climatically equivalent areas outwith the current range which, on a climatic basis, ought to be capable of supporting Choughs. This total range I have termed here the *Potential Climatic Range* (*PCR*). The *PCR* can then be compared with the historical range in order to address the question of whether climate change was the cause of the Chough's decline. The bioclimatic prediction of probable species limits dates back to original studies on "homoclimes" - areas which experience similar climatic conditions - by Koppen and Thornthwaite (see Lindenmayer 1991).

I also attempt to assess whether the climatic factors characterising the Chough's distribution might operate a) upon the birds themselves, b) on the invertebrates which make up most of their diet or c) upon non-favourable changes in land use. Some of the potential influences of climate on the Chough and its invertebrate prey were examined directly, as follows: a) the influence of short-term weather fluctuations on the body mass of one pair of roosting

Choughs was measured over the winter of 1988-89; b) the growth of *Tipula paludosa* (Diptera:Tipulidae) larvae ("leatherjackets") was measured on Islay during 1988-89, and compared with that of larvae in climatically different areas; c) cold-hardiness of *T. paludosa* larvae was investigated experimentally in relation to differences in their growth curves between climatically different areas as shown in b) above.

Tipula paludosa was selected as the invertebrate study species because it is an important prey item in the diet of the Chough (see Chapter 8) and there is an extensive literature on the relationship between the biology of this species and climate (Laughlin 1967, Freeman 1967, Meats 1974a, Barbash 1988). It was not within the scope of this study to sample invertebrates throughout Britain, but the existence of similar growth studies in climatically different areas (Glasgow (Barbash 1988) and Northumberland (Laughlin 1967)) meant that a comparative approach was possible.

5.2 METHODS

The current distribution of the Chough was determined using data from *The Atlas of Breeding Birds in Britain and Ireland* (Sharrock 1976), *The Atlas of Wintering Birds in Britain and Ireland* (Lack 1986), and results from the 1982 RSPB/Irish Wildbird Conservancy breeding survey (in Bullock *et al.* 1983 and Bullock *et al.* 1985). The breeding surveys collated data on a 10 km square basis, using a 1-3 categorical scale, representing possible, probable and confirmed breeding respectively. Data from the *Winter Atlas* were presented as maximum counts of birds in each 10 km square over the survey period: *1* = 1-4 birds; *2* = 5-11 birds; *3* = 12+ birds. More recent data on the Chough's breeding distribution and abundance were obtained from the 1982 RSPB survey, and from sources presented in Chapter 3. Results from all these sources were combined to provide a minimum estimate of the Chough's range by 10 km square in England, Wales and Scotland from 1968-88.

In a preliminary attempt to analyse the Chough's British range in relation to climate, climatic variables from the *Climatological Atlas of the British Isles* (Meteorological Office 1952) were used. However, methodological problems were encountered due to the overwhelming number of climatic variables presented in this atlas (each climatic variable, such as temperature, rainfall, humidity, barometric pressure, wind force, sunlight, snowfall etc. is further sub-divided into annual and monthly means, maxima, minima etc.), giving a total of 210 climatic maps, each with its own set of isograms; this posed a major problem regarding which variables and which isograms to compare with the Chough's range. Selecting any of these inevitably introduces bias into the results, and it was impossible to objectively justify choosing a variable such as the 38°F mean January isotherm, as used by Cullen & Jennings (1986), merely because it fitted the observed pattern of Chough distribution.

In an attempt to overcome these biases, I have used the more general climatic synopses provided by the bioclimatic classifications of Scotland (Birse & Dry 1970, Birse & Robertson 1970 and Birse 1971) and England & Wales (Bendelow & Hartnup 1980). These classifications are based on only 4 (England and Wales) or 5 (Scotland) climatic variables, these being chosen to give the most "realistic sub-division and categorisation of the overall climate for field biology" (Birse 1971) in the respective countries, providing a "basic tool for ecological research". The greater scale of these bioclimatic maps compared to those in the *Climatological Atlas* (Meteorological Office 1952) also enabled climatic analyses based on the 10 km square national grid to be carried out. Unfortunately, the bioclimatic classification for Scotland is not directly comparable with that for England and Wales due to the use of slightly different parameters. Comparable classifications are not available for the Isle of Man, Ulster or Eire.

The climatic parameters used in these bioclimatic classifications are described briefly below: **Available energy** is represented by "accumulated day degrees above base 5.6°C" (the threshold temperature for grass growth). **Soil moisture** is measured as "potential water deficit" by Birse & Dry (1970), and as the slightly different "potential maximum soil moisture deficit" by Bendelow & Hartnup (1980), both of which are cumulative measures of the availability of moisture in the soil. **Wind exposure** is represented by mean wind speed and its observed effects on vegetation growth. For Scotland, accumulated frost (day °C below 0°C) is used as a measure of **winter severity** (see Birse & Robertson 1970 for details), with altitudinal effects also taken into account. Bendelow & Hartnup did not include winter severity in their classification due to the occurrence of local frosts in areas of cold air drainage in the lowlands of England. Finally, Birse (1971) used **winter severity** to assess **oceanicity** empirically, whereas Bendelow & Hartnup used an interpolated "continentality index". The resulting oceanicity maps of the two classifications indicate that Birse's method enabled greater resolution of sub-regions of oceanicity in Scotland than was possible for England and Wales using Bendelow & Hartnup's method.

In both classifications, climatic maps for each parameter are produced individually, and these are combined (with some loss of detail) to produce the overall bioclimatic classification. To maximise the resolution of bioclimatic data the constituent maps for each parameter were used rather than the final summary map (except for oceanicity, which in both classifications is only shown on the summary map). Due to the differences between these classifications, it was necessary to analyse the distribution data for Scotland separately from those for England and Wales.

5.2.1 Bioclimatic analysis - Scotland

The small number of 10 km squares occupied by Choughs in Scotland restricted the analysis to a simple comparison of past and present occurrence in each climatic zone. The distribution of the Chough in Scotland, both past and present, was compared with the distribution of the bioclimatic zones in the classifications of Birse & Dry (1970) and Birse & Robertson (1970). Historical range was represented by all records of probable or definite breeding since 1750 (see Figure 3.2). Climatic sub-divisions currently and/or historically "occupied" were contrasted with those with no records, to characterise possible climatic constraints on the Chough's Scottish distribution. Likewise, the climatic characteristics of currently occupied areas were used to determine the current extent of climatically equivalent areas throughout Scotland - the *Potential Climatic Range*.

5.2.2 Bioclimatic analysis - England and Wales

Discriminant Function Analyses

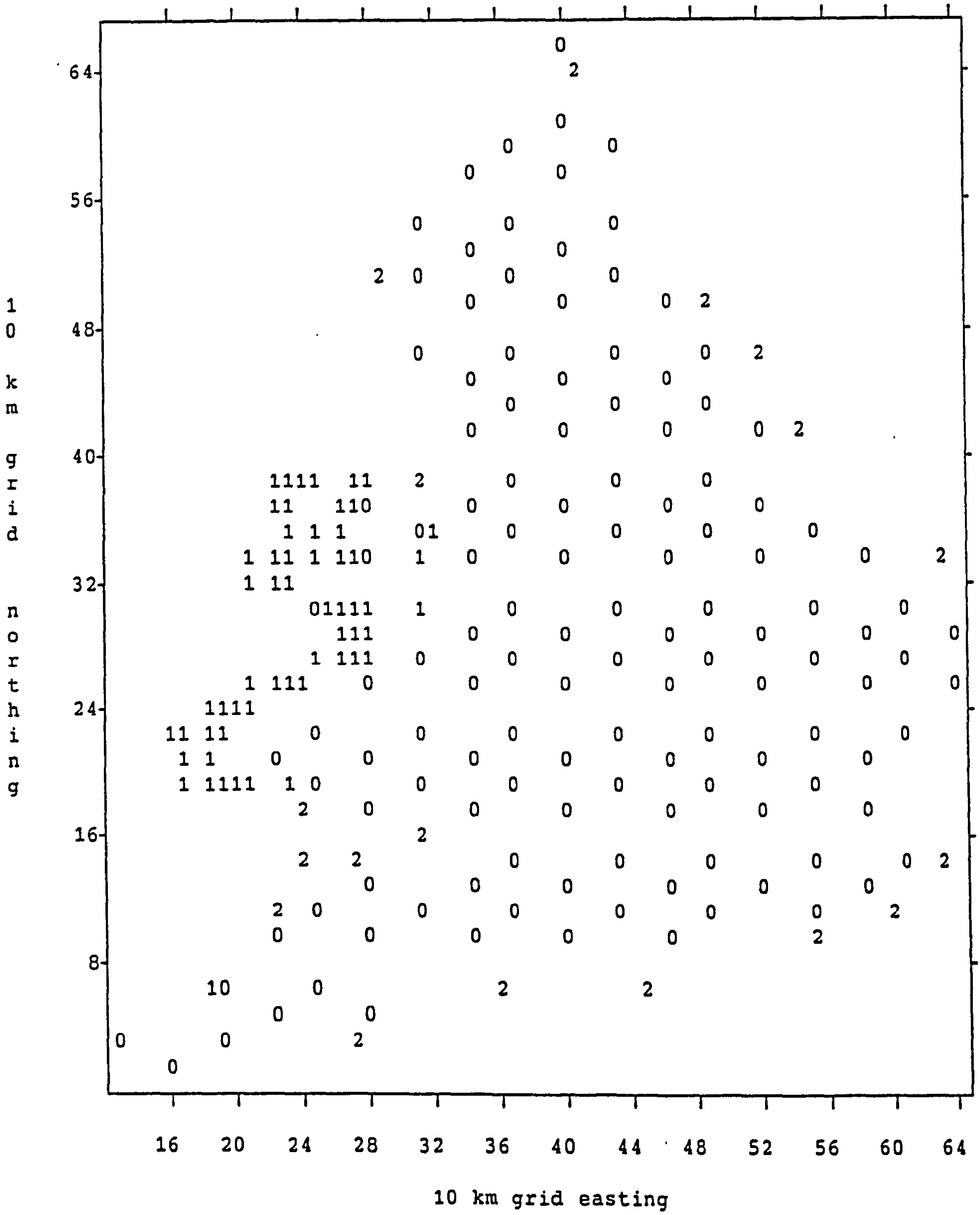
For England and Wales a *Discriminant Function Analysis* (DFA) using climatic variables to discriminate between occupied and unoccupied 10 km squares was carried out. In each analysis the discriminant groups were represented by presence/absence (groups 1 and 0 respectively) of Choughs in each square (see below). *Minimising Wilks' Lambda* was used as the stepwise selection rule; in all analyses, the SPSS/PC default settings were employed (see Norusis 1988).

The Chough's present range was represented by the 74 10 km squares known to have been occupied (summer and/or winter) during 1981-83 (see section 5.2 above). Unoccupied areas were represented by a sample of 130 (8.3%) of the remaining 1560 10 km squares in England and Wales; these were selected by devising a simple grid which gave a regular distribution of 10 km squares across the country (see Figure 5.1). Since, by chance, this grid resulted in very few coastal 10 km squares in the sample, 18 coastal squares were subjectively added, which increased the sample proportion to 9.5%. Where possible, these additional squares were positioned on headlands likely to provide suitable nest-sites for Choughs (high cliffs/caves), confirmed in some cases by previous records of Chough occupancy, eg. Beachy Head (Sussex) and St.Bees Head (Cumbria). The additional coastal squares fitted well into the existing regular sample (see Figure 5.1). The results of the subsequent DFAs were virtually identical whether these additional squares were included or not, but the extra detail they provided when comparing current with past distribution justified their inclusion.

The initial sample thus comprised 222 10 km squares (74 occupied by Choughs, and 148 unoccupied). Using Bendelow & Hartnup's (1980) bioclimatic maps of **accumulated temperature, exposure, soil moisture deficit,** and **oceanicity,** presence/absence (1/0) of <u>all</u> <u>divisions</u> of these four climatic parameters was scored for each of the 222 sample squares (each parameter and its divisions are described in Table 5.1).

In preliminary DFAs all divisions of the four climatic parameters were entered as separate variables e.g. 5 "variables" for exposure - X_1, X_2, X_3, X_4 and X_5 (see Table 5.1); this gave a total of 24 variables. However, this methodology posed several problems. Firstly, the use of 20 or more variables raises statistical problems since at the $P=0.05$ level one variable could produce a significant result by chance. Secondly, the use of a large number of binary (presence/absence) variables may reduce the performance of the linear discriminant function (Norusis 1988). Thirdly, it is unlikely that Chough distribution will be influenced by individual divisions of each climatic parameter in isolation. It seems more likely that there will be general preferences for "high", "low" or "moderate" levels of a particular parameter,

Figure 5.1 Distribution of different types of sample 10 km squares used in bioclimatic analysis, England & Wales



KEY:
0 = stratified sample square (n=130)
1 = 10 km square occupied by Choughs (n=74)
2 = additional sample squares from coastal headlands (n=18)

potentially embracing several separate divisions.

To overcome these problems the individual divisions for each parameter were converted to scores eg. for exposure $X_1 = 1$, $X_2 = 2$ etc. Scores for divisions of oceanicity were inverted eg. $O_1 = 4$, $O_2 = 3$ etc. so that for all climatic parameters a high score represents a high level of that parameter, ie. exposure ("windiness"), accumulated temperature ("length/ warmth of growing season"), soil moisture deficit ("soil dryness") and oceanicity ("hyperoceanicity").

From these scores, 3 variables were computed for each parameter: the maximum and minimum scores for each parameter occurring within a square form two variables - VAR_{max} and VAR_{min} respectively eg. if X_3, X_4 and X_5 all occur within a square, then $X_{min} = 3$ and $X_{max} = 5$. The mean of these two values gives a third variable - VAR_{mean}; in the above example $X_{mean} = 4.0$. A positive correlation between the number of squares occupied by Choughs and X_{min} indicates avoidance of squares with low levels of exposure; a positive correlation with X_{max} suggests a preference for squares with high exposure. These two relationships are similar, but not identical, thus both variables were used in all DFAs. The converse relationships exist if the correlations are negative. An example of the geographical distribution of scores for the O_{max} oceanicity variable for the 222 sample 10 km squares is given in Figure 5.2.

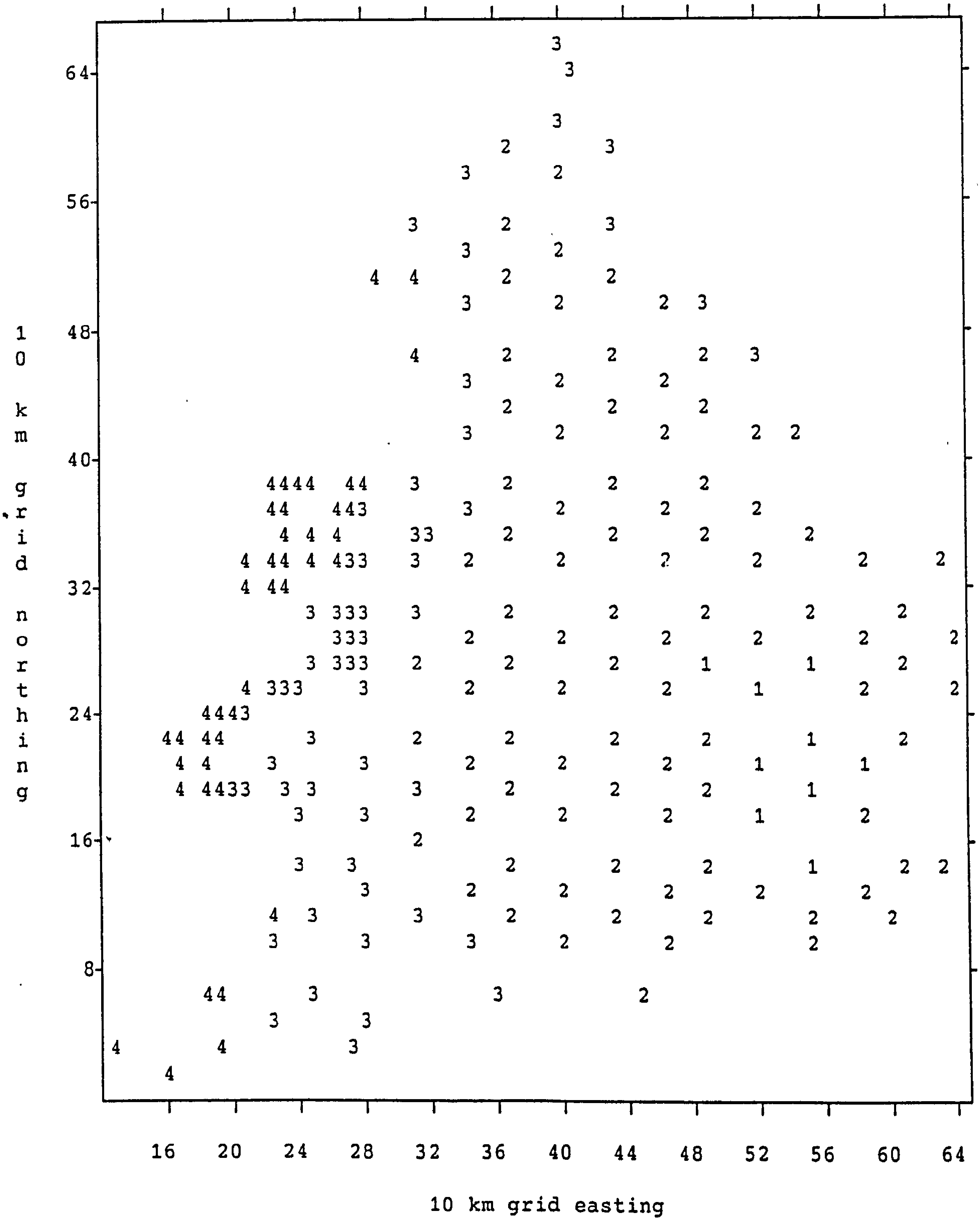
However, none of the above variables can identify a third possible type of climatic relationship, that of a preference for moderate levels of a particular parameter, ie. neither too high nor too low. Thus a third variable - VAR_{dev} was calculated, representing the difference between VAR_{mean} (the mean score for each square, see above) and PAR_{mean}, a constant representing the mean of the maximum and minimum possible scores for each climatic parameter (see Table 5.1). PAR_{means} were calculated as follows: exposure (1+5)/2 = 3.0, accumulated temperature (1+6)/2 = 3.5, soil moisture deficit (0+8)/2 = 4.0 and oceanicity (1+4)/2 = 2.5.

A zero difference between VAR_{mean} and PAR_{mean} indicates a preference for moderate levels of the variable in question. In order to give a positive correlation if there is a central tendency in the data the absolute value of the difference was subtracted from the PAR_{mean} to give VAR_{dev}, high values of which therefore represent values close to PAR_{mean}. An example of the calculation of all climatic variable scores for a hypothetical 10 km square is given in Table 5.2.

Table 5.1 *Climatic parameters and their divisions, as used in Bendelow & Hartnup's bio-climatic classification of England and Wales (1980).*

Symbol	PARAMETER & divisions	Measurement of parameter and range of values
	EXPOSURE (X)	(Average annual wind speed at 10 m. above ground)
X_1	Sheltered	<3.0
X_2	Moderately exposed	3.0 - 4.8
X_3	Exposed	4.8 - 6.6
X_4	Very exposed	6.6 - 8.4
X_5	Extremely exposed	>8.4
	ACCUMULATED TEMPERATURE (T)	(Accumulated day degrees above 5.6°C)
T_1	Moderately cold	<825
T_2	Slightly cold	825-1100
T_3	Slightly cold	1100-1375
T_4	Moderately cool	1375-1650
T_5	Slightly cool	1650-1925
T_6	Moderately warm	>1925
	SOIL MOISTURE DEFICIT (P)	(Average max. potential soil moisture deficit. MD range mm)
P_0	Moderately wet	<0
P_1	Moderately wet	0-40
P_2	Slightly wet	40-60
P_3	Moderately moist	60-80
P_4	Moderately moist	80-100
P_5	Slightly moist	100-140
P_6	Slightly moist	140-180
P_7	Slightly dry	180-210
P_8	Slightly dry	>210
	OCEANICITY (O)	See Bendelow & Hartnup (1980)
O_1	Hyperoceanic	
O_2	Euoceanic	
O_3	Hemioceanic	
O_4	Meioceanic	

Figure 5.2 Distribution of O_{max} scores for each sample square, England and Wales.



KEY :

4 = O_1 Hyperoceanic
3 – O_2 Euoceanic
2 – O_3 Hemioceanic
1 – O_4 Meioceanic

This reduced the number of variables used to a set of three (VAR_{min}, VAR_{max} and VAR_{dev}) for each of the four climatic parameters (total 12); a correlation matrix for these 12 variables (see Appendix 2) shows that there are some strong inter-correlations between them; highly inter-correlated variables ($r > 0.7$) should not be used in DFAs (Green 1979). As all the high inter-correlations occur between variables representing the same climatic parameter, the problem of inter-correlation was overcome by using only the first variable for each parameter selected by the DFA (ie. the one with the highest discriminative power); the other two variables for that parameter were removed from the analysis before repeating it, whereupon the next variable from another parameter was selected, and so on. This selection process reduced the total number of variables entered in the 1st DFA to three (O_{max}, X_{max} and T_{dev}), and to four for the 2nd DFA (O_{max}, X_{max}, T_{max} and P_{dev}, see below). For each analysis, none of the selected variables were inter-correlated at levels of $r > 0.7$.

Table 5.2 *Examples of variable and parameter scores for all parameters in one hypothetical sample 10 km square.*

Climatic parameter	Parameter divisions occurring in sample 10 km sq	Calculated score				
		VAR_{min}	VAR_{max}	VAR_{mean}	PAR_{mean}	VAR_{dev}
Acc. Temperature	T_3, T_4, T_5, T_6	3	6	4.5	3.5	2.5
Exposure	X_3, X_4	3	4	3.5	3.0	2.5
S. M. Deficit	P_3, P_4, P_5,	3	5	4.0	4.0	4.0
Oceanicity	O_1, O_2	3	4	3.5	2.5	1.5

Selection of an extended sample of 10 km squares for the 2nd DFA

To obtain a more detailed prediction of Chough distribution a 2nd DFA was performed. This analysis was effectively an "extrapolation" of the results obtained in the 1st DFA. In the 2nd DFA all squares predicted by the 1st DFA as "climatically equivalent" to occupied squares (whether currently occupied or not) were allocated to a new sample of "predicted occupied" squares (including all *actually* occupied squares), whilst a larger sample of control (unoccupied) squares was selected from those squares sharing the same climatic characteristics as those which explained most of the variation in Chough distribution in the 1st DFA: high exposure (X_4 and/or X_5) and high oceanicity (O_1 and/or O_2) (see 5.3.2). This sample comprised 163 squares containing X_4 and/or X_5, and a 50% sub-sample of the 434 squares containing O_1 and/or O_2 (total 217). [Only 50% of high oceanicity squares were used due to the large number of squares supporting these sub-divisions].

The sample squares were selected using a regular grid as described above for the selection of the original control sample, but with a smaller inter-point distance, to increase the resolution of the sample. Of the sample of 217 squares with high oceanicity and 163 squares with high exposure, 47 squares shared both characteristics, thus the new "unoccupied" group sample consisted of a total of 333 10 km squares, which were entered in the 2nd DFA against the 96 "predicted occupied" group squares from the 1st DFA. The larger size of the control group in the 2nd DFA should enable climatic relationships over and above those already identified in the 1st DFA to be investigated. The use of the "predicted occupied" group avoids possible biases in the 1st DFA brought about by the fact that Choughs are currently found only in Wales: the factors currently limiting the range may be non-climatic, as suggested by the results of the 1st DFA which showed that there are climatically equivalent areas outside Wales, e.g. Cornwall (see section 5.4 for a fuller discussion of this).

Test of the biological validity of DFAs

One would predict that if the climatic variables identified by each DFA are influencing the limits of the Chough's range, then this must be brought about by climatic effects on the population's productivity and/or mortality (presumably indirectly through effects on, for example, food availability). Thus the discriminant function score for each occupied sample square should correlate positively with population size and/or productivity within that square. To test these predictions indices of these two parameters were obtained as follows:

Estimation of Population Size. An index of year-round population size within each occupied 10 km square was calculated from the results of the 1982 RSPB/IWC breeding Chough census (Bullock *et. al.* 1983) and the *Winter Atlas* (Lack 1986). It was considered important to include winter distribution data in order to include sub-adult/non-breeding birds which may comprise up to 30% of the total population ((Bullock *et. al.* 1983). Data from the breeding census were transformed into numbers of individual birds, and scored on the same 1-3 point abundance scale as used in the *Winter Atlas* (see Section 5.2); the scores from both surveys were combined to give a "year-round" index of Chough abundance (possible range of values 0-6). Combining these data was justified since both surveys were carried out contemporaneously (breeding survey 1982, winter atlas 1981-84). The index of Chough abundance was regressed on the Discriminant Function score obtained from comparisons of Chough presence/absence in each DFA.

Estimation of Breeding Success. An estimate of breeding success was obtained using data from the British Trust for Ornithology nest record card scheme (aggregated by 10 km square) for all squares with more than 1 completed nest record card. A total of 220 cards were available for analysis. Mean values for each square for each of the following parameters were regressed on the Discriminant Function score: clutch size, earliest clutch date, brood size, fledging success and earliest fledging date. Not all cards included data on all these parameters, so the sample size of cards used per parameter varied between 74-101, and the number of 10 km squares for which cards were available varied from 8-13 (see Table 5.4).

Due to the small number of 10 km squares available for regression, and the possible biases resulting from the small sample sizes of nest record cards from which the means for each sample square were computed, simpler analyses between mean clutch size and fledging success in O_1 hyperoceanic *vs.* O_2 euoceanic zones and at **coastal** *vs.* **inland** sites were made using a 2-way ANOVA.

5.2.3 Weights of roosting Choughs

To assess the influence of weather fluctuations on Chough body mass, attempts were made to weigh three pairs of birds at their roost-sites using automatic balances during the 1988-89 winter. The system enabled the birds to be weighed at their roost-sites regularly without having to capture them or disturb them in any way. Only three of the six study pairs roosted at sites that were suitable for the use of balances. Of these, pairs A and B roosted in barns, and pair C on the outside of a building. Following roof decay caused by a storm, pair B moved to an inaccessible site after only a few roost weights had been obtained. The weights obtained for pair C "out-of-doors" proved to be too unreliable due both to exposure to the wind and to the cramped nature of the roost-site itself (which sometimes resulted in the full weight of the bird not resting on the balance). Thus, unfortunately, it was only possible to obtain reliable weights for pair A. However, weights were obtained for both members of this pair between November 1988 and March 1989, and as these are the first published weights for Choughs recorded regularly throughout a winter I have presented the results here. Both members of pair A had been colour-ringed as nestlings on Islay; they first paired up in 1987, and bred successfully in 1987, 1988 and 1989. Over the 1988/89 winter the female was 6.5 years old, and the male 5.5 years old.

The roost-site was in a Dutch barn at an altitude of 65 m, 4.5 km from the nearest coast. The birds roosted on two balances placed on an artificial ledge 7 m above ground level in the apex of the roof, where they were very sheltered from both wind and rain. The balances were designed by Dr. M. Burns of Glasgow University, and are described fully in Monaghan *et al.* (1989b); each consisted of a fibre-glass "rock" forming the perch, with a load cell and solid base below, connected to an Epson micro-computer. Weights were recorded automatically at hourly intervals, each recorded weight being the mean (plus standard deviation) of 30 readings taken at 1-second intervals. Weights with standard deviations greater than 1.0g were excluded from subsequent analyses, as were all weights from any night with erratic hourly recordings. Balances were calibrated using a standard 300g weight before and after the birds roosted on them; all weights from nights where the post-roost 0-300g readings were inaccurate by >= 2.0g were excluded from subsequent analyses. In practice, there was little overnight "drift" in readings; some inaccurate overnight sessions appeared to be due to faulty lead connections at the computer. Morning inspections showed that roosting birds ejected faeces and pellets over the rim of the balance, thus not interfering with recording.

The roost-weights used in these analyses were the best (those with the lowest standard deviation) weights obtained within 30 minutes of the birds' arrival at the roost. As I was present at the roost-site (out of sight) when the birds arrived, it was possible to obtain several weights (using a manual over-ride facility in the computer programme) as soon as the birds first settled on the balances. It was also possible at this time to confirm which bird was on which balance, though the large weight difference between the male and the female (>60 g) meant that this was not imperative.

Daily weather records were taken at Sunderland Farm, Islay, 11 km from the roost site, but at a similar altitude (50 m a.s.l.) and in the same bioclimatic zone - on the border of Birse's (1971) $O_1H_3T_1$ and $O_1H_2T_1$ zones. It is assumed that the local climate at Sunderland Farm is closely correlated with that of the roosting birds' home range. The following weather records were taken: daily maximum and minimum temperatures in the shade; an estimate of the average Beaufort windspeed during the daylight hours; duration of precipitation during daylight hours (0-5 scale representing 0-100% daylight hours); average heaviness of precipitation during daylight hours (0-5 scale, 0 = no rain, 1 = light rain, 2 = light-moderate, 3 = moderate, 4 = moderate-heavy, 5 = heavy rainfall). The last two were summed to give an overall estimate of the rainfall "severity" during daylight hours on a 0-10 scale. A further variable, "WINDRAIN", was computed by summing wind force and rainfall severity, to represent the combined effects of wind and rain. Daylength, the time between sunrise and sunset at Glasgow, at the same latitude as Islay, 120 km to the east (obtained from data published by the Science and Engineering Research Council) on the day that dusk roost weights were obtained, was entered into all analyses to take into account the amount of time available for feeding.

For each weather variable, 10-day means were computed for the 10 days prior to (and including) the day that roost-weights were obtained. Multiple regression analyses of weather variables and daylength on roost-weights for each sex on a) day of weighing and b) as 10-day means were carried out.

5.2.4 Growth of *Tipula paludosa* larvae on Islay

The growth of *Tipula paludosa* larvae was investigated during 1988-89 by taking 40 random samples (soil cores 10cm deep x 6.5 cm diameter) from 2 improved pasture fields on or close to the Rhinns of Islay. Samples were taken at 2-monthly intervals throughout the year, increasing to once per month in the breeding season. Larvae were extracted using a dry heat extraction apparatus (see Blasdale 1974). Subsequent hand-sorting of 400 treated cores showed that dry heat extraction had an efficiency of 94.2%. The extracted (live) larvae were washed in water, dried on filter paper and weighed to the nearest milligram. Larvae were identified (using Brindle 1960). Where possible, unidentified larvae were saved and their imagos identified after emergence. Virtually all identified larvae and imagos were *T. paludosa* so it was assumed that non-specifically identified individuals (mostly the small 1st and 2nd instar larvae) also belonged to this species. That this was likely to have been the case has been demonstrated in other parts of Scotland by isoelectric focussing techniques (Humphreys *et al.* 1993).

5.2.5 Cold-hardiness of *T.paludosa* larvae in relation to body size.

It is well established that *T. paludosa* larvae are particularly susceptible to relatively short exposure to sub-zero temperatures (Freeman 1967, Barbash 1988). Bearing in mind the predictions of Meats' (1974a) and Blackshaw's (1990) models that larval growth and/or survival will differ in areas experiencing different climates, I wanted to investigate whether larval size affects their ability to withstand cold. If larger larvae are more cold-hardy, then the shape of the growth curve in relation to the time of year when the coldest temperatures are experienced will have a strong influence on cold-induced mortality in wild populations. The methods used to investigate this follow those employed by Freeman (1967) and Barbash (1988).

Two replicate experiments were carried out in February 1988 on *T. paludosa* larvae collected from soil core samples in improved pasture on Islay. Larvae were divided into three size classes: 9-15 mm, 16-25 mm and 26-53 mm, and divided into experimental and control groups, each comprising 15 individuals. Larvae were placed individually on damp filter paper in compartmentalised 9.0 cm petri dishes. The compartments, c.2 cm^2 made of cardboard, were necessary to prohibit larvae from killing each other, which occurred in the control groups which remained active throughout the experiment. Experimental groups were exposed to -8°C for 5 hours (a temperature known to produce intermediate levels of mortality (Barbash 1988)). Control groups were simultaneously exposed to 2°C for 5 hours. At the end of exposure the larvae were transferred to room temperature, and after several hours the number of survivors was counted (dead larvae showed no response when the sensitive spiracular disc was prodded). Both experiments gave similar results, thus frequencies have been summed for presentation.

5.3 RESULTS

5.3.1 Bioclimatic analysis - Scotland

The distribution of all records of definite or probable breeding by Choughs in Scotland since 1750 is compared with that of the 4 climatic variables (accumulated temperature, soil moisture deficit, exposure and winter severity) used by Birse & Dry (1970) and Birse & Robertson (1970) to summarise the current climate of Scotland in Figures 5.3 and 5.4. The percentage of the current Scottish Chough population occurring within each climatic sub-division is shown, and historical records from climatic sub-divisions not currently occupied are also indicated.

Figure 5.3 shows that Birse and Dry's (1970) combination of **accumulated temperature** and **soil moisture** categories produces a total of 23 climatic sub-divisions in Scotland. Choughs currently occur in only two of these divisions: **Em** (*warm* and *moist*) and **Er** (*warm* and *rather wet*). The *warm* category is at the warmest end of the scale of accumulated temperatures found in Scotland. The *moist* and *rather wet* divisions are in the middle of the moisture range.

If we assume (as a form of null hypothesis, see Discussion) that the climatic divisions have not changed over the last 200 years, then historically Choughs occurred in a wider range of climatic *warmth/moisture* sub-divisions than they do today: three extra moisture divisions - *wet*, *rather dry* and *dry*, and one extra warmth category - *fairly warm*. However, only one combination of these divisions, **Eh** (*warm* and *rather dry*), was occupied by significant numbers of Choughs (the populations in Ayrshire and Wigtownshire). The other divisions represent the small populations that existed on Skye, Mull and at St. Abb's/Fast Castle, Berwickshire.

Figure 5.4 shows that Birse and Robertson's (1970) categorisation of **exposure** and

Figure 5.3 Bio-climatic moisture/temperature divisions (from Birse & Dry 1970) occupied by breeding Choughs (probable & definite records) in Scotland (current percentage of population and historical records since 1750).

Accumulated temp. divisions		Potential water deficit divisions					
		Dry	Rather dry	Moist	Rather wet	Wet	Very wet
		e	h	m	r	v	v+
WARM	E	h	H	90	10	h	0
FAIRLY WARM	L	0	0	0	h	h	0
COOL	M	.	0	0	0	0	0
COLD	S	.	.	.	0	0	0
VERY COLD	V	.	.	.	.	0	0
EXTREMELY COLD	Z	.	.	.	.	.	0

KEY: Figures indicate approx. percentages of current Scottish population
H = many historical records; h = few historical records;
0 = no records; . = climatic sub-division not found in Scotland

Accumulated temperature divisions

SYMBOL	DESCRIPTION	RANGE (Day degrees C)
E	Warm	> 1375
L	Fairly warm	1100-1375
M	Cool	825-1100
S	Cold	550- 825
V	Very cold	275- 550
Z	Extremely cold	0- 275

Potential water deficit divisions

SYMBOL	DESCRIPTION	RANGE (mm)
e	Dry	> 75
h	Rather dry	50-75
m	Moist	25-50
r	Rather wet	0-25
v	Wet	0
v+	Very wet	0

The v+ (very wet) category represents areas where summer rainfall (April-September) exceeds summer evapotranspiration by at least 500mm water.

Figure 5.4 Bio-climatic winter severity/exposure divisions (from Birse & Robertson 1970) occupied by breeding Choughs (probable & definite records) in Scotland (percentage of current population and historical records since 1750).

Accumulated frost divisions		Exposure divisions				
		Shelt -ered	Mod. expsd	Exp- osed	Very expsd	Extrmly expsd
		E	M	P	V	Z
Ext. mild winters	e	.	0	40	60	0
Fairly mild winters	f	0	0	h	0	0
Moderate winters	m	0	0	0	0	0
Rather severe winters	r	0	0	0	0	0
Very severe winters	v	.	.	0	0	0
Ext. severe winters	z	.	.	.	.	0

KEY: Figures indicate approx. percentages of current Scottish population
h = few historical records;
. = climatic sub-division not found in Scotland

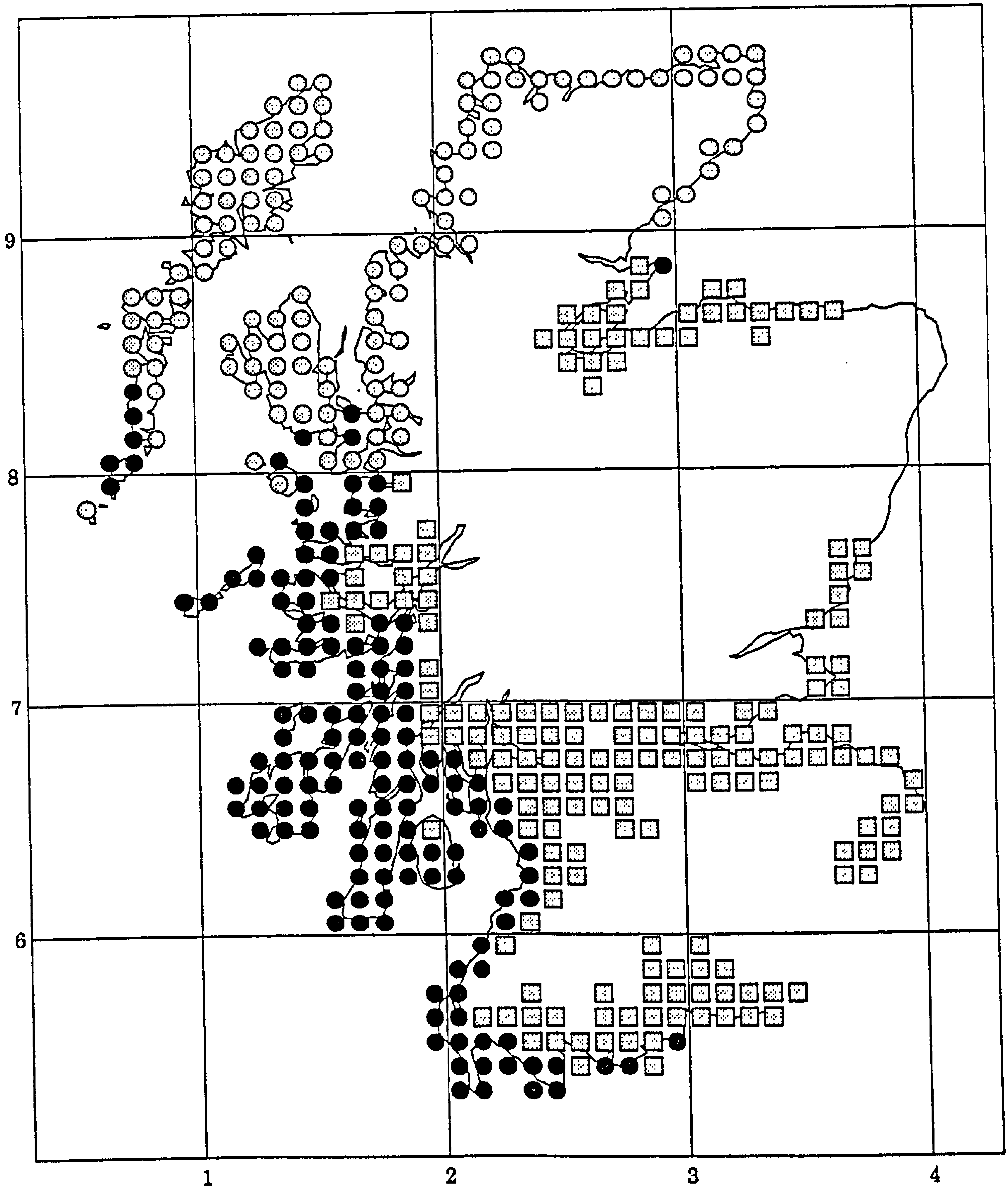
Exposure divisions

SYMBOL	DESCRIPTION	RANGE (wind speed, m/s)
E	Sheltered	<2.6
M	Moderately exposed	2.6-4.4
P	Exposed	4.4-6.2
V	Very exposed	6.2-8.0
Z	Extremely exposed	>8.0

Accumulated frost divisions

SYMBOL	DESCRIPTION	RANGE (Day degrees below zero C)
e	Extremely mild winters	< 20
f	Fairly mild winters	20- 50
m	Moderate winters	50-110
r	Rather severe winters	110-230
v	Very severe winters	230-470
z	Extremely severe winters	>470

Figure 5.5 10km squares in Scotland with extremely mild winters and/or warm summers.



grey circles = extremely mild winters (<20 day°C below 0°C)

grey squares = warm summers (accumulated temperature > 1375 day°C)

black circles = extremely mild winters <u>and</u> warm summers

NB. <u>Shetland and Orkney</u>: some squares have extremely mild winters, but none have accumulated temperatures > 1375 da

winter severity produces a total of 23 climatic sub-divisions in Scotland. Choughs currently occur in only two of these divisions: **Pe** (*exposed* with *extremely mild winters*) and **Ve** (*very exposed* with *extremely mild winters*). This suggests a strong preference for extremely mild winters and/or a high degree of exposure (where these two variables occur within hyperoceanic areas, as in areas occupied by Choughs, they are highly inter-correlated - in mild areas winds reduce the likelihood of frosts occurring). Historical breeding records come from only one other category - **Pf** (*exposed* with *fairly mild winters*). This category only occurs in two very small areas previously occupied by Choughs (Colvend on the Kircudbright coast, and St. Abb's on the Berwickshire coast), and probably only involved a handful of breeding pairs.

Of the four climatic parameters considered above, it appears that accumulated temperature and winter severity are the most limiting in terms of Chough distribution - the majority of past and present breeding records come from only one division of each - the *warm* accumulated temperature division (>1375 day°C) and the *extremely mild winter* accumulated frost division (<20 day°C below 0°C). This compares with five potential water deficit divisions and two exposure divisions. The distribution of the two limiting variables can be used to determine the Chough's *Potential Climatic Range* in Scotland.

5.3.2 Bioclimatic analysis - England & Wales

1st Discriminant Function Analysis

The following four sets of non-independent variables were entered in a preliminary analysis in order to identify which one from each set should be used in subsequent analyses:

Bioclimatic parameter	Variable set		
Oceanicity	O_{min}	O_{dev}	O_{max}
Exposure	X_{min}	X_{dev}	X_{max}
Soil Moisture Deficit	P_{min}	P_{dev}	P_{max}
Accumulated Temperature	T_{min}	T_{dev}	T_{max}

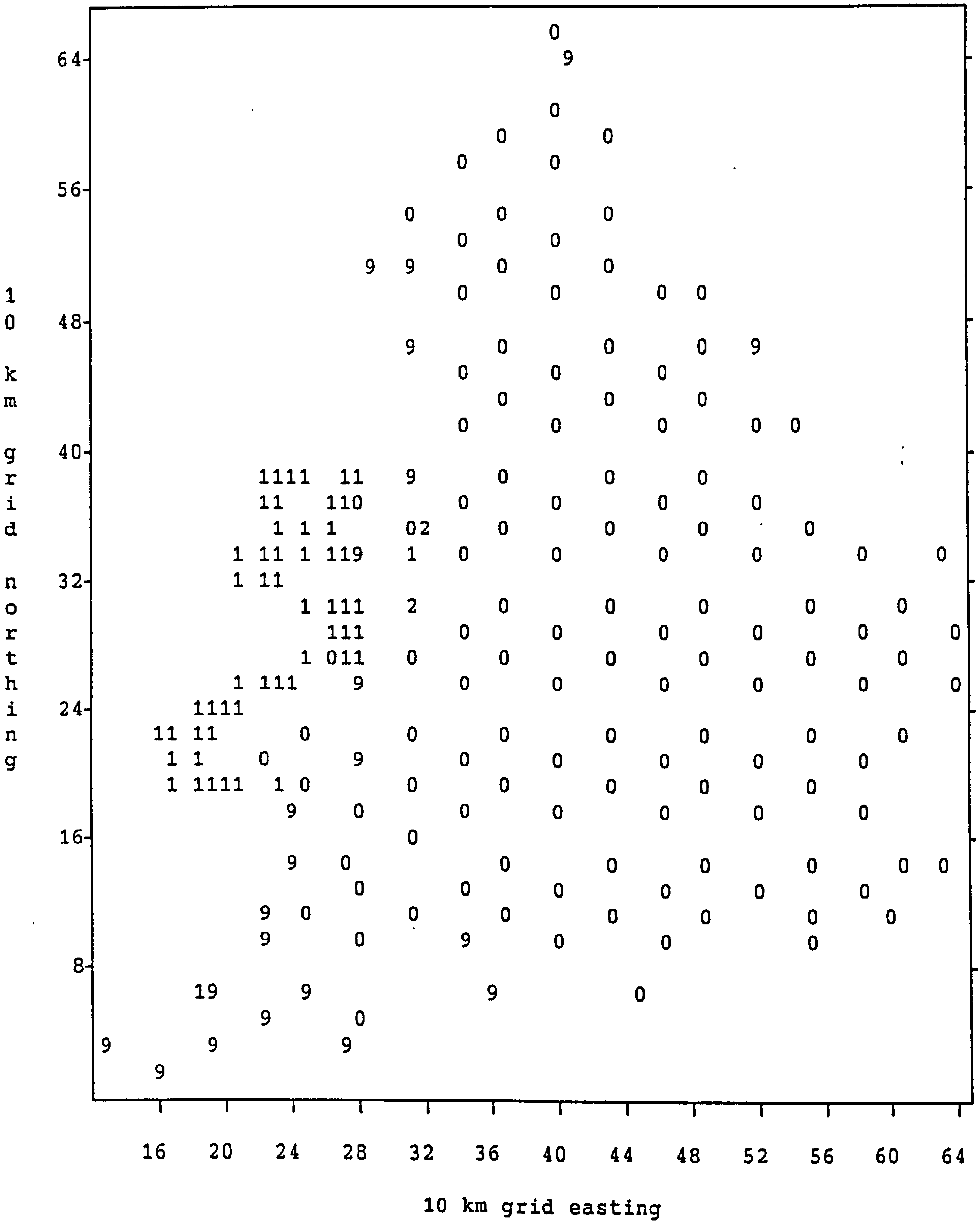
The preliminary DFA entered O_{max} at step one, X_{max} at step two, and T_{dev} at step three. For each of the three significant variables the other two variables from its set (e.g. O_{min}, O_{dev} for oceanicity) were removed before repeating the analysis (see Methods). None of the soil moisture variables achieved the entry criteria. The resulting 1st DFA (see Table 5.3) correctly classified "Chough occupancy" in 88.74% of the sample squares (prior probability 33.3%) . The discriminant function was highly significant (eigenvalue = 1.183, Chi^2 = 170.5, d.f.= 8, $P < 0.0001$). The standardised discriminant function coefficients indicate the relative contribution made by each variable to the discrimination. Only O_{max} and X_{max} exceeded the arbitrary significance level of 0.40 (see Green 1979 and Tabachnick & Fidell 1983), indicating that Chough distribution correlates most closely with high levels of oceanicity and exposure. Figure 5.6 shows the geographical distribution of predicted occupancy for the 222 sample squares. It is interesting to note the distribution of misclassified squares; in particular, it can be assumed that squares incorrectly classified as "occupied" are climatically equivalent to currently occupied squares. These areas include most of Cornwall, parts of Devon, Dorset and Cumbria, plus two outlying squares on the east coast of northern England. In addition, 3 currently occupied squares in Wales were predicted as unoccupied, suggesting that they are climatically less optimal than those predicted as occupied, including many areas in south-west England in which the Chough is now extinct.

Regression of the index of Chough abundance on the Discriminant Function score obtained in the 1st DFA for the 74 occupied squares gave a significant though small positive relationship:

$$\text{Index of Chough abundance} = 0.970 + 0.946 \text{ Discriminant Function score};$$
$$n=74,\ r=.382,\ P<0.001.$$

This suggests that the same climatic relationship that characterises the limits of the Chough's range, also influences abundance within the occupied range, and as such strongly suggests that there is a biological basis to the relationship.

Figure 5.6 Predicted occupancy by Choughs of sample squares in England and Wales, 1st Discriminant Function Analysis



KEY
0 = Predicted unoccupied correctly (n=126)
1 = Predicted occupied correctly (n=71)

2 = Predicted unoccupied incorrectly (n=3)
9 = Predicted occupied incorrectly (n=22)

Table 5.3 *Summary of first Discriminant Function Analysis for climatic variables on occupied vs. unoccupied 10 km squares (n=74 occupied squares, 148 unoccupied squares).*

Variable[1]	Unstandardised Discriminant Function Coefficient	Standardised Canonical Discriminant Function Coefficient
O_{max}	1.1066	.6817
X_{max}	.6635	.4341
T_{dev}	.1460	.0934
(constant)	-5.1345	

Percent of "grouped" cases classified correctly = 88.74%

Notes: Variables are listed in order of entry.
[1] : symbols are listed in Table 5.1.

Table 5.4 *Regression analyses of breeding parameters obtained from BTO nest record cards (N.R.C.s) on Discriminant Function Score obtained in 1st DFA*

Breeding biology parameter	No. of N.R.C.s	10 km squares *n*	*r*	Significance
Mean earliest recorded clutch date	74	12	.135	NS
Mean clutch size	79	8	.011	NS
Mean brood size	101	13	.262	NS
Mean earliest recorded fledging date	87	9	-.327	NS
Mean number chicks fledged	94	13	.452	NS

The results of regression analyses of breeding parameters (obtained from BTO nest record cards) on Discriminant Function score for those 10 km squares for which breeding data were available are given in Table 5.4. There were no significant relationships with any of the five parameters. Detection of significant trends was probably made difficult by the small sample sizes of 10 km squares on which the regressions were based, and because of the small number of nest record cards per square (mostly <5).

As the above analyses appeared to be limited by small sample sizes, a simpler comparison of breeding parameters of pairs nesting at **coastal** *vs.* **inland** sites and in the **O_1** *vs.* **O_2** bioclimatic zones was made (Table 5.5). For all parameters the means at coastal sites were higher than at inland sites, whilst they were also higher in the O_1 zone than in the O_2 zone. Two-way analysis of variance (ANOVA) (see Table 5.6) showed that there was no significant difference in mean clutch size between O_1 *vs.* O_2 bioclimatic zones, but mean brood size and mean number of young fledged were significantly greater in the O_1 zone. There were no significant differences between inland and coastal sites. There was a significant interaction between oceanicity and coastal/inland sites for brood size, but not for clutch size or fledging success.

Table 5.5 *Breeding parameters of Choughs nesting at* coastal vs. inland *and* O_1 vs. O_2 *nest-sites (data from BTO nest record cards).*

	Clutch size			Brood size			Fledged young		
Site	mean	SD	*n*	mean	SD	*n*	mean	SD	*n*
Inland	3.89	1.02	18	3.18	0.92	33	2.61	0.92	38
Coastal	4.21	0.95	61	3.38	1.12	64	2.98	1.11	52
O_1 hyperoceanic	4.23	0.93	65	3.46	0.99	70	3.26	0.85	39
O_2 euoceanic	3.71	1.07	14	2.93	1.14	27	2.49	1.07	51

2nd Discriminant Function Analysis

The O_{max} and X_{max} variables were automatically entered in the 2nd DFA to represent their respective climatic parameters due to their high level of significance in the 1st DFA (see Section 5.2.2); to these were added all **soil moisture deficit** and **accumulated temperature** variables. The analysis selected O_{max}, X_{max}, P_{dev} and T_{min} (the latter two from their respective variable sets). The results of the 2nd DFA are summarised in Table 5.7. The discriminant function was highly significant (eigenvalue = 0.297, $Chi^2 = 110.5$, d.f.= 4, $P < 0.0001$).

Table 5.6 *Results of two-way ANOVA for clutch size brood size and fledging success at O_1 vs. O_2 and coastal vs. inland sites.*

Variable	Source of variation	d.f.	*F*	*P*
CLUTCH SIZE	Oceanicity	1,75	1.78	NS
	Coastal/Inland	1,75	0.06	NS
	Interaction	1,75	0.20	NS
BROOD SIZE	Oceanicity	1,93	4.96	<0.03
	Coastal/Inland	1,93	0.29	NS
	Interaction	1,93	7.51	<0.01
NUMBER OF CHICKS FLEDGED	Oceanicity	1,86	10.22	<0.01
	Coastal/Inland	1,86	0.06	NS
	Interaction	1,86	0.58	NS

Table 5.7 *Summary of 2nd Discriminant Function Analysis for climatic variables on occupied vs. unoccupied 10 km squares (n=96 "predicted occupied" squares, 333 unoccupied squares).*

Variable[1]	Unstandardised Discriminant Function Coefficient	Standardised Canonical Discriminant Function Coefficient
O_{max}	.9350	.5123
X_{max}	1.2702	.8112
T_{min}	.2162	.3045
P_{dev}	.3354	.3215
(constant)	-10.5810	

Percent of "grouped" cases classified correctly = 75.52%

Notes: Variables are listed in order of entry.
[1]: Variable symbols are described in Table 5.1.

The 2nd DFA correctly classified 75.52% (prior probability 22.4%) of occupied squares. Though this accuracy appears to be lower than that obtained in the 1st DFA (88.74%), the lower prior probability of the 2nd DFA (22.4% compared to 33.3%) means that in absolute terms the accuracies are approximately equal (difference between *prior probability* % and *correct classification* %: 1st DFA = 55.44%, 2nd DFA = 53.12%). As in the 1st DFA, O_{max} and X_{max} contributed most to the discriminant function, emphasising the strength of these relationships. Also entered were positive relationships with T_{min}, suggesting avoidance of cooler areas (low levels of accumulated temperatures) and P_{dev} (suggesting a preference for moderate levels of soil moisture deficit ie. neither very wet not very dry), though neither exceeded the arbitrary 0.4 significance level (Green 1979). The geographical distribution of predicted square occupancy from the 2nd DFA is shown in Figure 5.7. Areas climatically equivalent to those currently occupied again include most of Cornwall and south Cumbria, some of the coasts of Devon and Dorset, and two outliers on the east coast of northern England. The predicted distribution in Wales is remarkably similar to that currently occupied, with the exception of the inland squares of mid-Wales, most of which are classified as climatically unsuitable.

Regression of the index of Chough abundance on the Discriminant Function score obtained in the 2nd DFA showed a significant though small positive relationship:

$$\text{Index of Chough abundance} = 1.816+0.560 \text{ Discriminant Function score}$$

$$n=74,\ r=0.313,\ P<0.01.$$

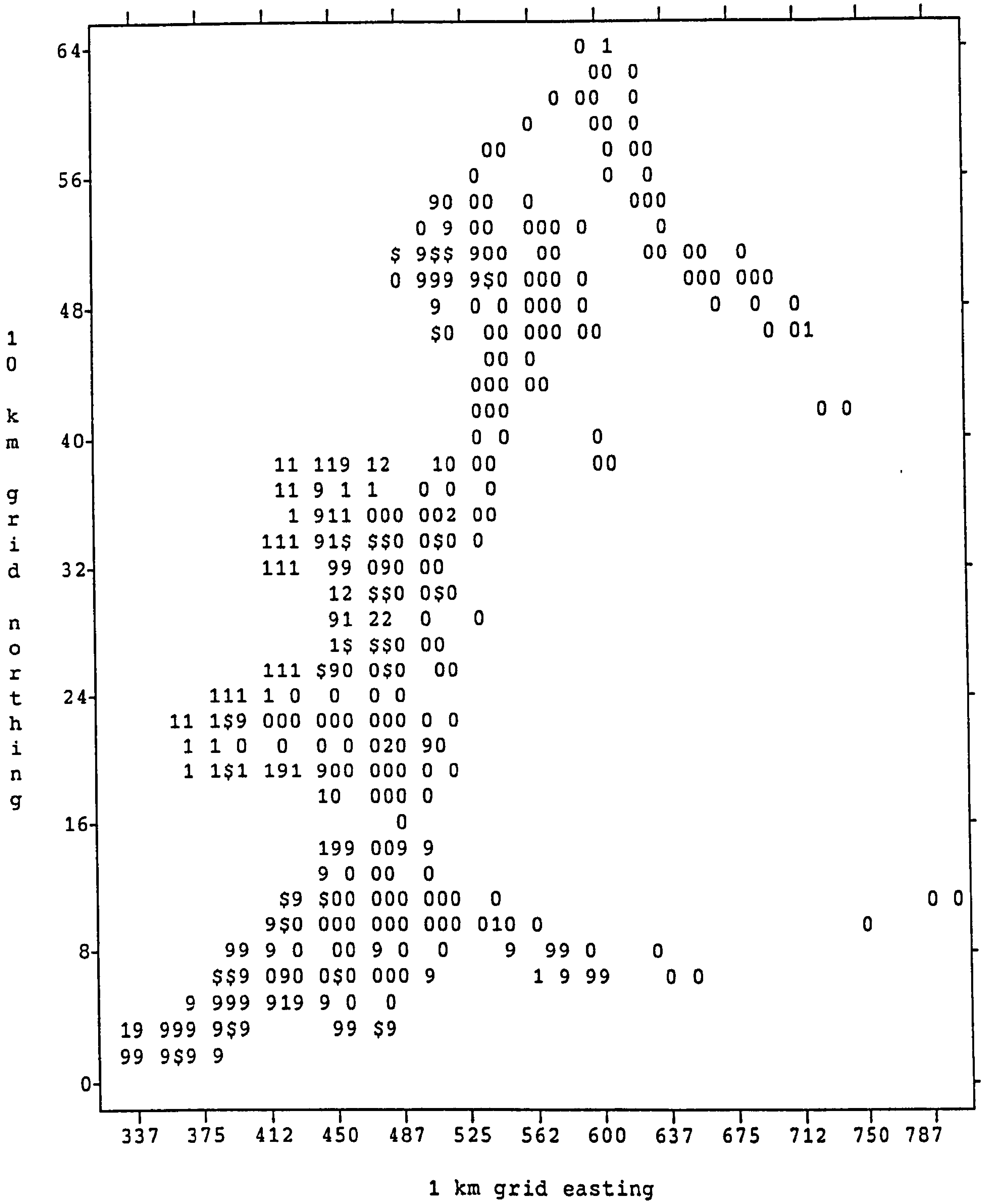
Chough abundance within currently occupied squares was correlated with the DF score from the 2nd DFA, even though these scores were calculated from areas which included squares which currently support no Choughs such as those in Cornwall and Cumbria.

5.3.3 Weights of roosting Choughs

Figure 5.8 shows a typical overnight weight-loss curve for the roosting male of pair A. The bird spent a minimum of 15 hours at the roost, and in this time lost 20g, 5.2% of its dusk weight. The slope of the curve is consistent with a rapid loss of weight in the first 6 hours due to evacuation of faecal matter, followed by a reduced rate of weight-loss thereafter, presumably representing respiratory losses. The smooth nature of the curve and the low standard deviations suggest a high degree of reliability in the methods employed, and that the roosting birds were inactive.

The dusk mass of the male and female birds from pair A between November 1988 and March 1989 are presented in Figure 5.9. The male's mass remained relatively constant throughout the period (mean 377.3g, SD 4.10). Maximum mass (385.2g) was recorded on

Figure 5.7 Predicted occupancy by Choughs of sample squares in England and Wales, 2nd DFA



KEY:
0 = Predicted unoccupied correctly (n=248)
1 = Predicted occupied correctly (n=76)

2 = Predicted unoccupied incorrectly (n=20)
9 = Predicted occupied incorrectly (n=85)
$ = Multiple occurrence of two of the above categories (due to insufficient resolution of the plotting system).

Figure 5.8 Mass of roosting male Chough, pair A, Islay, 29th January 1989.

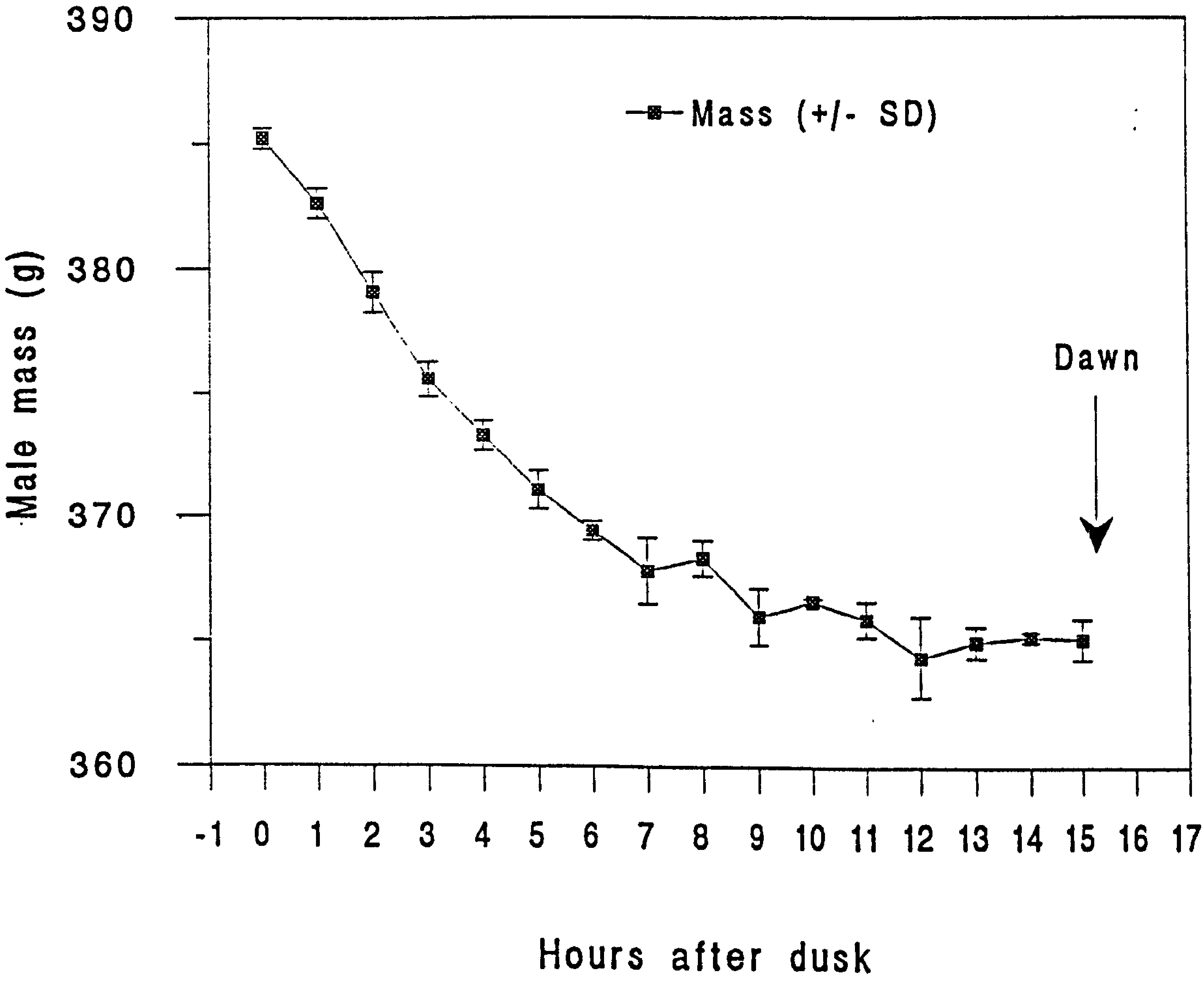
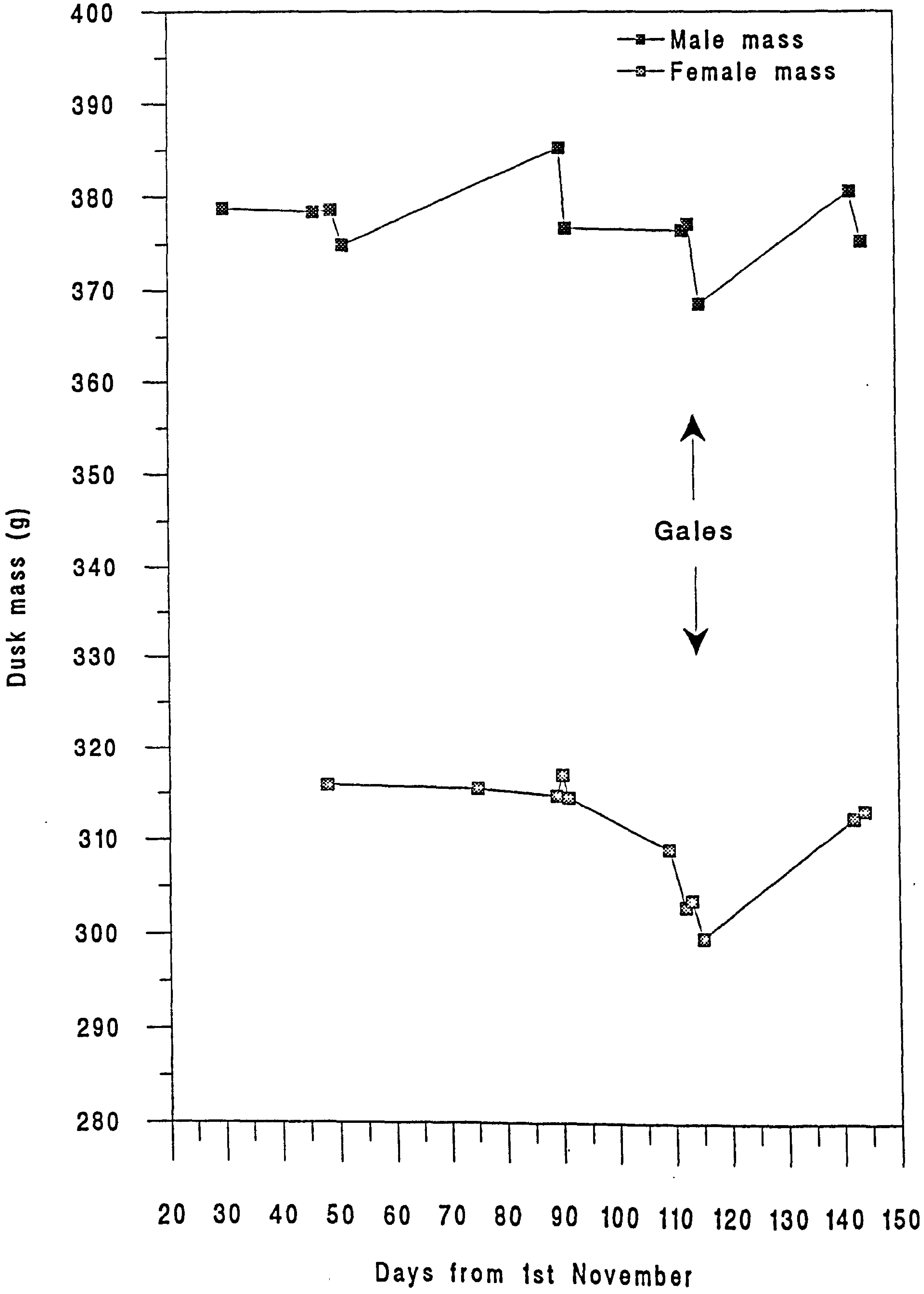


Figure 5.9 Dusk mass of male and female Choughs (pair A), November 1988 - March 1989.



29th January, and minimum mass (368.5g) on 23rd February). The overall range in mass represented only 3.7% of the mean.

The female's mass was also fairly constant (mean 310.8g, SD 6.16). Maximum mass (317.2g) was recorded on 29th January, as for the male, but it dropped markedly from 17th-23rd February to a minimum of 299.5g on 23rd February. By 24th March it had increased to 313.2g. The overall range in values represented a fluctuation of 5.7% of the female's mean mass.

The daily minimum and maximum temperatures recorded on Islay over the 1988-89 winter were milder than usual (Figure 5.10). In contrast to more normal winters there was virtually no snow and hardly any frosts in 1988-89. It was not possible to compare rainfall directly with past records due to the use of different recording methods in 1988-89, but it was thought not to have been a remarkably wet or dry winter. The most notable weather event was a force 12 hurricane which swept the island on 16th February. The birds spent at least part of this day sheltering at the roost site (*pers. obs.*), and it is likely that they spent little time feeding. If so, the effects of this event would have replicated that of a hard frost which would likewise have prevented feeding.

The results of multiple regression analyses of weather variables on dusk mass of both members of pair A are given in Table 5.8. There were no significant relationships between weather variables and/or day length with male mass, but female mass showed significant positive relationships with the 10-day means of both maximum and minimum temperatures.

5.3.4 Growth of *Tipula paludosa* larvae on Islay.

The mean monthly weights of *T. paludosa* larvae collected in the field in 1988-89 are presented in Table 5.9. Variability in sample sizes reflects intensity of sampling (see section 5.2.4) rather than actual differences in abundance of the larvae. The resulting growth curve (see Figure 5.11) is fairly typical of the species (see Discussion).

In Figure 5.12 the growth curves of *T. paludosa* larvae at three localities are compared - Islay (current study), Glasgow (Barbash 1988) and Northumberland (Laughlin 1967). The curves from the current study and Barbash's study are directly comparable as the same sampling and larval extraction methods were used, and the growth curves represent one

Figure 5.10 Mean monthly daily minimum temperatures Islay, November-March 1973-85 (+/- SD) and 1988-89

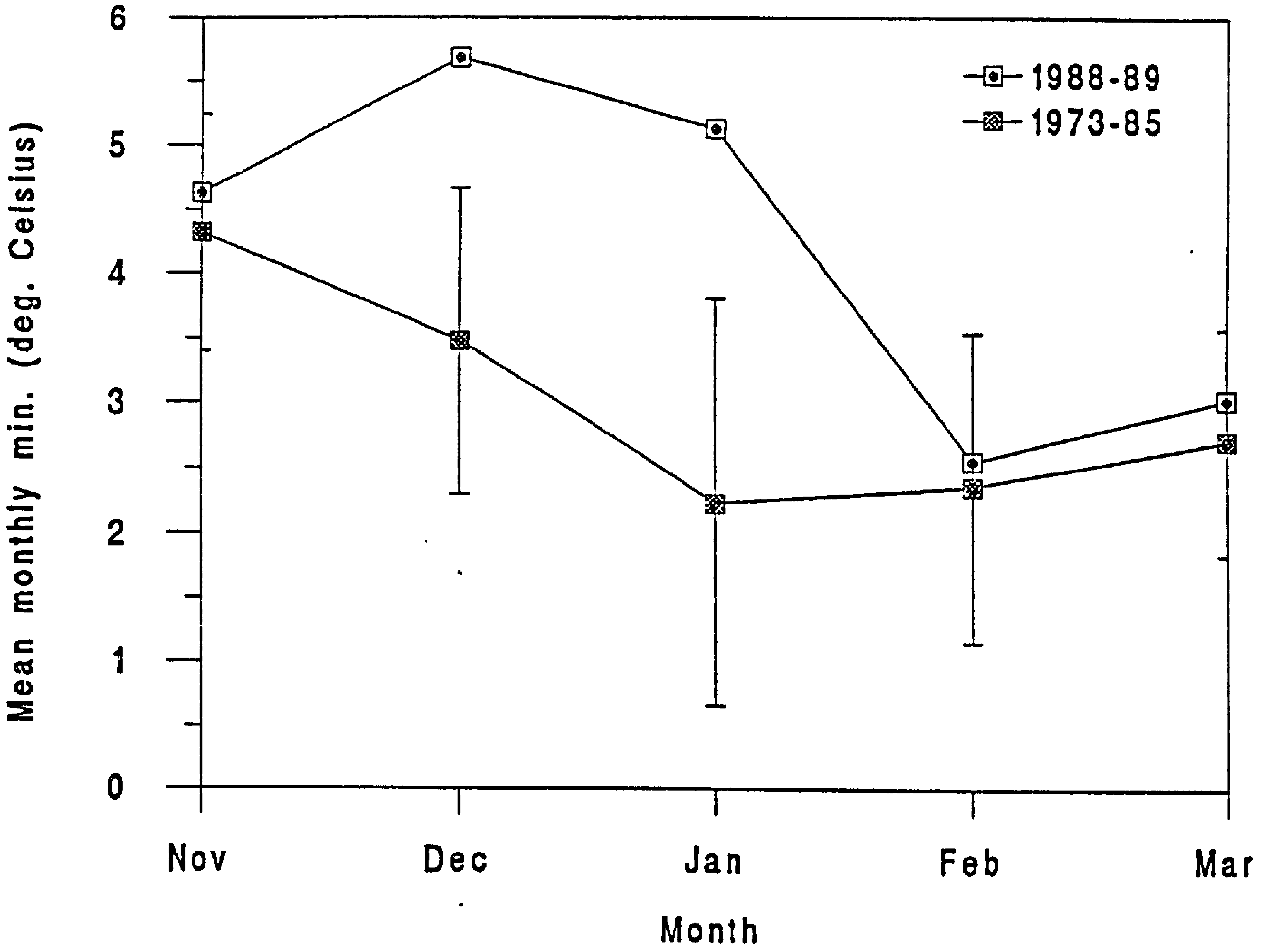


Figure 5.11 Growth of Tipula paludosa larvae, Islay 1988-89

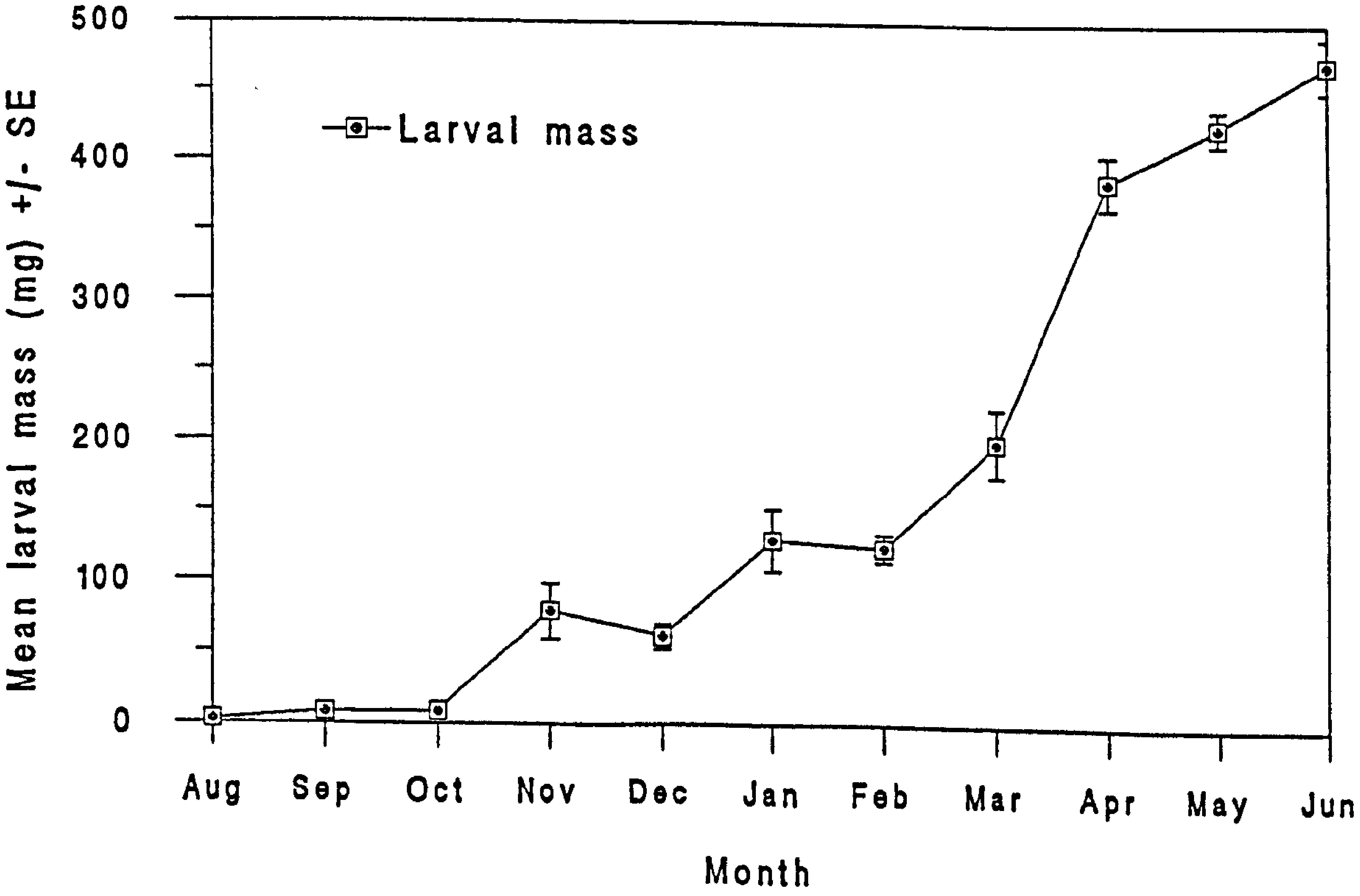
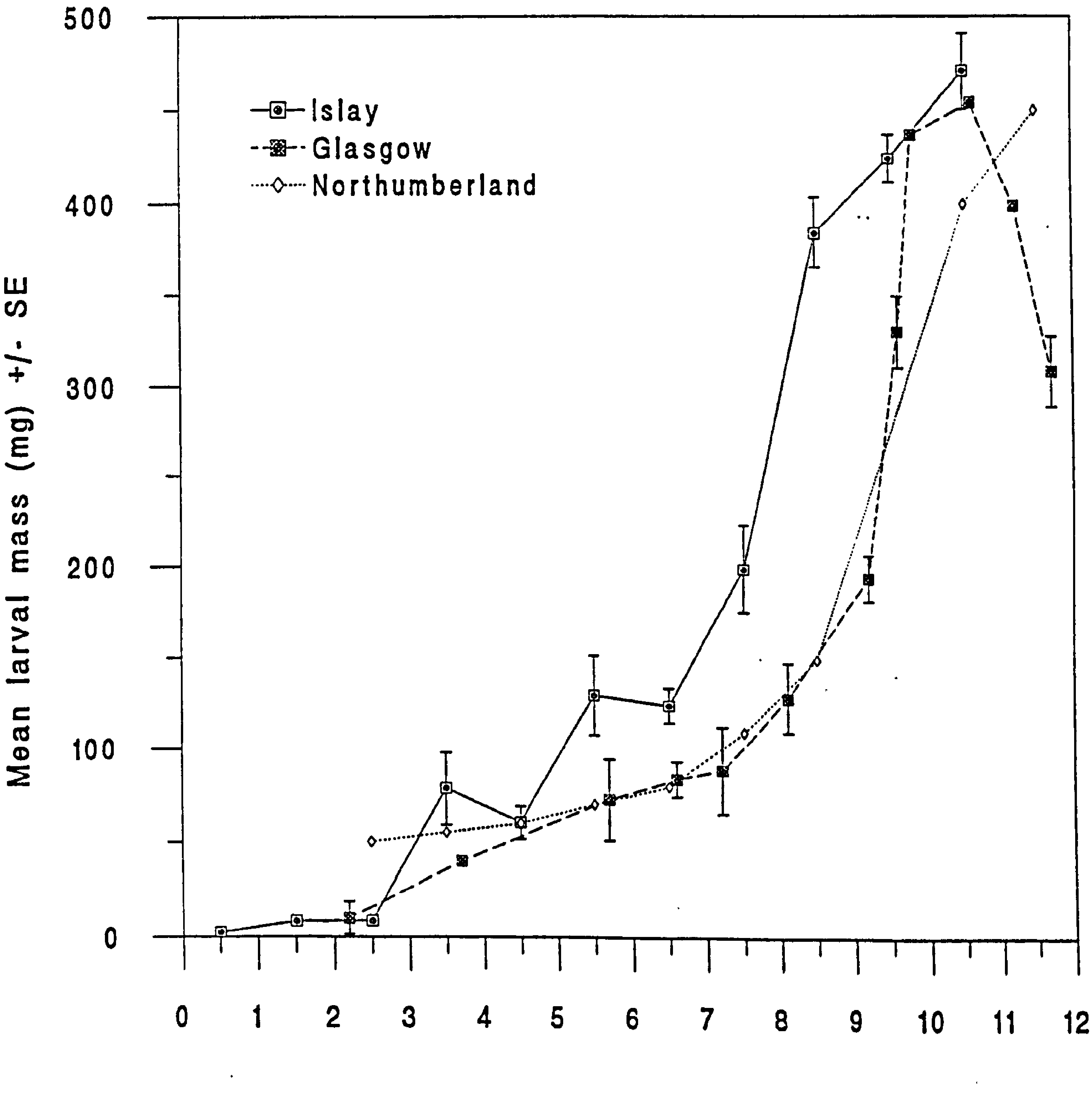


Figure 5.12 Comparison of Tipula paludosa larval growth curves from Islay (this study), Glasgow (Barbash 1988) and Northumberland (Laughlin 1967).



year's cohort of larvae. Laughlin's curve is the mean of 5 years' data, which he considered to represent "a good picture of a normal year's growth". In producing this curve he excluded data from 2 years when growth was poor. In addition, the chemical extraction technique that he used tends to underestimate the number of smaller larvae as these are harder to detect (Stewart 1969). For these reasons it is likely that Laughlin's curve represents a maximum estimate of larval growth.

From January onwards larval weight was approximately 4-6 weeks advanced on Islay as compared to Glasgow and Northumberland, although the shape of the growth curves was roughly similar in each area.

Table 5.8 *Stepwise multiple regression of weather variables on dusk mass for both members of pair A. (Male n=12, female n=11).*

Independent variable[a]	Beta	*F*	*P*	Multiple *r*	r^2
Female					
TMAX_{10}	0.82	18.2	.002	0.82	0.67
TMIN_{10}	0.50	19.9	.001	0.91	0.83
Male					
No variables entered	-	-	-	-	-

[a] All variables entered in the analysis (see section 5.2.3 for full descriptions):

TMAX - Maximum temperature on roost date
TMAX_{10} - Mean maximum temperature for 10 days up to and including roost date
TMIN - Minimum temperature on roost date
TMIN_{10} - Mean minimum temperature for 10 days up to and including roost date
RAIN - Rainfall severity on roost date
RAIN_{10} - Mean rainfall severity for 10 days up to and including roost date
WIND - Wind force on day of roosting
WIND_{10} - Mean wind force for 10 days up to and including roost date
WINDRAIN - Combined wind and rain index on day of roosting
WINDRAIN_{10} - Mean combined wind and rain index for 10 days up to and including roost date
DAYLENGTH - Day length on roost date

Table 5.9 *Mean live weights of* Tipula paludosa *larvae collected in the field, Islay 1988-89.*

Month	Mean weight (mg)	*n*	SE
Aug	2.6	18	0.45
Sep	8.3	12	1.56
Oct	8.8	35	1.53
Nov	78.4	10	19.44
Dec	60.6	28	8.60
Jan	130.0	26	21.77
Feb	124.5	56	9.65
Mar	199.4	25	23.94
Apr	384.5	47	19.03
May	424.4	131	12.72
Jun	470.5	67	19.96

5.3.5 Cold-hardiness of *T. paludosa* larvae in relation to size.

Mortality of *T. paludosa* larvae was highest in the smallest size class, and progressively lower in the larger size classes (see Table 5.10).

Table 5.10 *Percentage mortality in relation to body size of* T. paludosa *larvae exposed to -8°C (experimental) or 2°C (control) for 5 hours (n=30 in all groups).*

		Size class		
		9-15mm	16-25mm	26-35mm
EXPERIMENTAL	Live	6	25	26
	Dead	24	5	4
			(Chi^2 36.46, *df*=2, *P*<.0001)	
CONTROL	Live	30	30	30
	Dead	0	0	0

5.4 DISCUSSION

In this chapter I have attempted to take a broad climatological approach to the analysis of Chough distribution. Whilst it is tempting to simply select a climatic isogram that corresponds with a species' distribution, such as the 38°F January isotherm identified by Cullen and Jennings (1986) as corresponding with the Chough's British distribution, this is an unobjective approach and potentially misleading. There is no pre-determined basis for choosing this climatic variable, other than that it closely fits the Chough's distribution. Similarly, Hill (1991) states that selection of climatic variables for an analysis of climatic determinants of a variety of British bird and plant species distributions was "more arbitrary [than selection of study species]" and that "environmental variables were selected to include those *thought* to be most significant for species distributions" [my italics].

The use in this analysis of bioclimatic classifications is considered preferable to the above methods since it uses only a small number of variables, which are a) biologically meaningful, b) independent of each other and c) were originally selected to represent the country's overall climate rather than individual components of it. There have been recent advances in bioclimatic and biogeographic analysis, and a programme called BIOCLIM is now available specifically for the analysis of species distributions in relation to climatic variables (see Lindenmayer *et al.* 1991).

The second tenet of this analysis is the simple assumption that the climatic characteristics of areas currently occupied by Choughs can be used to predict the species' "*Potential Climatic Range*" (*PCR*) ie. all areas which share the same climatic characteristics and which are therefore assumed to be climatically suitable for Choughs. This is a similar concept to that of "homoclimes" proposed by Koppen & Thornthwaite (see Lindenmayer 1991). The simplest aim of this approach is to identify areas within the *PCR* in which Choughs a) have become extinct, or b) in which they have never occurred, which can then be used as climatic control areas in the determination of factors involved in determining the bird's absence from these areas.

5.4.1 The *Potential Climatic Range* of the Chough in Scotland

It was shown in section 5.3.1 that the Chough's *Potential Climatic range* (*PCR*) in Scotland is determined by two climatic variables - *extremely mild winters* and *high accumulated temperature*. The distribution of these two variables is shown in Figure 5.5. Each of the variables has a wide distribution in Scotland, but the area of overlap between them, which represents the Chough's current *PCR*, is limited to the coastal areas of south-west Scotland, from Kircudbright in the south to southern Skye/north Argyll in the north west. There is a very close correspondence between this area of overlap and the Chough's former breeding range (see Figure 3.2).

There are only a few areas within the *PCR* which have no historical Chough breeding records. These include Coll, Tiree, South Uist and Barra. The absence of Choughs from these areas does not necessarily refute the assumption that these areas are climatically suitable; it may suggest that they are unsuitable for Choughs in some non-climatic way. As these low-lying islands support few rocky cliffs, it is possible that nest-site availability is limiting here. This hypothesis is considered further in Chapter 6.

Similarly, there is only one area with historical records of breeding Choughs which falls outside the current *PCR* - the Isle of Skye. This may suggest that the *PCR* has contracted southwards in recent times as a result of some climatic change. Being at the north west perimeter of the Chough's British and European range, one might expect the Skye population to be particularly susceptible to small scale climatic changes. Most of the historical Chough records from Skye come from the period 1870-1920. It is possible that Skye was temporarily suitable for Choughs at this time as a result of the 1850-1950 climatic amelioration (Burton 1995) which would have made Skye warmer than it is today. This scenario is discussed further below.

The extent of the Chough's *PCR* in Scotland is much greater than its current breeding range - yet it is reasonable to assume that the whole *PCR* is currently climatically suitable for Choughs. The close correlation of the *PCR* with the Chough's historical distribution suggests that climate change was probably not the cause of the Chough's decline in Scotland (except perhaps in Skye, see above) since the climatic characteristics of areas where extinctions occurred are very similar to those of currently occupied areas. One assumes that both have also shared similar climatic histories in recent times. Even if intermittent climatic events had caused extinctions in some areas of the *PCR* without affecting others, it is still reasonable to assume that the *PCR* is currently climatically suitable for recolonisation. The recent return of a successfully breeding pair of Choughs to a site in Wigtownshire (see Chapter 3) within a part of the *PCR* which had been unoccupied for at least 50 years lends support to this hypothesis.

This simple climatic model enables some predictions to be made about changes to the Chough's *PCR* in the face of climatic change, such as a long run of mild winters or warm summers. If winters were to become milder, then the *PCR* would expand into areas marked with grey squares in Figure 5.5, ie. into inland areas of Argyll, the Central Lowlands, Ayrshire, Dumfries & Galloway, and onto the east coast of southern Scotland, where the winters are currently too severe to support Choughs. On the other hand, if annual accumulated temperatures increased, then the *PCR* would expand into areas marked with grey circles in Figure 5.5, ie. northwards into Skye, the Outer Hebrides and along the west coast of Ross & Cromarty where accumulated temperatures are currently too low to support Choughs. The observed occurrence and extinction of Choughs on Skye during the rise and fall of the 1850-1950 climatic amelioration fits perfectly into this scenario. Burton (1995) has documented the northward range changes of many species of European birds during this period, though insufficient data were available for him to draw any firm conclusions on the Chough. Northward range expansion has been predicted for a range of plant species as a response to global warming (Beerling 1990).

5.4.2 The *Potential Climatic Range* of the Chough in England and Wales.

In England and Wales, it was possible to carry out multivariate Discriminant Function Analyses (DFAs) based on the 75 10 km squares (all in Wales) occupied by Choughs in recent years. These squares exhibit a wider range of climatic characteristics than found within the more restricted Scottish range: their distribution includes Snowdonia, inland mid-Wales and the coastline from north Wales south to Pembrokeshire. In addition, data are also available for these areas on breeding success (through the BTO nest record scheme) which enables some of the predictions of the DFAs to be tested in terms of the species' breeding biology.

The results from these analyses were broadly similar to those obtained from the Scottish analysis. The 1st DFA classified 88.7% of cases correctly, and showed that Chough distribution in Wales corresponds closely with areas of hyperoceanicity and high exposure. It can be envisaged that the product of these two climatic variables is broadly similar to Birse and Robertson's (1970) winter severity parameter (unfortunately not used by Bendelow & Hartnup 1980), although an over-estimation of it, probably erroneously including inland areas with winters that are less than extremely mild.

As in the Scottish analysis, there was a close correspondence between the predicted *PCR* in England and Wales and the Chough's historical distribution (as estimated for the year 1780 by Owen (1989). Again, this leads to the conclusions that a) historical climatic constraints were the same as those that operate on the current range, and b) that it is therefore unlikely that climatic change caused the species' decline. This in turn suggests that the prediction of the *PCR* based on the results of the 1st DFA may be biased by the assumption that the climate of currently occupied areas is optimal for Choughs. This may not be the case if the cause of the species' absence from other parts of the *PCR* is non-climatic, as suggested by the above results.

Hence a 2nd DFA was carried out in which all 10 km squares predicted as occupied in the 1st DFA formed the "occupied" group sample (see Methods 5.2.2), to simulate an analysis based on the species' *PCR*/historical range. A larger sample of "unoccupied" group squares was selected for the 2nd DFA, based on the climatic variables which had the highest discriminative power in the 1st DFA - high levels of oceanicity (O_1) and exposure (X_4 and X_5). It was considered that this new sample would give a more detailed appraisal of the climatic characteristics of the Chough's range over and above the combined role of oceanicity and exposure already identified in the 1st DFA.

As one would expect, the 2nd DFA (based on the new sample of 429 10 km squares), again emphasised the importance of hyperoceanicity and high levels of exposure in determining Chough distribution. These variables had the highest standardised discriminant function coefficients, 0.51 and 0.81 respectively; in addition, Chough distribution in the 2nd DFA showed a positive relationship with minimum temperature (ie. "avoidance" of squares with low values of accumulated temperature (standardised coefficient 0.30)) and a positive relationship with moderate levels of soil moisture (ie. "preference" for these areas (standardised coefficient 0.32)). The predicted distribution of occupied squares is very similar to Owen's (1989) estimation of the Chough's distribution in England & Wales in the year 1780.

Both DFAs "incorrectly" predicted some currently occupied squares in inland Wales as "unoccupied". This could imply that the DFAs gave a conservative estimate of the Chough's *PCR*, or conversely, that these squares are climatically sub-optimal for Choughs. The latter hypothesis may be supported by the fact that a small isolated sub-population present in two "predicted unoccupied" 10 km squares far inland in Denbighshire became extinct in the late 1980s (Roberts & Hawkins 1990), suggesting that this population had low productivity and/or high mortality.

Analyses of Chough abundance and breeding success within the currently occupied range were carried out to test whether these variables shared the expected relationships with climatic gradients that exist within the occupied range. There was a significant positive relationship between Chough abundance within the occupied range and the Discriminant Function (DF) scores obtained in both DFAs (see Results). This strongly suggests that there is a biological basis to the climatic determinants of the Chough's range. The fact that the DF scores obtained in the 2nd DFA were also positively correlated with Chough abundance suggests that the inclusion of the "predicted occupied" squares from the 1st DFA in the sample group of "actually occupied" squares in the 2nd DFA was justified on biological grounds. The DF scores for many squares in Cornwall were higher than those of many currently occupied squares in Wales. This suggests that parts of south-west England are currently climatically more suitable for Choughs than parts of the currently occupied range in Wales.

There was no within-range climatic relationship between Discriminant Function Score and breeding success, perhaps due to the small number of sample 10 km squares for which nest record cards were available. However, a simpler analysis contrasting coastal/inland 10 km squares with hyperoceanic/ euoceanic squares using 2-way ANOVA showed that mean brood size and mean fledging success were significantly higher in hyperoceanic *vs.* euoceanic squares, regardless of whether these squares were at coastal or inland sites (though there was some interaction between oceanicity *vs.* "coastalness" for fledging success). Here again, the implication is that there is a biological basis to the climatic relationships identified in the DFAs, with hyperoceanic areas being characterised by higher breeding success. The interaction with "coastalness" may be related to the milder winters and/or warmer summers of coastal areas, or to some other favourable characteristic of coasts such as the presence of coastal feeding habitats (see Appendix 4).

The DFAs described above identified only those climatic variables which best discriminate between Chough presence/absence within any 10 km square, essentially an analysis of the boundaries of the range. This does not mean that these are the only climatic variables important to Choughs. For example, in both Scotland and Wales, most of the Chough's range is also characterised by moderate levels of soil moisture, but since there are large areas outwith the occupied range sharing this characteristic, it contributes little to the discrimination. The role of such variables within the occupied range can probably only be examined by comparing year-to-year variations in breeding success and/or survival with climatic fluctuations, or by looking at the effects of the variable in question on the biology of important invertebrate prey species (see below).

The analyses based on both Scottish and Welsh distributions gave remarkably similar results. However, there is a problem in interpreting these results due to the fact that winter severity was not used in the classification for England and Wales. To overcome this, I selected *average annual minimum temperature* from the *Climatological Atlas of the British Isles* (HMSO 1952) which I considered to be the climatic variable most closely related to Birse and Robertson's (1970) **winter severity** parameter, and identified the isotherm which most closely matched their *extremely mild winter* category. There was a close correspondence with the 20°F (-6.7°C) isotherm.

From this interpolation it appears that the predictions of the Chough's *PCR* obtained in the DFAs (see Figures 5.6 & 5.7) may over-exaggerate the climatic suitability of inland and upland areas, such as inland Wales and Cumbria: although they fall within Bendelow and Hartnup's O_1 hyperoceanic zone, they do not have extremely mild winters. The DFAs may also under-estimate the extent of the *PCR* along the south and south-east coast of England.

The bioclimatic analyses described above are the only British analyses that I am aware of that utilise bio-climatic variables rather than traditional isometric lines, such as mean minimum January temperate (eg. Turner *et al.* 1988, Hill 1991), to describe climate. The latter approach requires the use of a large number of climatic variables to characterise an area's annual climate. This in turn leads to the need for complex multivariate analyses, such as cannonical correspondence analysis (see Hill 1991, Myklestad & Birks 1993), whose results are presented on a series of axes which provide maximum separation of the data. These axes are, however, essentially hypothetical, and interpreting them in terms of the original data can be difficult and often intuitive. Interpretation of the bioclimatic data using discriminant analysis on the other hand was relatively straightforward and objective.

5.4.3 A Simple Climatic Model

The within-range analyses found that Chough abundance correlates positively with DF score. This is presumably brought about through variation in productivity/mortality in relation to winter severity and accumulated temperatures (hereafter referred to as summer warmth). This is supported by the fact that fledging success was found to be significantly higher in hyperoceanic areas as compared to coastal areas, suggesting that climatic oceanicity rather than coastal areas influences breeding success. Interestingly, Bignal *et al.* (1987b) showed that Chough breeding success is lower on Islay than in the rest of the British range (despite clutch size being largest on Islay). As Islay has relatively cool summers compared to other parts of the Chough's range, this may suggest a positive relationship between summer warmth and Chough productivity. It has also been noted that site occupancy at traditional nest-sites in Wales was lower in inland areas as compared to coastal areas following the severe 1981-82 winter (Bullock *et al.* 1983), suggesting that the harsher winters experienced inland may have increased mortality in these areas.

From the above results a simple climatic model is proposed relating summer warmth to higher Chough productivity and winter severity to higher mortality. The predictions of the climatic model in relation to recently occupied areas are presented schematically in figure 5.13. The model suggests that only in coastal Wales and Cornwall is the climate optimal for Choughs. In Islay and the Inner Hebrides, population size may be limited by the cooler summers experienced in the northern part of the range. In inland Wales, summer warmth and winter mildness are both sub-optimal, and it is proposed that these populations may be "sink" populations, dependent on recruitment from other areas for their continued existence (see Newton 1991 and Verboom *et al.* 1991). The recent extinction of the small sub-population in Denbighshire (see above) supports this hypothesis, as do sightings of Choughs ringed at coastal sites (Bardsey Island) recruited to the breeding population in Snowdonia (Roberts 1985). On a climatic basis alone, Cornwall should also be a "source" area for Choughs, yet it is extinct here. The suggestion is that unfavourable climate was not the cause of the Chough's extinction in south-west England.

It is notable that in both Scotland and England some of the main areas in which the Chough has become extinct, eg. Cornwall and Wigtownshire, appear to be more suitable climatically for the species than many currently occupied areas. This is shown most clearly by the DFAs: many 10 km squares in Cornwall had the highest DF scores of any in England and Wales. This apparent contradiction may imply that other variables correlated with climate may have been responsible for the Chough's extinction in these areas. Owen (1989) and Meyer (1991) both conclude that, following persecution at the turn of the century, it was land use change that caused the final extinction of the Chough in Cornwall, primarily through intensification of use of agricultural land and through abandonment of grazing on coastal headlands and the coastal strip.

I propose that these agricultural improvements were favoured by the very same climatic characteristics which make this area suitable for Choughs - namely warm summers and mild winters, which give a long growing season. One such change is the switch from extensive sheep and beef rearing to dairy farming, a land use inimical to Choughs (see Chapter 7). Such changes would have been slower to come about, or uneconomical, in areas with less favourable climates to the north and west. A similar scenario has been proposed to explain the decline of the Corncrake in Britain (Green 1994). Corncrakes nest on the ground in hay meadows, and mowing destroys a certain proportion of nests and young. The species' range contracted north-westwards during the 20th Century at the same time as farmers switched from horse-drawn mowing methods to faster mowing machines which were more destructive to ground-nesting birds.

Figure 5.13 Climatic scenarios in relation to the productivity of British Chough sub-populations.

	WARM SUMMERS[1] *(high productivity)*	SUB-OPTIMAL[2] SUMMERS *(low productivity)*
EXTREMELY MILD WINTERS[3] *(high survival)*	Coastal Wales Cornwall *(source popns)*	Islay Inner Hebrides *(stable/sink popns)*
SUB-OPTIMAL WINTERS[4] *(low survival)*	(no areas in this category) *(stable/sink popns)*	Snowdonia Inland mid-Wales Cumbria *(sink popns)*

[1] >1650 accumulated day°C above 5.6°C
[2] <1650 accumulated day°C above 5.6°C
[3] mean annual minimum temperature >20°F (6.7°C)
[4] mean annual minimum temperature <20°F (6.7°C)

5.4.4 What is the basis of the climatic relationship?

Having demonstrated that there is a relationship between the Chough's British distribution and climate, this begs the question "How are the negative effects of severe winters and cool summers on Chough mortality and survival brought about?" Below I consider three possibilities: a) habitat availability and land-use b) the physiology of the bird itself and c) feeding ecology.

a) Habitat availability and land use

It is possible that the climatic characteristics of areas occupied by Choughs may also produce characteristic plant communities. Meyer (1991b) found that the majority of Chough feeding sites in his study areas in west Wales occurred in a range of maritime grassland communities; in particular, the National Vegetation Classification *Aira praecox* sub-community MC5 was much used. However, this, and many other communities with maritime distributions, are not restricted to the western coasts of Britain; they also occur along northern and eastern coasts (where Choughs have never occurred). Moreover, most of these communities do not occur in the inland areas of Wales and Islay where Choughs occur. It seems unlikely therefore that there could be a causal relationship between the distribution of these habitats and that of the Chough.

The consequences of climate on land-use are difficult to assess. Distribution maps of agricultural land-uses in atlases of the British Isles (Coppock 1974a, 1974b) provide no obvious examples of land-uses whose distribution corresponds closely with that of the Chough. There is certainly a westerly bias in pastoral agricultural systems (sheep and cattle rearing, plus a high proportion of agricultural land given over to pasture), yet such land-uses have a much wider distribution than is commensurate with their having a role in determining the Chough's very restricted distribution.

There appear to be many parts of Britain which share similar land use characteristics with areas occupied by Choughs, such as Islay and west Wales. This has been noted previously by several authors. For example, Ratcliffe (1990) states that a lack of suitable habitat "can hardly explain the Chough's absence from the [English] Lakes and Southern Uplands [of Scotland]". To these areas I would add a) the flanks of the Pennines in Derbyshire, Lancashire, Yorkshire and Northumberland and b) many coastal, island and upland areas of central, west, north and north-east Scotland as far north as Orkney and Shetland.

It would appear that there are many areas of Britain with similar habitats and land-use characteristics to those currently supporting Choughs, and it is therefore unlikely that some form of climatic determination of the distribution of these two variables *per se* explains the Chough's distribution in Britain. On the other hand, it is quite possible that their distribution within the Chough's *PCR* will determine an area's suitability for Choughs. This is discussed further in Chapter 7.

b) Climatic effects on the bird itself

It has been shown that the North American Black-billed Magpie *Pica pica* and Yellow-billed Magpie *Pica nuttalli* show physiological adaptations to the climates of their allopatric distributions (Hayworth & Weathers 1984). In particular, these authors concluded that "climate acts directly to restrict Black-billed Magpies to the Cold Steppe Dry Climate, rather than ecologically through a secondary effect on food availability". It is possible that a similar physiological relationship could limit the Chough in Britain to areas with extremely mild winters. The only way to answer this question would be to replicate the experimental methods used by Hayworth & Weathers, but as these involved considerable stress to the birds (resulting in the death of three individuals) one could not justify their use on a bird as rare as the Chough.

However, circumstantial evidence suggests that it is unlikely that an interaction between climate and Chough physiology *per se* limits its distribution in Britain. Firstly, it seems very likely that British Choughs can withstand winters that are cooler than "extremely mild", since most Choughs outside the British Isles occur in mountain ranges or continental areas which experience very cold winter temperatures (e.g. -20°C January mean temperature in Ulan Bator, Mongolia). Secondly, whilst there was a positive correlation between maximum and minimum temperatures and body mass of the female of the pair of Choughs whose over-night roost weights were recorded, it seems very unlikely that these fluctuations could have been brought about through physiological effects on the bird itself, since the minimum ambient temperature was only -1°C (recorded on only 3 of 129 nights between November and the end of March).

c) Feeding ecology

The Chough is unusual amongst British corvids in having an almost completely invertebrate diet (see Holyoak 1968). It feeds on cereal grains to some extent, but this appears to be a "less preferred" food item utilised in only a few months of the year (see Chapters 7 & 8). In contrast to the above, it is easy to envisage that the short term fluctuations in Chough mass described above might be due to climatic effects on the availability/activity of the birds' ectothermic invertebrate prey, which by definition are sensitive to ambient temperatures.

The Chough's invertebrate diet may make it difficult for the bird to achieve its daily energy requirement in mid-winter when day-length is shortened. Moreover, it is relatively large for an invertebrate-feeder (c.320-380g.), and it feeds in non-wooded, very exposed non-aquatic habitats, which provide little buffering for invertebrates from climatic extremes

(Curry 1987). These factors suggest a possible mechanism for the climatic determination of the Chough's range, and the connection between invertebrate availability and winter temperatures has been forwarded by several authors in explaining the Chough's westerly distribution (Bullock *et al.* 1983, Cullen & Jennings 1986, Monaghan *et al.* 1989a).

5.4.5 Biology of *Tipula paludosa*

To test some of the above hypotheses, I have investigated the relationship between climate and the growth and mortality of one of the Chough's principle prey items (see Chapter 8), the larva of *Tipula paludosa* (Diptera:Tipulidae), commonly known as the "leatherjacket". It is intended that this species should be seen as a model of the way that climate can affect the biology of an invertebrate which inhabits the upper soil surface (where Choughs obtain most of their food (Goodwin 1986)). My concentration on this species does not imply that it is the most important species in the diet of the Chough, but rather reflects the fact that the biology of this species has been studied in climatically different parts of Britain, and that the species' population dynamics in relation to climate are well known (Meats 1974a). It could be seen as an unpromising species to act as a model since it has a wide distribution throughout the British Isles which bears no relation to the restricted distribution of the Chough. However, I hoped that the study of a common species might provide information about the broader principles of Chough feeding ecology.

Figure 5.11 shows the growth curve obtained for *T. paludosa* larvae on Islay from 1988-89. The curve is fairly typical of the species (see Laughlin 1967): eggs are laid in August/September, from which the first instar larvae hatch c.2 weeks later, when they are at their lowest weight (<3mg). From November to March there is a gradual increase in weight from c.75mg to c.200mg, before a rapid "spring growth phase" in April-May during which body weight increases 2- to 3-fold (Dunnet 1955). Peak larval weight (470.5mg in this study) is achieved in June, and is positively correlated with subsequent fecundity of female imagos (Meats 1974a), thus influencing the size of subsequent generations. From June-July the larvae lay down fat reserves before entering a weak diapause (Laughlin 1967) during which body weight falls. They remain inactive until pupation in late July followed by emergence in August/September.

In Figure 5.12 I have compared the growth curves of *T. paludosa* larvae from three localities - Islay (current study), Glasgow (Barbash 1988) and Northumberland (Laughlin 1967). The Islay samples all come from localities in Birse & Robertson's (1970) *extremely mild winter* bioclimatic sub-division (<20 day°C frost); those from the Glasgow area were taken at Lawmuir, in Birse & Robertson's *moderate winter* sub-division (50-110 day°C frost). The Northumberland samples were taken at a variety of sites, mostly in Bendelow & Hartnup's (1980) *euoceanic* category, whose winter climate is probably similar to Birse & Robertson's *moderate winter* category.

By late-winter/early spring the growth of *T. paludosa* larvae on Islay was approximately six weeks ahead of larvae in Glasgow and Northumberland, bringing forward the rapid spring growth phase from mid-May to early April. This doubling of Tipulid biomass on Islay therefore occurs <u>before</u> Choughs lay their eggs in mid-April, when the male has to take on the extra burden of feeding the female at the nest. The pair's food demand increases dramatically from early May onwards when the chicks hatch, and at this time *T. paludosa* larvae are close to their peak weight. In contrast, if Choughs bred in Glasgow or Northumberland the extra Tipulid biomass resulting from the spring growth phase would not be available until their chicks were approximately half grown. Choughs have the longest fledging period (31-41 days) of any of the medium-sized British corvids (including the larger Rook and Carrion/Hooded Crow), so it seems unlikely that they could breed later to take advantage of the later availability of high leatherjacket biomass in such areas.

It is clear from the bioclimatic models that the winters on Islay will, on average, be milder than those in Glasgow or Northumberland. From Meats' model, it is equally clear that these climatic differences will favour over-winter growth of *T. paludosa* larvae, and that the high accumulated temperatures will facilitate achievement of maximum peak larval weights in the spring/summer, ensuring maximum fecundity and thus a large population size in the next generation. It is assumed that these climatic conditions will likewise favour the growth and survival of many of the other invertebrates which make up the Chough's diet.

Meats' model fails to take into account one important climatic factor that affects overwinter mortality, namely sub-zero temperatures. Freeman (1967) demonstrated experimentally that *T. paludosa* larvae experience 61.5% mortality after 10 hours of exposure to -5.0°C, and 100% mortality following 10 hours exposure to -7.5°C. Barbash (1988) obtained similar results, though in his study larvae showed higher survival at -7.5°C (see Table 5.12). Both studies found that mortality also increased with increased duration of exposure to sub-zero temperatures.

These factors show the dependence of *T. paludosa* on frost-free winters, and the negative effect that severe frosts might have on population size/biomass the following spring. In addition, I have shown that larval mortality is inversely related to body size (see Table 5.10, section 5.3.5), such that the earlier in the autumn/winter that severe frosts occur, the more damaging they are to leatherjacket populations, since larvae are smaller earlier in the autumn/winter. The smaller over-winter size of larvae in Northumberland and Glasgow as compared to Islay on any given date will render them more susceptible to any severe frosts that might occur, a situation exacerbated by the fact that in these areas frosts are a) more frequent, b) more likely to occur earlier in the autumn/winter and c) more likely to be of greater severity (see HMSO *Climatological Atlas*, 1952).

Table 5.12 *Percentage mortality of* T. paludosa *larvae after 10 hours exposure to sub-zero temperatures.*

	Temperature		
	-2.5°C	-5.0°C	-7.5°C
Freeman (1967)	0	61.5	100.0
Barbash (1988)	0	63.0	76.0

It is possible that the inclusion of cold-induced mortality in Meat's model would have increased the percentage of variation in inter-generation population size from the 71.6% which it explained. The implications of the above findings for *T. paludosa* larvae are clear: severe frosts cause high levels of mortality. Indeed, Freeman (1967) noted that *T. paludosa* larvae were less cold-hardy than the other species of Tipulid larvae which he studied; he considered this finding anomalous bearing in mind the species' occurrence in open habitats (pastures) which are unprotected from the effects of frosts (see Curry 1987). Severe and/or extended winter frosts will also reduce the biomass of Tipulids (e.g. see Larsen 1949). However, the consequences of this will not be experienced by Choughs until the following spring when *T. paludosa* larvae begin to feature in the diet (prior to this time the larvae are presumably too small to represent a profitable food item for Choughs. This exemplifies the delay that may occur between climatic events and their impact upon Chough feeding ecology, and highlights the fact that a severe winter may affect breeding success in the following spring in addition to any immediate over-winter effects that it may have.

A third climatic factor important to survival of *T. paludosa* larvae is autumn dryness. Both eggs and newly hatched 1st instar larvae (present in the soil from August to September) are particularly susceptible to desiccation (Milne *et al.* 1965); dry autumns were found to be the prime cause of population crashes in Northumberland (Milne *et al.* 1965). They recorded population crashes when total rainfall in August and September was c.25-45 mm rather than the usual c. 150 mm. Average total rainfall on Islay (1973-1985) in August and September averages 227 mm (data supplied by Mrs. V. Turner, Upper Killeyan weather station, Mull of Oa). Rainfall data for the 13 year period 1973-85 are presented in Table 5.13. Even in the exceptionally dry summer of 1976 Islay had 76 mm of rain in August and September, and in all other years it exceeded 139 mm. Apart from 1976, these conditions would have been very favourable for the survival of eggs and 1st instar larvae. All areas within the Chough's *PCR* in Britain are characterised by moderate to low levels of soil moisture deficit (ie. generally moist-wet conditions). Such areas are likely to be suited to high levels of survival of *T. paludosa* eggs and larvae.

Table 5.13 *Total rainfall recorded in August and September at Upper Killeyan weather station, Mull of Oa, Islay, 1973-85.*

YEAR	TOTAL RAINFALL	
	inches	mm
1973	5.85	148.6
1974	8.70	221.0
1975	9.11	231.4
1976	2.99	76.0
1977	8.77	222.8
1978	12.80	325.1
1979	7.74	196.6
1980	10.60	269.2
1981	11.20	284.5
1982	9.90	251.5
1983	5.50	139.7
1984	7.60	193.0
1985	15.60	396.2

Finally, temperatures greater than 20°C cause mortality of *T. paludosa* pupae, (Meats 1975a, Barbash 1988). The soil can reach such temperatures at the height of summer (July-August). Barbash (1988) recorded pupal mortality of 52% at 20°C and 92% at 25°C, suggesting that the latter temperature is close to the upper limit of the species' tolerance. Ward & Simmons (1990) noted a similar relationship with the Yellow Dung Fly *Scathophaga stercoraria* (Diptera:Scathophagidae) in which temperatures greater than 27°C caused high levels of adult mortality. Most of the Chough's current breeding range and its *Potential Climatic Range* fall within the hyperoceanic zone. The annual temperature curve in this area will be flatter than that of (inland) areas outwith the zone with equivalent levels of accumulated temperature. Thus summer maxima will be lower and the winter minima higher (Birse 1971), giving a long but not intense growing season. The 25°C (80°F) average annual maximum temperature isotherm corresponds closely with the O_1 hyperoceanic zone of the bio-climatic classifications for Scotland, England and Wales (see above). These temperature characteristics will favour the survival of *T. paludosa* pupae and Yellow Dung Fly adults.

It can be seen that the climatic characteristics of the Chough's British range are ideal for the survival and growth of *T. paludosa* larvae, and fecundity of imagos, favouring a high biomass of this species from year-to-year. This may help to resolve the apparent contradiction posed by the fact that this widespread and abundant species forms such an important component of the diet of a bird whose distribution, by contrast, is very restricted.

It should be noted that a population crash of *T. paludosa* larvae brought about by dry weather in August and September would not manifest itself to Choughs until 6-8 months later when they begin feeding on leatherjackets. Such knock-on effects would be even more protracted, if, as in the case of Elaterids (Coleoptera) (wireworms), the Ghost Swift Moth *Hepialus humuli* (Lepidoptera:Hepialidae), and the Cockchafer *Melolontha melolontha* (Coleoptera:Scarabaeidae), all Chough prey items (Bullock 1980, Roberts 1982), the larvae take several years to develop to maturity. In studies of bird breeding biology there is a natural tendency to relate poor breeding success to spring weather events, yet, in Choughs at least, breeding success may be equally dependent upon cumulative weather effects which occurred in the previous autumn/winter, or perhaps even several years earlier.

Climate and weather, as stated by Curry (1987) "have a major role in determining occurrence, life history, phenology and population ecology of grassland [invertebrates]" and it is perhaps not surprising therefore that the distribution of a large specialised invertebrate feeder such as the Chough should be indirectly controlled by climate, through its effects on the ecological requirements of the host of invertebrates which make up its diet. As such it is likely that the climatic characteristics of the Chough's range probably represent a compromise between a range of climatic factors which benefit different invertebrates in different ways.

The climatic model presented above is a simplified representation of a series of complex relationships. Some of these are discussed in relation to a range of invertebrate groups which make up the Chough's diet below. Mild winters enable some species of Carabid beetles (Coleoptera) to over-winter as active larvae rather than as dormant imagos (Thiele 1977); the larvae are nocturnal carnivores, and frosts would presumably inhibit their activity and therefore their growth. Carabid larvae are an important winter and spring food item of Choughs on Islay (see Chapter 8, Warnes 1982) and in Wales (Bullock 1980, Roberts 1982).

Likewise, the over-winter activity of the Yellow Dung Fly *Scathophaga stercoraria* (whose cow-pat inhabiting larvae form an important winter food item on Islay, see Chapters 7 & 8) is closely related to ambient temperatures. Adult flies are killed by the first frosts of winter, and larval development is arrested (Gibbons 1987). Adults emerge following the last spring frosts. On Islay the period between first and last frosts of the winter extends on average from 1st December to 1 April (HMSO *Climatological Atlas* 1952), whereas on the east coast of Scotland, for example at St. Abbs, it extends from 15th Oct to 1st May, a difference of 10 weeks.

Mild winter temperatures may also enable soil hibernating larvae such as dung beetle larvae (*Aphodius spp.*), to hibernate close to the soil surface as noted on Islay (see Chapter 8) where they are more likely to be preyed upon by Choughs. Similarly, Barbash (1988) demonstrated experimentally that *T. paludosa* larvae subjected to sub-zero temperatures migrate downwards through the soil horizon, the depth depending on the duration of exposure and the severity of the "cold". Even at the relatively "high" temperature of -2°C, most larvae moved from a soil depth of 1-3 cms to a depth of 3-5 cms after only 3 hours exposure, increasing to 4-8 cms at a temperature of -4°C. Such a vertical migration would presumably make the larvae more difficult for foraging Choughs to detect/extract.

The climatic analyses described above suggest that Chough distribution is positively correlated with regions with high levels of accumulated temperature. Such areas generally support a more diverse invertebrate fauna than cooler regions. For example, the warmest parts of southern Britain may support over 30 species of ants (Hymenoptera:Formicidae), whereas northern and western Britain supports less than 10 species (Brian 1977). Brian (1977) related these differences to sunlight hours during spring, a climatic parameter which one would expect to be closely correlated with accumulated temperature. Ants are an important food source for Choughs during the summer months (Cowdy 1973), and they feature prominently in the diet in southern parts of the British range (Bullock 1980, Meyer 1991b). However, it should be noted that high summer temperatures may result in mortality of other prey items such as *Tipula paludosa* pupae and adult Yellow Dung flies.

It is possible that the more diverse invertebrate faunas of southern areas may account for the higher fledging success of Choughs in these areas noted by Bullock *et al.* (1983).

Some Chough prey items are completely absent in the north, including the Cockchafer *Melolontha melolontha* (Coleoptera:Scarabaeidae), and the pasture-inhabiting cranefly *Tipula vernalis* (Diptera:Tipulidae). Likewise the higher breeding success of Choughs in hyperoceanic as compared to euoceanic areas (see Results above) may be due to higher invertebrate abundance, biomass or diversity in these areas.

5.4.6 Summary

In summary, the mild winters, warm summers and generally equable climate characterising the Chough's British range provide ideal conditions for invertebrate growth, survival and over-winter activity. The hyperoceanic nature of these areas means that extreme climatic events are rare, and thus invertebrate biomass is probably relatively constant from year-to-year. It was not possible to test this directly during the short duration of this study.

Analysis of the Chough's *Potential Climatic Range* in Britain showed that there are many climatically suitable areas for Choughs outwith the current breeding range. This strongly suggests that climate was not implicated in the decline of the Chough, except on the Isle of Skye, at the north-western periphery of the species' British range. These results are important in terms of Chough conservation in that they identify areas where conservation efforts can be directed to re-establish or consolidate Chough populations - the Wigtownshire coast in Scotland and the Cornish coast in England. A pair of Choughs has already become established in Wigtownshire, and it is recommended that every effort be made to consolidate this "population". Proposals have been made to reintroduce the Chough to Cornwall. In both cases, it will be necessary to demonstrate that the appropriate habitats and land-uses are present to ensure the survival of such populations. This is the subject of Chapter 7.

Ironically, the above analyses suggest that global warming could lead to an expansion of the Chough's range in Britain. However, this might be offset by unfavourable agricultural changes which might also be favoured by a warmer climate, as I have proposed to be the case in the extinctions of the populations in Cornwall and Wigtownshire earlier this century.

Chapter 6

THE INFLUENCE OF NEST-SITE AVAILABILITY ON CHOUGH BREEDING DISTRIBUTION

6.1 INTRODUCTION

Choughs have very specific nest-site requirements, preferring caves, natural arches and cavities in cliffs (Coombs 1986). Such sites may be important in avoiding nest-predation by the larger Carrion/Hooded Crow *Corvus corone*, which Bossema *et al.* (1986) argued has been a major factor in determining the nest-site characteristics of other medium-sized corvids: colonial nesting in Rooks, hole-nesting in Jackdaws, and building of roofed nests by Magpies *Pica pica*. On Islay most Choughs also roost at, or close to, their nest-sites throughout the year (*pers. obs.*). Nest-sites are very traditional and are used year after year; there is evidence of sites in use today that were occupied 100 years ago (Bullock *et al.* 1983, Scot-Skirving 1876 and *pers. obs.*). Male Choughs show greater natal site philopatry than females (Bignal *et al.* 1989); if Greenwood's (1980) hypothesis on sex differences in dispersal applies, the implication is that male Choughs are defending a physical resource in order to attract a mate, which in this case is represented by the nest-site or feeding territory. Competition for nest-sites amongst Choughs on Islay is high. When one or both members of a pair disappear from a site they are rapidly replaced. I have recorded one instance of an incoming male apparently killing the resident male at a nest-site during the breeding season. All these facts point to the importance to Choughs of the possession of a nest-site, preferably within a suitable feeding habitat.

Suitable nest-sites are presumably abundant in the mountain ranges inhabited by Choughs throughout Eurasia, or, as in western Europe, along rocky coastlines. On the Iberian peninsula, calcareous rocks provide abundant caverns and pot-holes formed by water erosion in karst systems, and friable clay cliffs along dry water-courses are also important (Garcia Dory 1989, Soler 1989, Zuniga 1989). However, in Britain Choughs very rarely use natural nest-sites inland (here taken as sites >2 km from the coast): none of the 95 sites found in the 1986 survey of Scotland were at natural inland sites (see Monaghan *et al.* 1989a), and Bullock *et al.* (1983) reported that all inland nests found in Wales in the 1982 survey were at man-made sites (quarries or mine-shafts). It would appear that the cliffs in inland areas of Britain occupied by Choughs rarely provide the large crevices and caves required for nesting. Where natural nest-sites are absent, Choughs will readily use human artifacts such as quarries, mine-shafts, lighthouses, bridges and disused buildings (Cabot 1965, Goodwin 1986, Warnes 1983).

In the previous chapter, it was suggested that the absence of Choughs from some areas within its *Potential Climatic Range (PCR)* might be due to the absence of suitable nest sites in these areas. In this chapter I assess the influence of nest-site availability on Chough breeding distribution and abundance in coastal areas of Scotland within the Choughs *PCR*. This was achieved by devising an index of nest-territory availability based on observed nest-site use on the Rhinns of Islay (see below). This index is used to predict the number of "nest-territories" that other areas can theoretically support. The aim of this work is to assess the influence of nest-site availability on the past and present distribution of the Chough in Scotland. Provision of artificial nest-sites is a cheap and effective way of increasing the size of breeding populations (see Newton 1994), and has been shown to be effective for Choughs (Bignal and Bignal 1987, Cross *et al.* 1993). One of the main objectives proposed for Chough conservation action in the RSPB's *Chough Species Action Plan* is to "increase the Chough population [in the U.K.] by encouraging the provision of suitable nesting sites and feeding areas... to encourage the expansion of range along the western coasts of the British Isles. It is important to identify those areas where this type of work is appropriate.

In Appendix 4, I use a similar analysis to assess the influence of habitat on nest-site occupancy on the Rhinns of Islay, and compare this with nest-site occupancy on the nearby islands of Jura and Colonsay.

6.2 METHODS

6.2.1 Calculation of nest-territory index

It was not possible to identify and count all potential nest-sites in the field. Many sites are mere crevices in cliffs, and to find and classify all these would have involved climbing and surveying all cliffs in the study area, which, even if possible, would have been exceptionally time consuming. Instead a nest-territory availability index was calculated, based on the number of nesting pairs per unit length of cliff (high or low) or per nesting feature on the Rhinns and Oa of Islay during the 1986 census (Monaghan *et al.* 1989a). Since the index is based on the number of nesting pairs, it is not strictly speaking an index of nest-site availability, so I have called it a "nest-territory index". Nevertheless, since the index is calculated from two areas with a high nesting density of Choughs (Monaghan *et al.* 1989), it is likely that there was much competition for nest sites in these areas (see above), and thus a high proportion of the available nest-sites were likely to have been occupied. As such, the nest-territory index is broadly equivalent to a nest-availability index. Four categories of nest-site were identified: caves, natural arches, high cliff (> 10 m) and low cliff (≤ 10 m). No distinction was made regarding Monaghan *et al.*'s "gulley" category, which was lumped with cliffs. Subsequent personal observations also clarified the nest-site types of some of their "unknown" sites. The analysis was restricted to coastal areas because inland cliffs are rarely used for nesting (see above). Artifact nest-sites were excluded from the analysis since their use in Scotland is a comparatively recent phenomenon and is restricted to Islay (Warnes 1983). In the analysis I wanted to look at a wide range of areas over a long historical period.

The following measurements were taken from the Ordnance Survey 1:25 000 "Pathfinder" series maps of the Rhinns and Oa of Islay: 1) The total length of both high and low sea-cliffs measured to the nearest 0.1 km (only cliffs given the cliff symbol were measured, steep embankments and low rock were excluded; cliff height was assessed from map contours). 2) The total coastline length measured to the nearest 1.0 km. 3) The total numbers of caves and natural arches, counted from written-names (ie. "cave") rather than their map symbols (caves - one small open circle, arches - two), since the open circle symbols were not always clearly visible, and could easily be confused with the "rock" symbol. Groups of caves or natural arches written as "caves" or "natural arches" were arbitrarily assumed to represent two cases of the feature in question. Only features within 2 km of the coast were measured (see above).

From these data a conversion factor relating the number or length of each feature on the map to the number of known nesting-pairs found in each feature on the Rhinns and the Oa of Islay was calculated (Table 6.1). For each climatic control area (see below), the number/length of the same nest-site features was counted/measured on the appropriate OS Pathfinder 1:25000 map. Applying the conversion factors obtained in Table 6.1, the number of potential nest-territories in each control area was calculated. That these sites actually existed was confirmed by a foot survey of the coastlines of Islay and Jura.

Table 6.1 *Calculation of nest-territory conversion factors based on data from the Rhinns and Oa regions of Islay (Monaghan* et al. *1989a, pers. obs.), (natural and coastal nest-territories only).*

Nest-site	Number of prs of Choughs using feature	Number/length of feature/s in study area	Conversion factor (terrs/feature)
Caves	13	79	0.165/cave
Natural Arches	7	14	0.500/arch
"High" cliffs	19	12.0 km	1.583/km
"Low" cliffs	18	22.9 km	0.786/km

6.2.2 Climatic control areas

The importance of climate in controlling the distribution of the Chough in Britain was established in Chapter 5. Hence in this analysis, nest-site availability has only been investigated in areas which are a) within the Chough's potential climatic range or b) have some history of breeding by Choughs (ie. probable or definite breeding records, see Chapter 3 and Appendix 1; "Chough occupancy" as used here refers only to breeding records). In fact, the overlap between the two is almost complete (except in Skye and St. Abbs, Berwickshire, see Chapter 5), and here on they are treated synonymously. These areas were divided into two categories: 1) *climatically "identical" areas*, with climates identical to that of the Rhinns and Oa of Islay, ie. extremely mild winters (<20 day°C frost), high (for Scotland) annual accumulated temperatures (> 1375 day°C) and potential water deficits of 0-50mm (see Birse & Dry 1970 and Birse & Robertson 1970), and 2) *climatically "non-identical" areas*, with climates similar to, but not identical to Islay (being generally either slightly wetter, cooler or less mild).

The phrase "climatically identical" is used here with respect to the bioclimatic sub-divisions used in Birse & Dry's and Birse & Robertson's classifications. Since each sub-division represents a range of values, there will be small differences between sites within the same sub-division, thus they are not absolutely identical. In the "climatically identical" category I have included two areas which have slightly *drier* climates than Islay (parts of the Rhinns of Galloway and Burrow Head, both in Wigtownshire, with potential water deficits of 50-75mm) since many other parts of the Chough's British range (eg. coastal Wales) share this characteristic, and the difference is probably beneficial rather than detrimental (see Discussion).

6.3 RESULTS

6.3.1 Areas climatically identical to Islay

The predicted number of nest-territories in the 1986 survey areas and in areas climatically identical to Islay are given in Table 6.2, the total for all these areas being c.336. The areas from which the nest-territory index was calculated, the Rhinns and Oa of Islay, not surprisingly have occupancy rates close to those predicted since these were the areas from which the index was calculated. Territory occupancy on Colonsay is close to that predicted. In contrast, both Jura and the Elsewhere region of Islay, which have the highest number of potential nest-territories (75.5 and 47.2) have very low occupancy rates (8.5% and 4.0% respectively).

Of the areas within the *PCR* that were unoccupied in 1986, it is notable that all those with more than 10 predicted nest-territories have some history of Chough occupancy (except Ardnamurchan, for which no historical data are available). For most of these areas the predicted number of nest-territories is consistent with general impressions of historical population size given in the literature (Chapter 3). The remaining areas with less than 10 predicted nest-territories, have either no history of Chough occupancy - South Uist, Barra, Muck, Coll, Tiree and Morar, or are areas where the Chough was never abundant - Ayrshire (Paton & Pyke 1929) and Cumbria (MacPherson and Duckworth 1886).

6.3.2 Areas not climatically identical to Islay but with some history of Chough occupancy

The predicted number of nest-territories in areas not climatically identical to Islay, but with some history of Chough occupancy are given in Table 6.3. The areas fall into two categories: 1) those to the north of Islay which have equally mild winters to Islay, but cooler and/or wetter summers, and 2) the Berwickshire coast on the south-east coast of Scotland, which has less-mild winters, but equally warm and drier summers. All areas have relatively high numbers of predicted nest-territories, which are higher than the general impressions of historical Chough population sizes given in the literature (small populations on Skye, Mull and possibly Lismore Island, possibly 3-4 pairs on Eigg and at St. Abbs, Berwickshire, and none on Rhum or Canna) (see Chapter 3 and Appendix 1).

Table 6.2 *Predicted number of coastal Chough "nest-territories" (natural sites only, see Table 6.1) and site occupancy in 1986 in areas climatically "identical" to Islay.*

Locality	Total coast length (*km*)	Total cliff length[1] (*km*)	Caves (*n*)	Arches (*n*)	Predicted nest-terrs (*n*)	Breeding pairs in 1986[2] (*n*)	Per cent territory occupancy (*prs/terrs*)
Areas occupied by breeding Choughs in 1986							
Colonsay[3]	62.0	5.9	6	0	7.2	6	83.1
Jura	136.6	40.9	113	27	75.5	3	4.0
Islay-Rhinns[4]	68.5	24.5	27	11	33.1	37	111.7
Islay-Oa[4]	24.2	10.3	52	3	23.8	20	83.9
Islay-Elsewhere[4]	99.5	13.9	80	42	47.2	4	8.5
Areas unoccupied in 1986, but with previous breeding records							
R. of Mull/Iona[5]	87.0	11.0	4	2	14.5	0	0
Mull of Kintyre[6]	53.2	11.4	31	3	21.0	0	0
Ayrshire[7]	57.0	5.9	8	0	5.9	0	0
E. Wigtownshire[8]	134.5	20.4	54	1	28.3	0	0
W. Wigtownshire[9]	52.0	11.4	51	0	21.2	0	0
Kircudbright	134.7	9.7	13	4	14.4	0	0
Cumbria[10]	123.3	7.0	1	0	7.6	0	0
Areas with no Chough breeding records, past or present							
South Uist	147.5	1.3	2	0	1.3	0	0
Barra	106.0	5.3	0	2	8.5	0	0
Isle of Muck	12.0	5.8	9	1	7.3	0	0
Morar[11]	90.5	1.4	9	0	2.6	0	0
Ardnamurchan[12]	36.5	12.5	7	0	16.8	0	0
Coll	54.9	1.4	4	0	1.7	0	0
Tiree	55.0	1.3	10	5	5.9	0	0

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[1] High + low cliff summed (for this table only).

[2] Data from Monaghan *et al*. 1989a.

[3] Including Oronsay.

[4] For details of regions on Islay see Monaghan *et al*. 1989a.

[5] Ross of Mull (west of easting NM 50), and Iona.

[6] South of northing NR 20.

[7] South of Ayr.

[8] Excluding Rhinns of Galloway, east of line between Sandhead and Stranraer.

[9] Rhinns of Galloway, west of line between Sandhead and Stranraer.

[10] West of easting NY 20.

[11] Coast west of easting NM 70 and north of northing NM 70.

[12] Coast from Kilchoan to NM 6070.

Table 6.3 *Predicted number of coastal Chough "nest-territories" (at natural sites only, see Table 6.1) and their occupancy in 1986 in areas* <u>*not climatically "identical"*</u> *to Islay, but with some history of Chough occupancy.*

Locality	Total coast length (*km*)	Total cliff length[1] (*km*)	Caves (*n*)	Arches (*n*)	Predicted nest-terrs (*n*)	Breeding pairs in 1986[2] (*n*)	Per cent territory occupancy (*pairs/terrs*)
Extremely mild winters (as Islay), summers cooler and/or wetter than Islay							
Skye	520	137.2	64	18	191.4	0	0
Rhum	42	20.0	96	7	40.4	0	0
Eigg	25	18.8	9	1	26.7	0	0
Canna	25	12.0	26	1	16.0	0	0
Lismore I.	35	22.5	4	0	19.3	0	0
Mull[3]	180	61.0	37	6	90.1	0	0
Winters less mild than Islay, summers warmer and drier than Islay							
Berwickshire[4]	48.6	20.0	12	2	25.8	0	0

[1] High + low cliff summed (for this table only).
[2] Data from Monaghan *et al.* (1989a).
[3] All west coast (excluding Ross of Mull and Ulva) from Loch Spelve in south to Tobermory in north.
[4] East of easting NR 70.

6.4 DISCUSSION

The availability of suitable nest-sites may be one factor which limits the size of breeding populations of Choughs within occupied areas, as it does in other corvids such as the Magpie (Birkhead 1991) and Carrion Crow (Charles 1972), and in many raptor species (Newton 1979). Absence of potential nest-sites may render otherwise suitable areas unoccupiable. The fact that Choughs use land features for nesting (cliffs, caves and arches) which are specifically marked on OS maps has enabled a map-derived index of nest-territory availability to be determined, which would have been much more difficult for a species with less specific nesting habits.

The index was calculated from the two areas of Scotland which were found to have the densest breeding populations of Choughs during the 1986 Scottish survey, the Rhinns and the Oa of Islay (Monaghan *et al.* 1989a). Since the index was determined from areas where habitat/land-use are evidently favourable to Choughs, predictions on nest-territory availability in other areas probably represent relatively high estimates. Even so, there were stretches of cliffs (particularly on the Oa) where few nest-sites and/or pairs were present, thus the index predictions are not necessarily maximum estimates.

The Islay-based nest-territory index predicts that there will be one Chough territory for every 6 caves, 2 arches, 1.3 km of "low cliff" or 0.6 km of "high cliff" marked on OS 1:25 000 Pathfinder series maps. Perhaps the greatest bias involved in the calculation of this index is the influence that differences in geology, rock stratigraphy and erosion have upon the likelihood that cliffs will provide suitable nest crevices. The differing geologies of the two areas from which the index was calculated (Rhinns - igneous gneisses and epidiorites, Oa - metamorphic quartzites and slates) should help to reduce such bias, but it is clear that sandy or friable cliffs will probably provide far fewer sites than suggested by the index. The index for caves and arches should be less susceptible to such bias. A foot survey of the coasts of Islay and Jura showed that the map-predicted nest-sites did actually exist.

A second bias concerns the consistency with which the nest-site features were mapped in the field by the original OS surveyors. In the Islay study areas some nest-sites are in caves or arches which are not marked on the 1:25 000 maps. However, in all such cases ($n = 4$) another potential nesting feature was present. It is likely that this source of bias will have a negligible effect on the predicted number of nest-territories when dealing with such large areas as those being studied here. The important factor in this analysis is how many pairs of nesting Choughs are present. To overcome such biases it would be necessary to carry out a detailed ground survey, which was beyond the scope of this study.

The index of nest-territory availability is useful in providing estimates of potential population size, both past and present, based on physiographic features alone. The index could perhaps have been improved by calculating the original conversion factor only from occupied areas within the Oa and Rhinns of Islay (see Appendix 4). This would have the effect of increasing the number of predicted potential nest-territories, and as stated earlier, this indicates that the index-based predictions used here are not maximum estimates.

6.4.1. Nest-site availability in areas climatically identical to Islay

The influence of nest-territory availability on Chough abundance in areas climatically identical to Islay was examined in relation to whether the area 1) is currently occupied, 2) has a history of Chough occupancy but where it is now absent or 3) has no history of Chough occupancy. Past and present status in localities mentioned below is given in Chapter 3, with individual records given in Appendix 1.

a. Areas currently occupied by Choughs.

The three currently occupied areas outwith the Rhinns and Oa of Islay, namely Colonsay, Jura and the Elsewhere region of Islay, have contrasting numbers of potential nest-territories. Colonsay, an island with a coastline twice as long as that of the Oa of Islay, has a very small breeding population of Choughs, only 6 pairs. However, the predicted number of nest-territories is only 7, thus the size of the Chough population here is almost certainly constrained by natural nest-site availability, a result of the island's generally low-lying coastline. A different picture emerges for Jura and the Elsewhere region of Islay, both of which provide an abundance of potential nest-territories (75 and 47 respectively, much greater than the totals for the Rhinns and Oa of Islay, for example), yet the number of breeding pairs of Choughs (3 and 4 respectively) is very low, giving occupancy rates of only 4% and 8.5%. The majority of potential coastal nest-territories in both regions occur in areas dominated by blanket bog and wet acidic grassland, which serves as rough pasture for Red Deer *Cervus elaphus*, deer "forest" being the main land-use. The inevitable conclusion is that these habitats and/or land-uses are not favourable to Choughs (see Chapter 7 and Appendix 4). It should be noted that the Elsewhere region of Islay has a relatively large inland-breeding population of Choughs - but here the birds nest in artifact sites (mostly derelict barns/cottages), adjacent to habitats/land-uses that are very different from those in the coastal areas considered above.

b. Areas formerly occupied in which Choughs were absent in 1986.

These provide control areas in which to look at the causes of the Chough's decline in Scotland, especially in relation to land-use/habitat change over time. Clearly these areas were once more suited to Choughs than they are now. It is assumed that the decline was not due to changes in the number of available nest-sites, since by their nature it is unlikely that natural sites will become any more or less available with time. [Tourism might be considered to have led to increased disturbance, but within the Chough's *PCR* in Scotland few areas suffer intense tourist pressure (except perhaps the island of Iona, and the very tip of the Mull of Galloway). Moreover, in other parts of Britain Choughs shows remarkable tolerance of humans - such as on the cliffs at St Govan's Head in Pembrokeshire where Choughs continue to nest on some of the most popular rock-climbing sea cliffs in Britain (R. Haycock *pers. comm.*)].

Table 6.2 shows the predicted number of nest-territories in previously occupied areas; all the estimates are consistent with the subjective impressions given in the literature on the Chough's past abundance in each area. It would appear that the Chough's stronghold outside Islay was the coast of Wigtownshire, particularly the Rhinns of Galloway. The county as a whole may have supported 50 Chough territories. Smaller populations existed in nearby Kircudbright and Ayr, in which, however, potential nest-territories are scarce (14.5 and 6 respectively) relative to the length of their coastlines. The Mull of Kintyre may have supported c.21 territories. Interestingly, the Cumbrian coast has a very low number of potential nest-territories (7.6); this may explain the fact that the species was never common there (MacPherson & Duckworth 1886), and that it has been absent from this area for most of this century (Bullock *et al.* 1983), despite its proximity to the Isle of Man.

Of all the above areas, the Wigtownshire coast provides the most promising control area in which to assess land-use/habitat changes in relation to Chough abundance (see Chapter 7), since it is climatically identical to Islay (but for its drier summers, see below) and nest-sites are not limiting here. It is clear that simple provision of nest-sites is likely to be of little benefit to Choughs in Wigtownshire.

c. Areas with no history of Chough occupancy.

These areas are all characterised by low nest-site availability. This is particularly notable in Coll and Tiree which both have climates identical to the Rhinns of Islay, and coastlines almost equally long, but Coll has only 2 predicted nest-territories, and Tiree only 6. For islands with coastlines of c.55 km this represents a very low availability of nest-territories. This alone is likely to explain the absence of breeding Choughs from these islands (though see below). The same applies to South Uist, Barra, Muck and the west coast of Morar, all of which have less than 10 potential nest-territories. Only the Ardnamurchan peninsula has a substantial number of potential nest-territories (17), but unfortunately there are no historical records from this area to indicate whether Choughs were ever present. However, the habitats/land-uses on the Ardnamurchan peninsula are similar to those of other unoccupied areas such as Jura and the Elsewhere region of Islay (see above), ie. wet heath/bog and wet acid grassland supporting deer forest, and these appear to be unfavourable to Choughs.

It should be borne in mind that the lack of Choughs on some of the more remote islands may also be due to their distance from the nearest Chough populations. It was established in Chapter 4 that the open sea acts as a barrier to Chough dispersal, thus colonisation of, and recruitment to islands such as Coll, Tiree and the Outer Hebrides is always likely to be slow. The situation may be aggravated by the fact that dispersal to these areas will not be aided by the prevailing south westerly wind direction.

6.4.2. Nest-site availability in areas not climatically identical to Islay, but with a history of Chough occupancy.

Many areas formerly occupied by breeding Choughs are climatically identical to currently occupied localities, suggesting both that climate has always been an important factor in determining the Chough's distribution in Britain, and that climatic change was not the cause of the many local extinctions which took place over the last 150 years (Chapter 5). However, some formerly occupied Scottish areas have slightly different climates from those currently occupied (see Table 6.3). All these areas have relatively high levels of nest-territory availability, particularly Skye and Mull (excluding the climatically identical Ross of Mull and Iona) which provide 520 and 180 potential nest-territories respectively, yet historical records suggest that they have only ever supported relatively small populations of Choughs. Whilst this may have been due to unfavourable land-use, as described above for Jura and the Elsewhere region of Islay, this appears not to be the case, particularly on Skye, where the mosaic of heath, rough and improved pasture with pastoral land-uses closely resembles many occupied parts of Islay (see Chapter 7). The same is true of Eigg, Canna and parts of Lismore island, yet there is a paucity of records from these sites also.

The lower than expected occupancy of these islands in former times may indicate that they are climatically "sub-optimal" for Choughs. Compared to Islay and former breeding areas in south-west Scotland, these islands all have lower levels of accumulated temperature, and some also have wetter summers. Despite a much greater availability of potential nest-territories in the northern islands of the Inner Hebrides, it was the localities further south in Scotland (Islay, Kintyre, Wigtown, Ayr & Kircudbright) which supported the largest populations of Choughs. The populations north of Islay are at the extreme northern limit of the species' range in Britain, but their scarcity here was clearly not due to an absence of potential nest-sites. Likewise, a brief look at OS maps of those areas further north which have no breeding records at all (eg. Sutherland, the Outer Hebrides, Orkney and Shetland) confirms that potential nest-sites are also abundant here. These findings support the hypothesis that the northern limit of the Chough's range in Scotland has a climatic basis (see Chapter 5).

The Berwickshire coast differs from all the above sites in having winters that are less mild than Islay's. It is also slightly drier than Islay (potential water deficit >75mm), thus its summer climate may have been more favourable for Choughs than Islay's. However, its less-mild winters may account for the absence of a large breeding population here, despite the presence of 26 potential nest-territories.

6.4.3 Summary

This analysis emphasises the importance to breeding Choughs of the juxtaposition of suitable habitat/land-use and nest-sites, within climatically favourable zones (categorised Type A areas in Figure 6.1). This was also shown in the analysis of nest-site occupancy presented in Appendix 4. The occurrence of all three factors in any one area appears to be a matter of chance, but two of these factors, nest-site availability and habitat, can be manipulated by man. The current pattern of Chough occupancy within climatically suitable areas of Scotland in relation to nest-site availability and habitat/land-use is presented schematically in Figure 6.1.

Figure 6.1 Schematic representation of the relationship between nest-site availability and habitat/land-use within the Chough's *Potential Climatic Range* in Scotland.

	Abundant nest-sites	*Few nest-sites*
Favourable habitat/ land-use	TYPE A Rhinns of Islay Oa of Islay	TYPE B Inland Islay Colonsay Coll Tiree
Unfavourable habitat/ land-use	TYPE C Jura Elsewhere coast, Islay Mull of Kintyre Rhinns of Galloway	TYPE D Kirdcubright? Ayrshire?

In other areas, it will be important to tailor the conservation measures to the needs of that area. In Type B areas (see Figure 6.1) nest-site availability appears to be limiting Chough numbers. It is interesting that where Choughs are present in these areas they have adapted to nesting in artifact sites such as ruined buildings and mine-shafts. In 1986 27% of the Islay breeding population nested in such sites (Monaghan *et al.* 1989a), enabling birds to exploit inland areas where natural nest-sites are scarce. This also enables nesting in some coastal areas with soft-geology, eg. dunes, which are good feeding habitat (see Chapter 7 and Appendix 4), but which provide no nest-sites. Indeed, the population pressure in dune areas may have initiated barn-nesting on Islay. The provision and maintenance of artifact sites is a simple and effective way to increase population size in such areas.

Steps in this direction have already been taken on Islay and Colonsay by Bignal & Bignal (1987), who, funded by Scottish Natural Heritage and the World Wide Fund for Nature, have encouraged the use of barn nest-sites by renovating and maintaining derelict buildings. However, this is a relatively expensive method which limits its potential for increasing population size. A less expensive alternative has proved successful in mid-Wales (see Cross *et al.* 1993), where artificial nest boxes and nest-ledges have been erected at coastal sites and at inland mines in areas where natural nest-sites were scarce. Nineteen per cent of the mid-Wales population used this type of artificial site in 1993. As a result of the current study, a nest-box was erected in a Type B area on Colonsay in 1994 by RSPB staff. The area had supported no breeding Choughs for at least 5 years (following the closing up of a former nest-site in a building). A pair of Choughs occupied the site in the spring of 1995, and bred successfully (see Appendix 1).

In Type C areas, positive management would require wholesale changes in habitat/land-use. Whilst this is much harder to achieve than provision of nest-sites, it may now be possible under the auspices of the Argyll Islands Environmentally Sensitive Area (ESA) (including Coll, Tiree, Mull, Iona, Colonsay, Jura and Islay) and the Stewartry ESA (which includes the Wigtownshire coast). Moreover, the new E.C. Special Protection Area (SPA) scheme provides a framework for positive management of Chough populations which was difficult to achieve with the SSSI mechanism. As the Rhinns and Oa of Islay are soon to be designated as SPAs for Choughs (and other species), there is now a real opportunity for positive habitat management for this species.

Needless to say, Type D areas are those where conservation measures are least likely to succeed, and should not be attempted at the expense of measures in Type B and C areas.

Chapter 7

HABITAT SELECTION BY CHOUGHS AND THE INFLUENCE OF LAND-USE

7.1 INTRODUCTION

This study aims to assess habitat use, habitat selection and patch use by Choughs, with particular reference to the influence of land-use, and the potentially detrimental effects of afforestation. The Rhinns of Islay was chosen as the main study area as it has traditionally supported a large and stable population of Choughs. In 1986 just before the start of this study, 56 pairs of Choughs were present at nest-sites on the Rhinns (Monaghan *et al.* 1989a).

The Rhinns supports a wide range of habitats an, ideal situation for the study of habitat selection. The scope of some previous studies of habitat use by Choughs (Bullock 1980, Roberts 1983, Meyer 1991) may have been limited to some extent by the small range of habitats present in their study areas, and by the relatively small sizes of their study populations. Land-use on the Rhinns is also varied, including crofting, and sheep, beef and dairy farming, each of which incorporates variable proportions of arable farming. In the early 1980's approximately 11 km^2 (15.3%) of the southern half of the Rhinns peninsula (south of national grid northing NR 63) was planted with alien conifers (mostly Sitka Spruce *Picea sitchensis*), adjacent to the nest-sites of approximately 30 breeding pairs (*c.* 10% of the UK population). Prior to this the whole peninsula had been virtually tree-less, and the loss of 11 km^2 of potential Chough foraging habitat was perceived as a possible threat to this nationally important breeding population. Unfortunately, all afforestation occurred before this study began, so it was not possible to look at "before and after" effects. Instead, observations were made on habitat selection by Choughs and the influence of land-use upon these habitats, so that the possible impact of afforestation could be assessed retrospectively.

Habitat use and habitat selection were assessed in a thirty nine 1 km^2 study area on the south Rhinns by making detailed observations of habitat and patch use by feeding birds on a transect route passing through the area. This provided data on habitat selection at the population level over a wide geographic area. The disadvantage of this method is that it is based on the implicit assumption that if a bird is seen feeding in a habitat, then it is necessarily a "good" feeding habitat. This is not always the case, as shown for the Woodpigeon (see Murton 1965). Thus additional observations were made on the foraging behaviour of a sample of breeding pairs. These had the advantage that they could be related to the size of the feeding range and the breeding success of the pairs involved. Particular attention was paid to the influence of grazing regime, and sward height and ground bareness on the use of improved pasture fields by the study pairs.

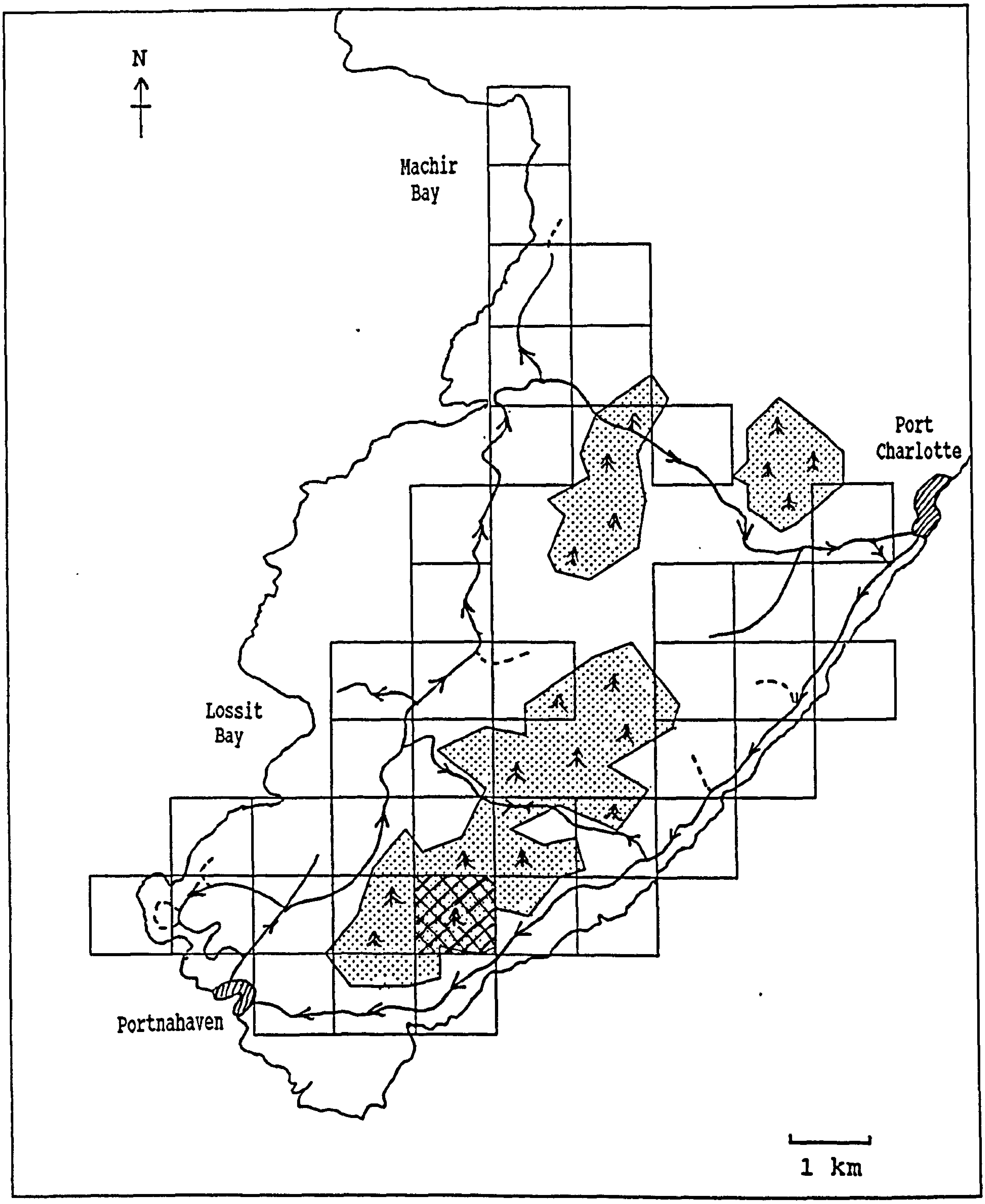
Finally, comparisons of historical land-use were made between the Rhinns of Islay and the Rhinns of Galloway from 1915-85 to assess the impact of land-use change on chough populations. The Rhinns of Galloway was selected for comparison since it was identified in Chapter 5 as being almost identical climatically to the Rhinns of Islay, but it is an area in which Choughs became extinct this century (see Chapter 3 and Appendix 1).

7.2 METHODS

7.2.1 Rhinns transect

Habitat use by the Chough on the Rhinns was assessed by means of a transect which followed a circular road route starting and ending at Port Charlotte (see Figure 7.1) and which passed through a wide range of habitats. Thirty nine 1 km squares clearly visible from roads/vantage points along the transect route comprised the survey area. Transects were carried out between January and December 1988. The survey method consisted of a) driving along the road and stopping at regular intervals to scan all habitats for feeding Choughs using 10x40 binoculars, and b) walking to vantage points within each square and scanning for Choughs using binoculars and mounted 20-60x telescope (if necessary). The use of a vehicle ensured that the observer was able to move quickly from one vantage point or road-side viewing point to the next without duplication of observations. Transects were carried out on days with wind < force 5 with good visibility 2-4 times per month - until a total of "bird feeding observations" (BFOs, see below) in excess of 100 was achieved. No observations were made in September or November, and only 60 and 79 BFOs were obtained in January and March respectively due to bad weather (see Table 7.3). The transect included all or part of the territories of c.30 breeding pairs of Choughs, and was within the foraging range of a non-breeding flock (of up

Figure 7.1 The Rhinns transect route, showing 1 km squares surveyed and afforested areas.



Main roads and tracks used on transects

Main paths used on transect

NB. Hatched square = not a survey square to 45 birds) from a communal roost just outside the study area (see Still 1989).

The main bias involved in this method is that of differential visibility of Choughs in different habitats. However it is thought that the impact of this is minimal with Choughs since they very rarely feed in tall vegetation (Bullock, 1980). In this study, 89.5% of 1266 feeding observations were in vegetation ≤5cm (see section 7.3.2).

Observations

To ensure independence of data, the aim was to obtain one bird feeding observation (BFO) only for each Chough seen on a transect. Once found, Choughs were observed using a mounted 20-60x telescope until their first successful feeding event was seen (as indicated by swallowing, which in Choughs is an obvious backwards movement of the head as prey is rapidly tossed from bill to oesophagus). For each BFO the following were recorded: habitat, sub-habitat (see below), patch, feeding behaviour, colour-rings (if possible) and vegetation height estimated to the nearest 1 cm (using Chough tarsus length (c.6 cm) as a guide). If birds were in a flock, the process was repeated for each individual. Birds in flight or not feeding were not included in the analysis. The location of feeding birds was noted on a 1:10 000 OS map on which the whole study area had been divided into individually numbered fields or compartments.

Observations were made at distances of up to 1 km from the birds, which ensured that their behaviour was not influenced by the observer's presence. Observations were facilitated by the Chough's intentness when feeding, which generally made them oblivious to the observer. However, in the spring and summer Curlews and gulls alarm-calling when I left the vehicle frequently alerted feeding Choughs, and sometimes put them to flight, but they usually quickly resumed feeding when it was obvious that no avian predator was present. This had the effect of slowing down the observer's progress, but this was counter-balanced by the longer day-length at this time of year.

The presence of colour-ringed birds on the Rhinns was valuable in determining the age of birds, and in highlighting possible duplication of records. In 1988 at least 6 breeding pairs had one member of the pair ringed, and it was usually possible to identify individuals in non-breeding flocks (which contain a relatively high proportion of ringed birds) by their ring combinations.

The movements of flying birds were carefully followed in order to avoid duplication of sightings on transects. As most breeding pairs were territorial throughout the year they were unlikely to be seen twice on a transect. Non-breeding flocks ranged more widely, which increased the chance of duplicate records. However there were no records of colour-ringed birds being sighted twice on the same transect. If a degree of duplication did occur with unringed birds, duplicate sightings would probably have been several hours apart, ensuring a degree of independence in the data.

Habitat classification

A habitat survey of the Rhinns of Islay Site of Special Scientific Interest (SSSI) (which covers most of the current study area) was carried out by the Nature Conservancy Council in 1987/88; their successors Scottish Natural Heritage (SNH) kindly made these data available for this study. Areas outwith the SSSI (primarily agricultural land) were surveyed by the author. The habitat classification used was the Nature Conservancy Council/Royal Society for Nature Conservation Habitat Classification (NCC/RSNC 1984), in which habitats are mapped in the field to a resolution of approximately 0.1 ha using 1:10 000 OS maps.

It was necessary to use additional "sub-habitat" and "patch" categories to classify all Chough feeding sites. These were sub-ordinated to the "main-habitat" categories within which they occurred to ensure compatibility with the NCC/RSNC classification. A four-level hierarchy was devised:

First level - NCC/RSNC first/second level *main-habitat* categories
Second level - *sub-habitats* of the main-habitats (see text)
Third level - *habitat-patches* within the above categories
Fourth level - *dung patches* within the above categories (see text)

For each of the 39 1 km squares in the study area habitat and sub-habitat data were recorded at each intersection on a grid overlay representing 50 m intervals (total 400 points in each 1 km square, resolution = 0.25 ha). The total land area surveyed was 3239 ha (less than

39 km^2 due to the fact that some squares also included sea and open water). Habitat changes were noted on the monthly transects (these were restricted to changes between improved pasture and arable crops). Some similar habitat categories with few or no Chough BFOs were subsequently aggregated, eg. woodland and scrub were lumped together under the wood category. Details of aggregated categories are given in Table 7.1.

Whilst rock outcrops and field boundaries (walls, fences, field headlands, earth-banks) are first level habitat categories in the NCC/RSNC classification, in this study they are treated as patches within habitats, as the habitat within which these features occurred appeared to influence their use by Choughs (see Results).

Sub-habitats

Choughs on Islay make extensive use of improved pastures (ie. ploughed, reseeded and/or fertilised). There is only one category for improved grassland in the NCC/RSNC classification; to assess the importance of pasture age this category was sub-divided into 3 age classes (see Table 7.1). Reseeds (RS) are fields ploughed and reseeded less than one year before observations were made. Recently improved pastures (RIP) are fields reseeded >1 and <5 years ago; old improved pastures (OIP) are approximately 5-15 yrs old. Improved pastures older than 15 years are considered to have reverted to semi-improved permanent pasture (SIPP) (NCC/RSNC 1984). Rank pasture (RP) is improved pasture (usually quite old) that has been left ungrazed for some time, and so become tussocky with a high vegetation profile and usually infested with a range of weed/ruderal species. This category does not include pastures grown for silage crops (improved pasture), nor with "rough pasture", a term usually applied to unenclosed hill grazings (which would equate with Dry heath/acid grassland or Wet heath/acid grassland in this classification).

Table 7.1 *Comparison of habitat categories used in this study with those of the NCC/RSNC habitat classification*

		This Study	
NCC/RSNC Habitat[a]		Main-habitat (variable name)	Sub-habitat (variable name)
A.	Woodland and scrub[b]	Wood & scrub (WOOD)	
B.1.1	Acid grassland unimproved	Permanent pasture (PP)	
B.1.2	Acid grassland semi-improved	Semi-improved perm. pasture (SIPP)	
B.1.3	Acidic marshy grassland	Marshy Grassland (MG)	
B.2.1	Neutral grassland unimproved	Permanent pasture (PP)	
B.2.2	Neutral grassland semi-improved	Semi-improved perm. pasture (SIPP)	- Sand/moss pasture
B.4	Improved grassland	Improved pasture (IP)	- Reseed (RS) - Recently improved (<5yrs) pasture (RIP) - Old improved (5-15yrs) pasture (OIP) - Rank pasture
C.1	*Pteridium* (bracken)	Bracken (PT)	
D.1	Dry heath	Dry heath (DH)	
D.2	Wet heath	Wet heath (WH)	
D.5	Dry heath/acid grassland mosaic	Dry heath/acid grass mosaic (DHAG)	
D.6	Wet heath/acid grassland mosaic	Wet heath/acid grass mosaic (WHAG)	
E.1	Bog[c]	Bog (BOG)	
E.2	Flush[d]	Flush (FLUSH)	
F.1.2	Tall fen	Tall fen (TF)	
G.1	Open water	Open water (OW)	
H.6	Sand dune	Dunes (DUNES)	- Fore dune (FD) - Grey dune (GD) - Dune pasture (DP)[e] - Yellow dune (YD)
	Beach (sand)[f]	Beach (sand) (BS)	
H.8.4	Coastal grassland	Coastal grassland (CG)	
J.1	Arable	Arable (ARAB)	- Oats (AO) - Barley (AB) - Stubble turnips (AST) - Potatoes (AP)
J.2	Boundary	Boundary (BDRY)	- Dyke/earth bank (DK) - Fence (FC) - Wall (WL)
J.3	Building	Built up (BU)	

(cont. over)

(Table 7.1 continued)

[a] NCC/RSNC first-level habitats not listed did not occur in the study area (except rock outcrops, see text).
[b] Woodland includes all NCC/RSNC woodland and scrub categories.
[c] Includes all bog categories.
[d] Includes acid and basic flushes.
[e] Equivalent to NCC/RSNC dune grassland category
[f] Not classified under the NCC/RSNC system.

The NCC/RSNC classification of semi-natural grasslands is sub-divided into various categories of acidity and level of improvement, which it was not possible to determine for each Chough feeding observation in this study. These grassland categories have therefore been aggregated under the simpler main-habitat headings of *Permanent Pasture (PP)* (not ploughed or artificially fertilised in recent times (c.25 years)) or *Semi-Improved Permanent Pasture (SIPP)* (permanent pasture which appears to have been artificially fertilised or possibly surface-seeded in the recent past, giving it a greener appearance than permanent pasture).

The dune main-habitat was divided into four sub-habitats corresponding to the RSNC/NCC classification. These categories represent increasing dune maturity/stability: fore dune is mostly unstable sand with few colonising plants (typically *Elymus farctus*); yellow dune is partially stabilised ridges of sand dominated by marram grass *Ammophila arenaria* with some herbs; grey dune is stable ridges of sand almost completely vegetated, which on Islay included a high per cent cover of moss and lichen, producing a very short "sward"; dune pasture (dune grassland in the NCC/RSNC classification or machair) is similar to a semi-improved permanent pasture due to its high nutrient status, and supports a wide variety of herbs on a stable (usually flat) consolidated sandy substrate.

Habitat-patches

A habitat-patch was defined as a small area of habitat (<0.1 ha) which differed from the dominant habitat within the field or map compartment in which the BFO was recorded. It is termed a "habitat-patch" to differentiate it from a "dung-patch" (see below). Typical examples included rock outcrops in improved fields, or patches of permanent pasture within heath/acid grassland mosaics. Sheep carcases were treated as habitat-patches. Habitat-patch names which are not self explanatory are described below:

Moss pasture (MP) - a moss-dominated pasture with sedges *Carex* dominant in the sward on a peaty substrate. The end result of heavy grazing of wet heath or bog.

Sand/moss pasture (SD/MP) - as MP, but on a mixed peat/wind blown sand substrate, therefore less acidic. Occurs on raised plateaux near Lossit Bay where wind blown sand from the bay has mixed with what were originally heath/bog habitats. Now heavily grazed, and classed in the NCC/RSNC survey as Semi-improved Neutral Grassland (SIPP in this classification).

Rock/PP, Rock/CV, and Rock/moss, - these three categories all describe rock outcrops which are by their nature an admixture of micro-habitats. The suffix gives an indication of which micro-habitat the Choughs were feeding in (PP = permanent pasture, CV = heather *Calluna vulgaris*). However, where this wasn't easily seen, or the birds used a mixture of habitats, rock outcrops were given the default description of rock/pp - rock with permanent pasture, since most rock outcrops are surrounded by an area of permanent pasture inaccessible to farm machinery.

Dung-feeding - Dung-feeding posed a particular classification problem as animal dung constitutes a patch which may be super-imposed on another patch. As it was considered important to record the habitat or patch type within which the dung occurred, "dung-patches" were added as a fourth level to the habitat classification. Three examples of how this would be recorded are given below:-

Habitat classification hierarchy level	Hierarchy description	Example BFO #1	Example BFO #2	Example BFO #3
First level	Habitat	PP	IP	IP
Second level	Sub-habitat	-	RIP	OIP
Third level	Habitat-patch	-	ROCK/PP	-
Fourth level	Dung-patch	SHEEP-D	SHEEP-D	COW-D

Analysis of habitat use and habitat selection

Habitat use is presented as the total number of BFOs in each habitat by season. Habitat selection was determined by comparing the distribution of habitats in the study area with the distribution of Bird Feeding Observations made on transects using a Chi^2 goodness of fit test. However, a Chi^2 test only shows whether or not there is a difference between observed and expected distributions, and not which habitats are more or less preferred. Therefore I have used the method of Neu *et al.* (1974) to evaluate habitat preference, non-prefernce and avoidance. This method uses confidence limits based on Bonferroni's adjustment, which reduces the value of P at which significance is accepted to $P < 0.05/n$, where n is the number of repeated tests (in this case habitat types). The resulting confidence limits will be wider for each multiple estimate than for an estimate of only one parameter (see Kirk 1982). A significant preference or avoidance is indicated by expected values not included in the 95% confidence limits of the observed values. The method depends on feeding observations being independent. This requirement is met since each BFO represents one feeding observation per bird per transect date.

Analysis of patch use

It was not possible to determine % cover for the wide range of patch types used by Choughs due to their exceptionally fine resolution in some cases (almost to Chough bill probing level). This means that it was only possible to quantify patch use and not patch selection. Analysis of patch use on a monthly basis showed that some were only used in one month; in order not to under-estimate such short-lived phenomena, patch use data are presented on a monthly rather than a seasonal basis. An annual summary of patch use within main-habitats/sub-habitats was represented by the total number of BFOs in each patch-type as a percentage of the total number of BFOs for that habitat/sub-habitat in each month, and summed. This weighting process allows for the different number of BFOs made in different months. It should be noted that where birds were not feeding in a patch within a habitat, habitat-patch was coded the same as the dominant main-habitat or sub-habitat. In this way, it is possible to compare the number of observations in the dominant habitat with the number in patches of other habitats.

7.2.2 Study pairs

The aim of this work was to determine habitat use and foraging behaviour during the breeding season and how this is influenced by land-use. The study of nesting pairs provides an opportunity to assess how habitat availability within a finite area surrounding the nest influences the pair's foraging behaviour and breeding success. It is assumed that the extra burden placed on the breeding pair by the need to provision their chicks will "force" them to feed in the most profitable habitats, based on quantity and/or quality of food. It also enables the responses of individual pairs to short term changes in their environment, such as sward height in feeding fields, to be examined.

A sample of 5 pairs (A - E) was chosen for intensive observations during the breeding season. Study pairs were selected on the basis of differences in land-use and habitat adjacent to their nest-sites. Pair A nested in a non-agricultural area dominated by permanent pasture and bog. Pairs B and C nested in agricultural environments, one with an extensive grazing regime (pair B) and one with an intensive (dairy farming) grazing regime (pair C). Pairs D and E nested in agricultural environments adjacent to dune systems.

Making continuous observations on study pairs was made possible by the fact that the birds could be easily located as they returned to the nest at 30-45 minute intervals. It would have been preferable to use radio transmitters on these birds, but this was not possible at the time of this study due to the sensitivities of the local human population, which required that field work be as unobtrusive as possible. In the first year of the study, I found that it was very difficult to make continuous observations on pairs nesting on coastal cliffs, as these birds frequently disappeared from sight below the cliffs. Thus, only pairs using barn sites were used for this part of the study. Current data suggest that there are no differences in Chough breeding success at barn *vs.* natural sites (Bignal *et. al.* 1987b), so there should be no bias in using these study pairs.

Each pair was observed for a minimum of two 2-hour study periods per week from mid-April (egg-laying) to mid-June (fledging), whereupon the families became more difficult to locate. Most observations were made from vantage points located far enough away from the nest-site (*c.* 0.5 km) to ensure that the birds ignored the observer, or from a vehicle. Following birds on foot was usually impossible, and keeping one's distance was the most reliable way to obtain continuous observations. A tripod-mounted high magnification telescope (20-60x) was used at all times. Study period observations commenced on the quarter hour after the birds were first located. During each study period the location, behaviour and habitat of both members of the pair was recorded at one minute intervals. To overcome the problems of non-independence of these foraging data, observations were also classified by "foraging trip" and "foraging trip habitat". A foraging trip was defined as a trip made by either or both birds away from the nest which included at least one feeding event. Feeding events in different habitats on the same foraging trip were classed as "foraging trip habitats", which were considered independent of each other. Thus if birds were recorded feeding in two habitats on one foraging trip this would represent two foraging trip habitats, and these formed the basis of most analyses on habitat and patch use by the study pairs. Total amount of time spent feeding in each habitat is also used for some analyses.

Habitats were classified using the same classification as described above (section 7.2.1). Habitat availability within a 1 km radius of each nest was measured. If part of a field used by the pair fell outside the 1 km radius, then the extra-limital part was added to the total area. A 1 km radius was chosen as this was the maximum foraging distance which encompassed all feeding observations of the pair which foraged least far from the nest (Pair B). Moreover, beyond this distance it was difficult to maintain continuous observations on the feeding birds whilst simultaneously keeping the nest-site in view (in order to observe the return leg of the foraging trip). As pair B bred successfully within their "1 km range", this was used as the basic sampling unit for comparison of habitat - availability between pairs. If birds foraged outwith this range then the suggestion is that the habitats within 1 km of the nest were not adequate, or that those used outwith this radius were preferred to those within it. The total feeding range of each pair was calculated using Kenward's (1987) convex polygon method.

Treatment of habitat and patch use was the same as described above for the Rhinns transect, except that fields within a 1 km radius of the nest were also classified according to whether or not they were grazed and, for pairs B and C, by what kind of stock. Habitat selection was determined for main habitats using the methods of Neu *et al.* (1974) described in section 7.2.1. Where sample sizes were restrictive, habitat selection data are presented as Jacobs Preference Indices D (Jacobs 1974). This index is given by:

$$D = \frac{(r - p)}{(r + p - 2rp)}$$

where r is the proportion of foraging trip habitats and p is the proportion of the 1 km range occupied by that habitat.

Vegetation height was measured in a range of habitats and fields with differing grazing regimes close to the nest-sites of pairs B and C to assess the influence of vegetation height and ground bareness on field use. To compare the difference in growth of silage fields with and without goose grazing, sward height was measured in fields around the nest-site of pair C (all goose-grazed) and in a silage field without goose grazing at Octofad Farm (grid reference NR 222549) on the Rhinns. No geese were recorded feeding in this field or general area during the course of the study. The altitude and distance from the sea were similar to that of the goose grazed fields. Vegetation height was measured using my own adaptation of Castle's (1976) sward stick. This version of the sward stick comprised a square plastic plate (20 cm x 20 cm, mass 70 g) with a central circular collar fitted over a graduated aluminium pole which is held in a vertical position with its base on the ground. The plate slides freely down the pole and was gently spun as it was released from approximately 20 cm above the vegetation. When the plate comes to rest on the vegetation, height is read off the graduated scale. Ground bareness (0 = not bare, 1 = bare) was recorded vertically below the 4 corners of the plate, giving total bareness scores of 0-4 for each measurement. Measurements were taken at a minimum of 25 random points along a transect across each field or compartment.

7.2.3 Land-use on the Rhinns of Islay and the Rhinns of Galloway

Land-use in these two areas was compared using data from the *Ministry of Agriculture, Fisheries and Food* annual agricultural census, in which areas of crops and numbers and type of livestock on each farm holding are collated on a parish basis. I have compared the parish of Kilchoman on the Rhinns of Islay, which covers the entire Rhinns transect area, with the parish of Portpatrick on the Rhinns of Galloway. The Portpatrick parish lies on the west coast of the Rhinns of Galloway, and references in the literature suggest that there were at least 7 breeding pairs in the vicinity of Portpatrick at the turn of the century (see Appendix 1), though they had probably become extinct by 1920.

The total areas of the main agricultural land classes were compared. These were improved pasture, rough pasture, arable crops (potatoes, swedes and others), and cereal crops (oats, barley or a mixture of the two). Improved pasture was sub-divided into hay/silage and grazed. There were large differences in the proportion of rough grazing between the two parishes, so comparisons have been restricted to improved habitats only - pasture, silage/hay, arable and cereal etc. These are presented as proportions of the total area of improved land within each parish, rather than as a proportion of all land.

The numbers of the main grazing animals (sheep, beef cattle, dairy cattle and horses) were converted into standard "livestock units" for analysis. Livestock units are based on the feed requirements of stock, one unit being that required to maintain a mature 625 kg Friesian cow and the production of a 40-45 kg calf, and 4,500 litres of milk at 36 g/kg of butterfat (source: MAFF 'Definitions of Terms used in Agricultural Business Management', see Chadwick 1990). A dairy cow represents 1.00 livestock unit, a beef cow 0.65 units, yearling cows and calves (both dairy and beef) 0.65 and 0.34 units respectively, horses 0.80 units, sheep (medium weight) 0.08 units, and lambs 0.04 units. The use of livestock units thus takes into account differences in body size of livestock giving a rough indication as to what proportion of land is given over to the maintenance of each type of livestock. Census returns prior to 1935 did not differentiate between beef and dairy cattle, so the livestock units for these two types of stock were averaged for these years, and presented as 'all cattle'.

7.3 RESULTS

7.3.1 Habitat use and habitat selection on the Rhinns

The % cover of the main habitat categories on the Rhinns transect in each season is shown in Table 7.2. The three main pasture types (improved, semi-improved and permanent pasture) totalled 34.2-34.4% of the land area. Bog covered 16.3%, and woodland 15.0%. Most of the woodland comprised recently planted forestry plantation 0.5-1.5m high. The four heath and heath/acid grassland mosaic categories totalled 18.5% of the land area. The areas of each category remained the same throughout the year apart from a change of 0.2% from improved pasture to arable in June.

Table 7.2a *Comparison of the area of different habitats in the study area (total 3239 ha) and the number of winter Bird Feeding Observations (BFO) in these habitats (n=326). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974).*

Habitat	% habitat	no. of BFOs	% BFOs	Confidence limits of % BFOs lower	upper
Arable	.6	1	.3	-.5	1.1
Bog	16.3	0	.0	.0	.0
Beach	.3	3	.9	-.5	2.4
Coastal grass	1.8	0	.0	.0	.0
Dry heath/Acid grass	5.1	2	.6	-.6	1.8
Dunes	2.6	41	12.6	7.5	17.6
Flush	3.0	0	.0	.0	.0
Improved pasture	19.6	253	77.6	71.3	84.0
Marshy grassland	6.8	2	.6	-.6	1.8
Permanent pasture	8.5	22	6.7	2.9	10.6
Semi-imp'd perm. past.	5.8	2	.6	-.6	1.8
Wet heath	7.2	0	.0	.0	.0
Wet heath/Acid grass	6.0	0	.0	.0	.0
Wood/scrub	15.0	0	.0	.0	.0

Table 7.2b *Comparison of the area of different habitats in the study area (total 3239 ha) and the number of spring Bird Feeding Observations (BFO) in these habitats (n=427). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974).*

Habitat	% habitat	no. of BFOs	% BFOs	Confidence limits of % BFOs lower	Confidence limits of % BFOs upper
Arable	.6	0	.0	.0	.0
Bog	16.3	0	.0	.0	.0
Beach	.3	0	.0	.0	.0
Coastal grass	1.8	4	.9	-.3	2.2
Dry heath/Acid grass	5.1	17	4.0	1.4	6.6
Dunes	2.6	138	32.3	26.1	38.5
Flush	3.0	0	.0	.0	.0
Improved pasture	19.6	241	56.4	49.8	63.0
Marshy grassland	6.8	0	.0	.0	.0
Permanent pasture	8.5	15	3.5	1.1	6.0
Semi-imp'd perm. past.	5.8	4	.9	-.3	2.2
Wet heath	7.2	2	.5	-.4	1.4
Wet heath/Acid grass	6.0	6	1.4	-.2	3.0
Wood/scrub	15.0	0	.0	.0	.0

Table 7.2c *Comparison of the area of different habitats in the study area (total 3239 ha) and the number of summer Bird Feeding Observations (BFO) in these habitats (n=279). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974).*

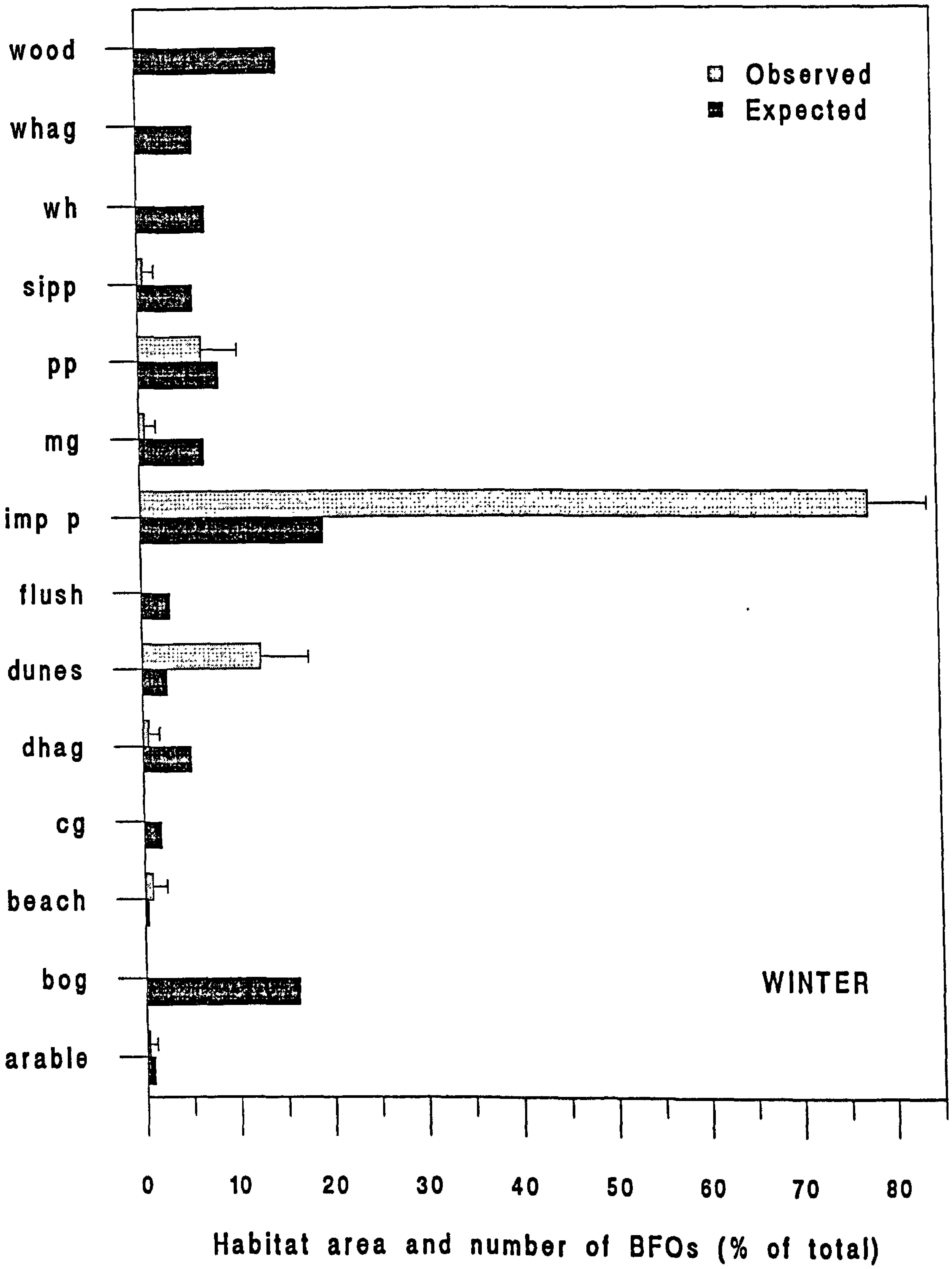
Habitat	% habitat	no. of BFOs	% BFOs	Confidence limits of % BFOs lower	Confidence limits of % BFOs upper
Arable	.8	0	.0	.0	.0
Bog	16.3	11	3.9	.7	7.1
Beach	.3	0	.0	.0	.0
Coastal grass	1.8	2	.7	-.7	2.1
Dry heath/Acid grass	5.1	35	12.5	7.1	18.0
Dunes	2.6	57	20.4	13.8	27.1
Flush	3.0	0	.0	.0	.0
Improved pasture	19.4	89	31.9	24.2	39.6
Marshy grassland	6.8	0	.0	.0	.0
Permanent pasture	8.5	52	18.6	12.2	25.0
Semi-imp'd perm. past.	5.8	27	9.7	4.8	14.5
Wet heath	7.2	0	.0	.0	.0
Wet heath/Acid grass	6.0	6	2.2	-.2	4.5
Wood/scrub	15.0	0	.0	.0	.0

Table 7.2d *Comparison of the area of different habitats in the study area (total 3239 ha) and the number of autumn Bird Feeding Observations (BFO) in these habitats (n=275). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974).*

Habitat	% habitat	no. of BFOs	% BFOs	Confidence limits of % BFOs	
				lower	upper
Arable	.8	27	9.8	4.7	15.0
Bog	16.3	10	3.6	.4	6.9
Beach	.3	4	1.5	-.6	3.5
Coastal grass	1.8	4	1.5	-.6	3.5
Dry heath/Acid grass	5.1	15	5.5	1.5	9.4
Dunes	2.6	39	14.2	8.1	20.2
Flush	3.0	0	.0	.0	.0
Improved pasture	19.4	114	41.5	32.9	50.0
Marshy grassland	6.8	7	2.5	-.2	5.3
Permanent pasture	8.5	38	13.8	7.8	19.8
Semi-imp'd perm. past.	5.8	10	3.6	.4	6.9
Wet heath	7.2	2	.7	-.7	2.2
Wet heath/Acid grass	6.0	5	1.8	-.5	4.1
Wood/scrub	15.0	0	.0	.0	.0

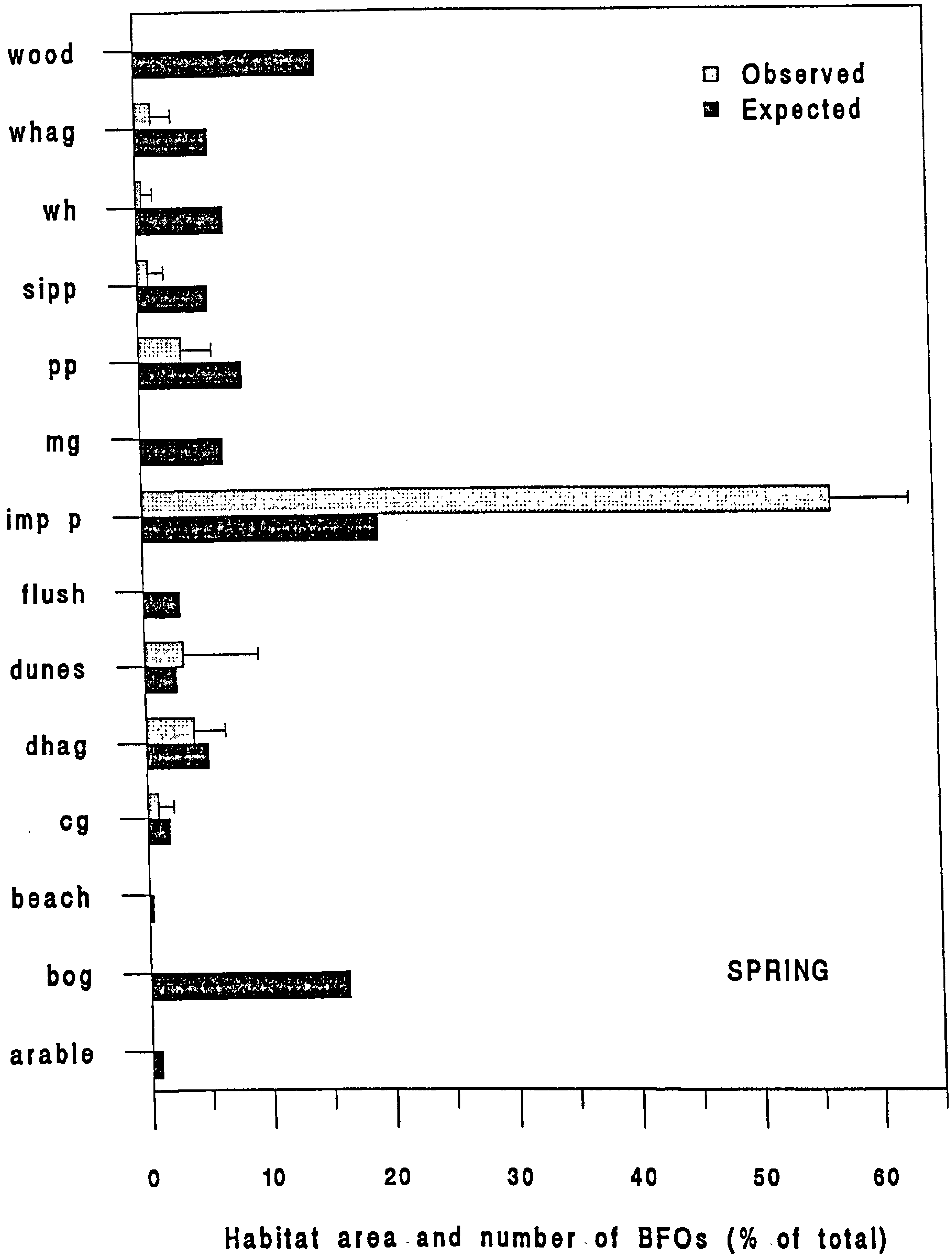
A total of 1307 bird feeding observations (BFOs) were made on the transects. Their distribution by season and habitat is shown in Table 7.2. Habitat use and selection are presented graphically in Figure 7.2. The observed habitat distribution of BFOs differed significantly from the expected habitat distribution in the study area in all seasons (winter: $Chi^2 = 791.3$, df=13, $P < .001$; spring: $Chi^2 = 1311.2$, df = 13, $P < .001$; summer: $Chi^2 = 409.5$, df = 13, $P < .001$; autumn: $Chi^2 = 608.0$, df = 13, $P < .001$). Habitats used significantly more or less than expected fall outside the 95% confidence limits for the observed values of habitat use by feeding birds (Figure 7.2; Neu *et al.* 1974). Those used more than expected are referred to here as "preferred" habitats, those used less than expected as " non-preferred". Habitats not used at all are referred to as "avoided habitats". Six main-habitats were avoided by feeding Choughs - woodland/scrub and flush plus 4 habitats of limited extent for which data are not presented (dry heath, bracken *Pteridium aquilinum*, tall fen and built up areas). Four habitats were significantly non-preferred or avoided in all seasons - wet heath, wet heath/acid grassland, bog and marshy grassland. The remaining habitats were significantly preferred in at

Figure 7.2a Distribution of winter Bird Feeding Observations (BFOs) in relation to distribution of different habitats in the Rhinns study area. The habitat areas (total 3239 ha) are labelled "Expected" and the BFOs (n=326) are labelled "Observed".



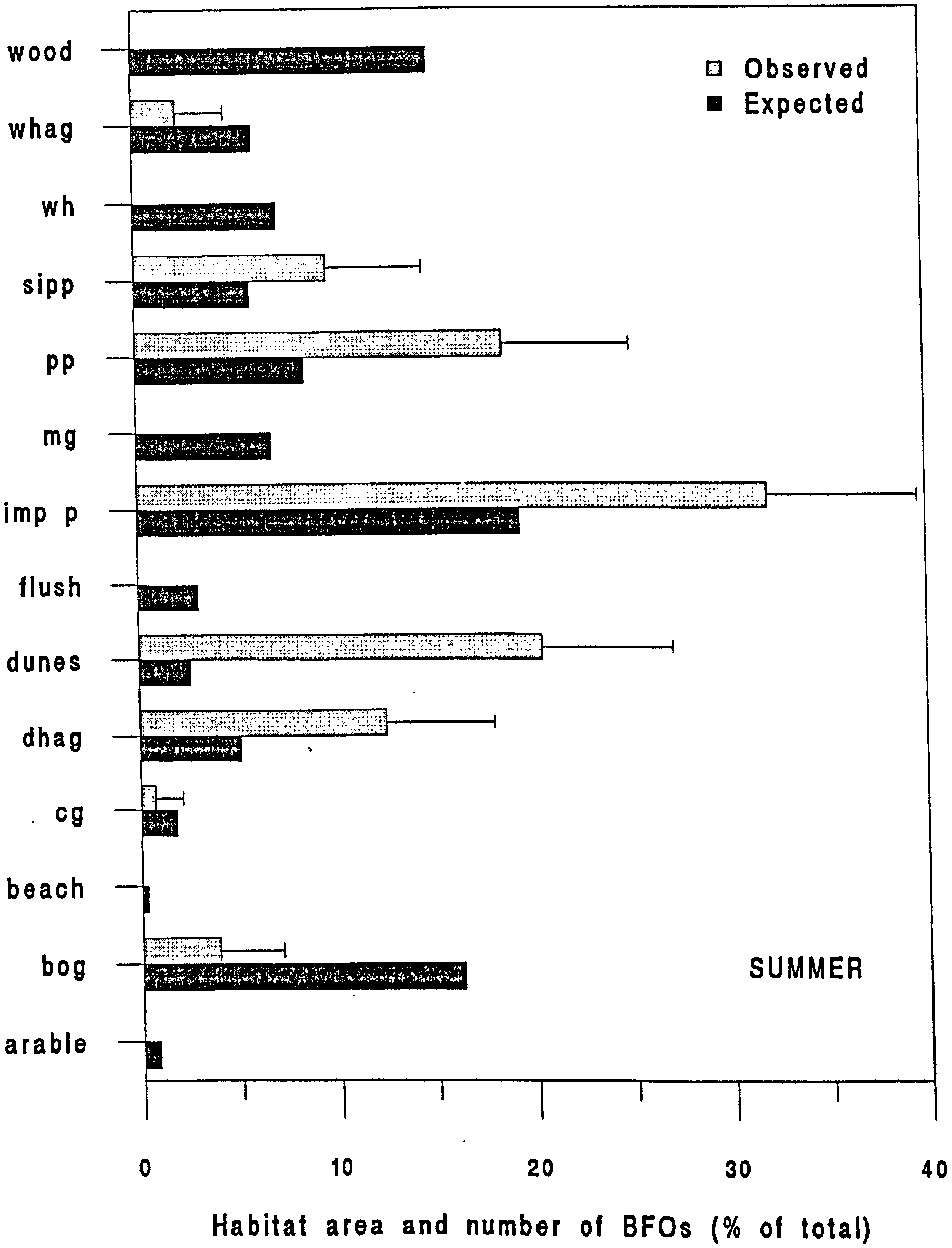
For explanation of habitats see Table 7.1. The 95% confidence limits for the observed values were calculated according to Neu et al. (1974).

Figure 7.2b Distribution of spring Bird Feeding Observations (BFOs) in relation to distribution of different habitats in the Rhinns study area. The habitat areas (total 3239 ha) are labelled "Expected" and the BFOs (n=427) are labelled "Observed".



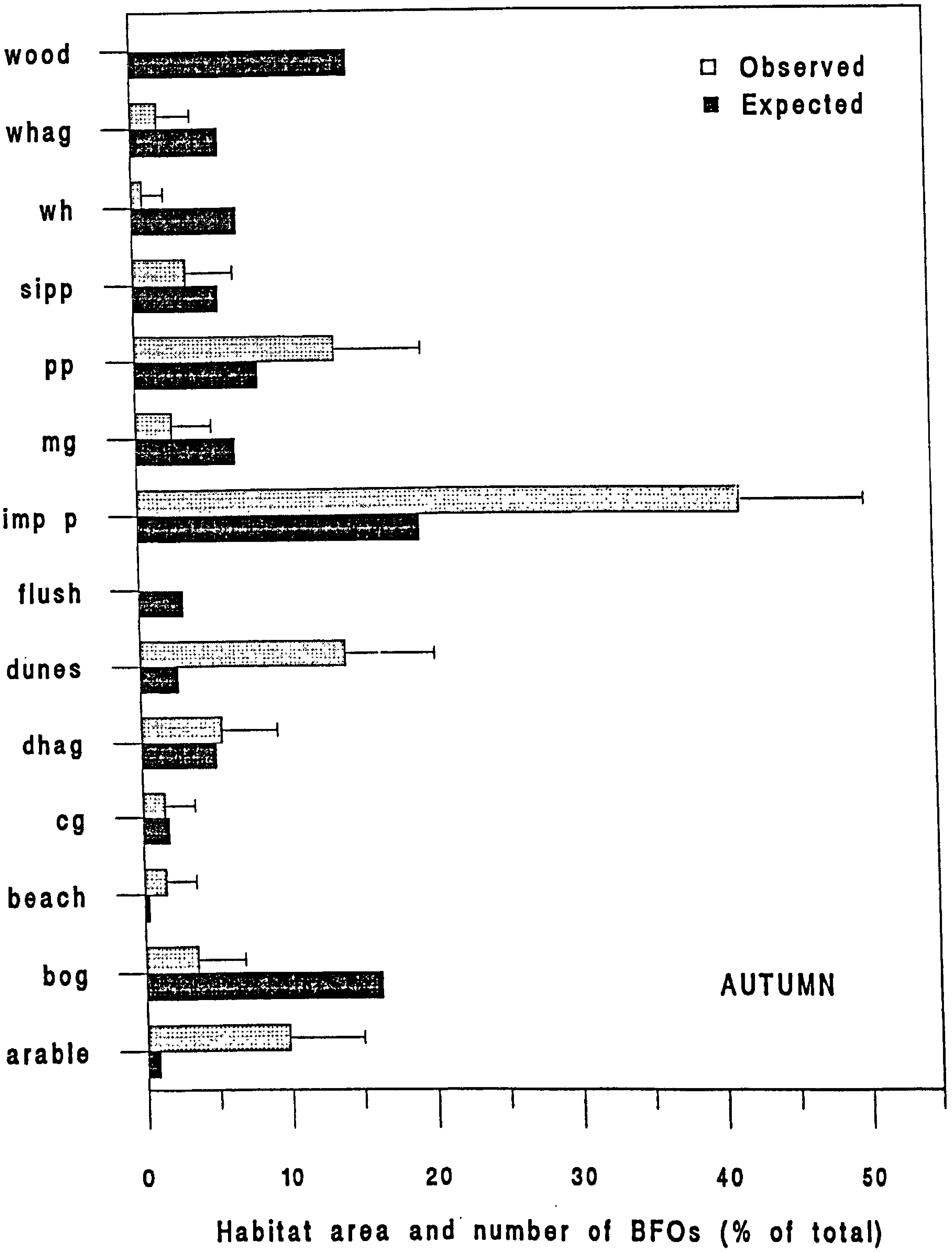
For explanation of habitats see Table 7.1. The 95% confidence limits for the observed values were calculated according to Neu et al. (1974).

Figure 7.2c Distribution of summer Bird Feeding Observations (BFOs) in relation to distribution of different habitats in the Rhinns study area. The habitat areas (total 3239 ha) are labelled "Expected" and the BFOs (n=279) are labelled "Observed".



For explanation of habitats see Table 7.1. The 95% confidence limits for the observed values were calculated according to Neu et al. (1974).

Figure 7.2d Distribution of autumn Bird Feeding Observations (BFOs) in relation to distribution of different habitats in the Rhinns study area. The habitat areas (total 3239 ha) are labelled "Expected" and the BFOs (n=275) are labelled "Observed".



For explanation of habitats see Table 7.1. The 95% confidence limits for the observed values were calculated according to Neu et al. (1974).

least one season; they fall into three broad categories - pasture, dunes/beach and arable. In all seasons the majority of BFOs were in some form of pasture habitat.

Improved pasture was the most-used habitat, and was significantly preferred in all seasons. In spring it accounted for 78% of all BFOs. Semi-improved permanent pasture was significantly non-preferred in winter and spring, and was used in proportion to its availability in summer and autumn. Permanent pasture was used more than semi-improved permanent pasture, but less than improved pasture. It was significantly preferred in summer, and significantly non-preferred in spring. Dunes were significantly preferred in all seasons except spring, generally supporting 10-20% of BFOs. Arable land was significantly preferred in autumn (10% of BFOs), but was virtually unused in all other seasons. Beach habitats were used in proportion to their availability and only in winter and autumn. Dry heath/acid grassland was used in all seasons (0.6 -12.5% of BFOs); it was significantly preferred in summer, and significantly non-preferred in winter.

In winter two habitats (improved pasture and dunes) accounted for over 90% of BFOs, with improved pasture alone accounting for 78%. The same two habitats plus dry heath/acid grassland accounted for over 90% of spring BFOs. A wider range of habitats was used in summer, with 5 (those above plus permanent pasture and semi-improved permanent pasture) accounting for over 90% of BFOs, and 7 habitats accounted for over 90% of BFOs in autumn (those above plus arable and bog).

Patch use

The above analyses provide an overview of habitat use and habitat selection, but do not identify whether feeding Choughs were utilising the habitat itself, or a patch of some other habitat within it. Habitat and patch use within each main habitat are described below. Non-preferred habitats are considered first, followed by preferred habitats. The results are presented on a monthly basis (see Methods) in order that short-lived feeding preferences are not over-looked. The monthly number of BFOs is shown in Table 7.3. No transects were carried out in September and November due to my absence from the island and bad weather.

Table 7.3 *Total number of Bird Feeding Observations (BFOs) in each month on Rhinns transects.*

Month	Bird Feeding Obs (n)
Jan	60
Feb	187
Mar	79
Apr	125
May	178
Jun	124
Jul	155
Aug	124
Oct	122
Dec	153
TOTAL	1307

Non-preferred habitats

Table 7.4 and Figure 7.3 show habitat and patch use by Choughs feeding in non-preferred habitats. It is clear that in these habitats Choughs were not utilising the dominant habitat, but were feeding in patches of other habitats, primarily rock outcrops and permanent pasture. Moreover, within these patches most BFOs were of birds dung-feeding rather than feeding in the habitat-patch itself.

Preferred habitats

Habitat and patch use within preferred habitats are considered in reverse order of their overall preference by feeding Choughs.

Dry heath/acid grassland mosaic (see Table 7.5, Figure 7.4).

This habitat was significantly non-preferred in winter and significantly preferred in the summer months. No BFOs were recorded in the dry heath component of this habitat mosaic. Most BFOs were associated with patches of permanent pasture or rock outcrops, whilst 62.7% of all BFOs in this habitat were associated with dung. The Thyme *Thymus drucei* BFOs probably represent birds feeding on Yellow Mound Ants *Lasius flavus* (see Chapter 8).

Table 7.4 *Habitat and patch use by feeding Choughs in non-preferred habitats (see Table 7.3).*

Habitat[a]	Habitat-patch[b]	Dung-patch	BFOs (*n*)	weighted[c] % of total BFOs in each habitat
BOG	Bog	-	0	0
	Bank+bracken	-	3	13.2
	Moss pasture	Cow-dung	8	37.8
	Permanent pasture	-	2	8.8
	Permanent pasture	Cow-dung	2	8.9
	Rock outcrop+PP	-	2	11.0
	Sheep carcase	-	4	20.1
			--	
	TOTAL		**21**	
MG	Marshy grassland	-	0	0
	Dyke	-	1	17.0
	Permanent pasture	Cow-dung	1	11.0
	Permanent pasture	Sheep-dung	1	17.0
	Rock outcrop+moss	-	2	17.6
	Rock outcrop+PP	Cow-dung	3	26.4
	Wet heath+PP	Cow-dung	1	11.0
			--	
	TOTAL		**9**	
WH	Wet heath	-	0	0
	Permanent pasture	-	2	55.2
	Rock outcrop+PP	-	2	44.8
			--	
	TOTAL		**4**	
WHAG	Wet heath/acid gr.	-	0	0
	Moss pasture	Cow-dung	3	19.2
	Permanent pasture	Cow-dung	6	37.8
	Rock outcrop+PP	-	6	30.4
	Rock outcrop+PP	Sheep-dung	2	12.6
			--	
	TOTAL		**17**	

[a] MG = Marshy grassland; WH = Wet heath; WHAG = Wet heath/acid grassland

[b] If birds fed in the dominant habitat, patch is coded as such.
PP = permanent pasture

[c] Weighted to allow for different no. of BFOs made in each month (see Table 7.3)

Figure 7.3 Patch use by feeding Choughs in Bog, Wet heath, Wet heath/Acid Grassland mosaic and Marshy Grassland, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

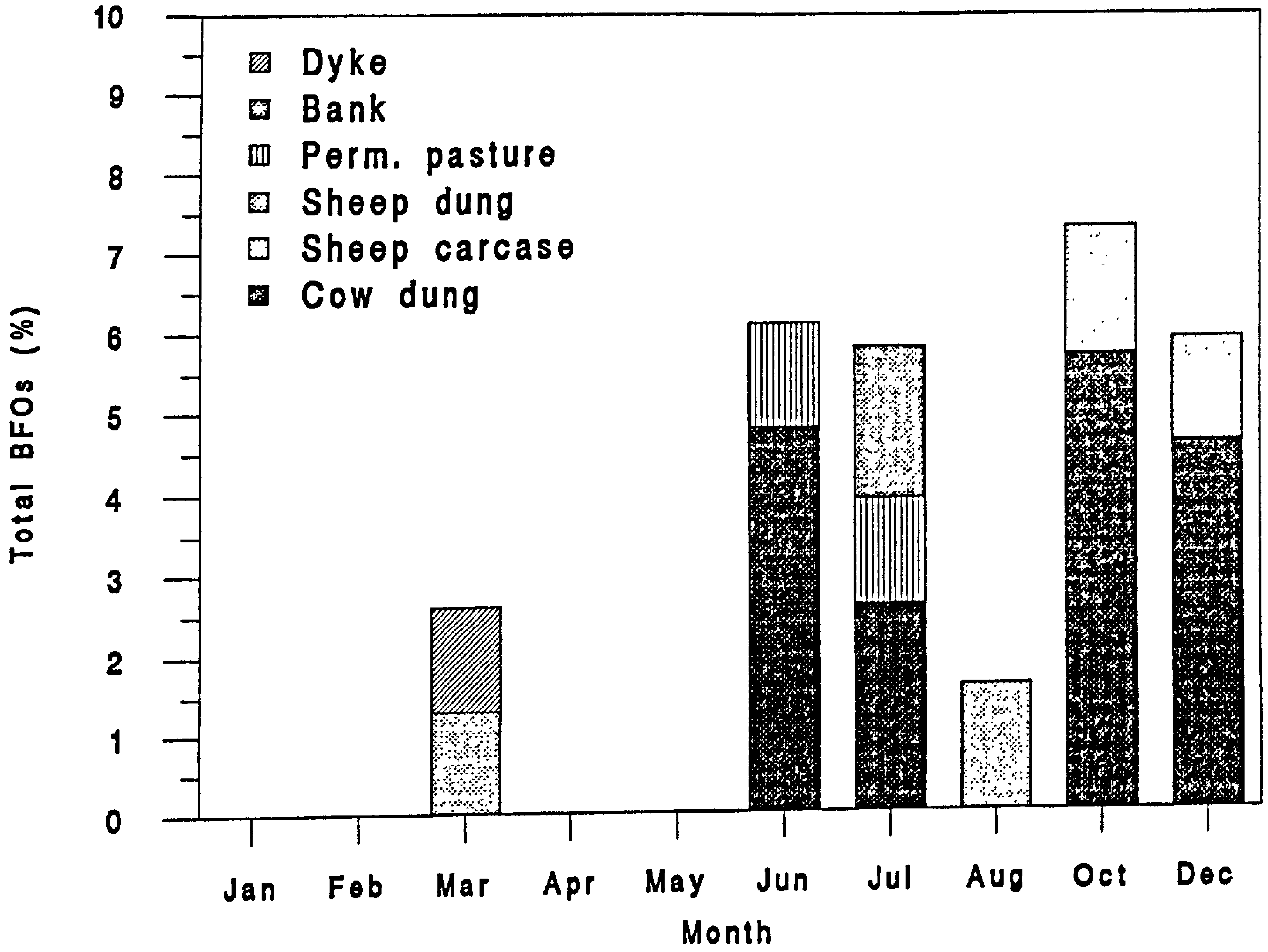


Figure 7.4 Patch use by feeding Choughs in Dry heath/Acid grassland habitat mosaic, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

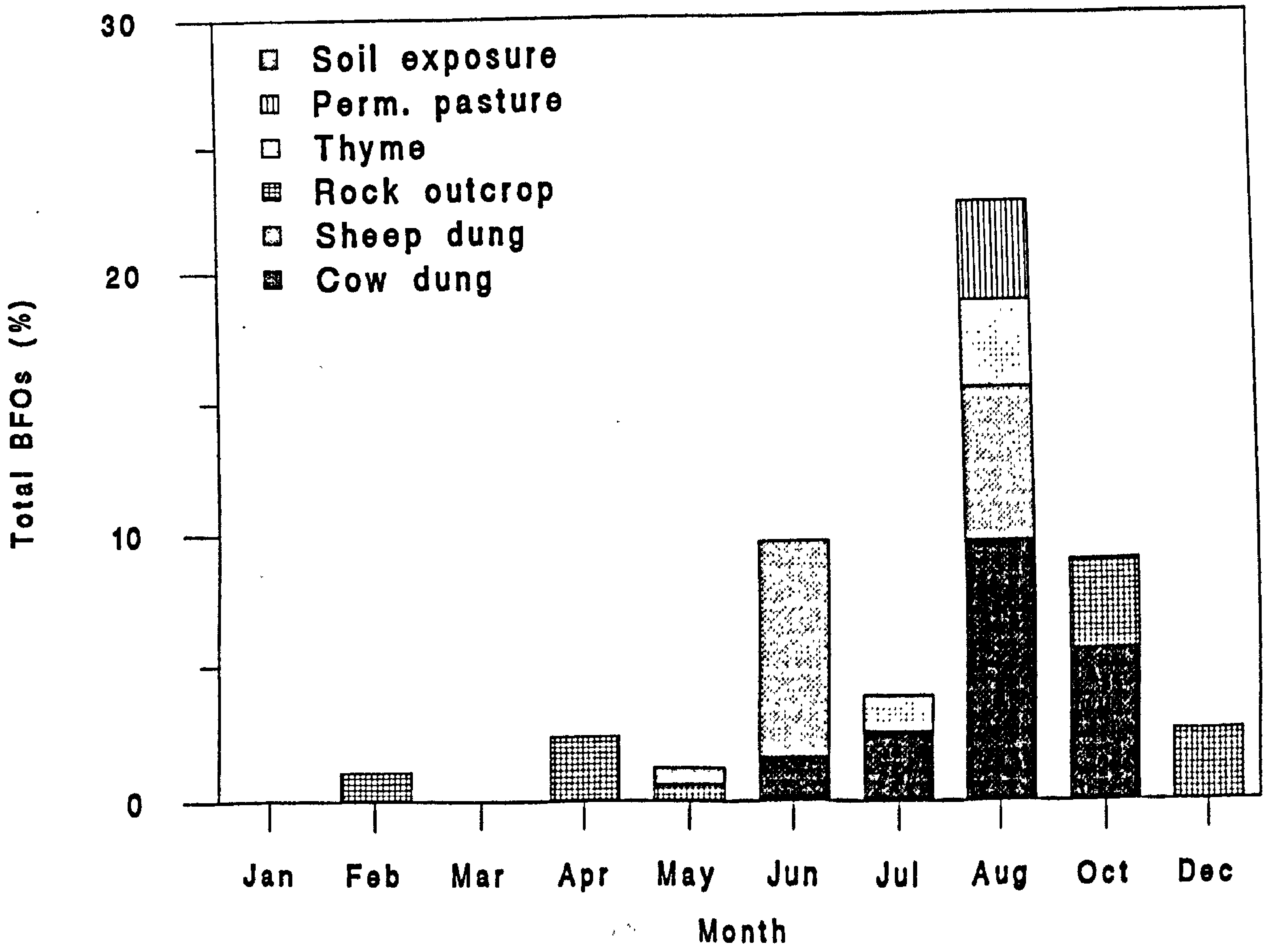


Table 7.5 *Patch use by Choughs feeding in dry heath/acid grassland.*

Habitat-patch	BFOs Dung-patch	weighted[a] % of total (*n*)	BFOs in DHAG
Dry heath/acid grass	-	0	0
Dry flush	Cow-dung	4	4.9
Moss pasture	Cow-dung	2	3.0
Permanent pasture	-	6	9.1
Permanent pasture	Cow-dung	8	12.1
Permanent pasture	Sheep-dung	14	21.2
Rock/PP	-	14	18.7
Rock/PP	Cow-dung	11	16.9
Rock/PP	Sheep-dung	3	4.6
Stream bank	-	1	1.1
Thyme hummock	-	6	8.5
TOTAL		69	

[a] Weighted to allow for different number of BFOs made in each month (see Table 7.3)

Coastal grassland (Figure 7.5)

Patch use in this habitat has been lumped with that in permanent pasture for presentation (see Figure 7.5). Coastal grassland was avoided in winter, and used in proportion to its availability in other seasons. There were only 10 BFOs in this habitat. Three BFOs related to cow dung-feeding, one was in a rock outcrop and the remaining 6 were in the dominant habitat.

Permanent pasture (Table 7.6 and Figure 7.5).

Permanent pasture was significantly non-preferred in spring, and significantly preferred in the summer. It was utilised by Choughs in all study months. Only 14.5% of BFOs were in the dominant habitat. Herbivore dung was the most used patch within this habitat; 35.2% of the total of 127 of dung BFOs were associated with the dominant habitat. Rock outcrops accounted for 35.9% of BFOs. Most of the remaining observations were associated with birds feeding in exposed substrate patches - bank (5.5%), hummocks (1.2%), and rabbit burrows (1.5%).

Table 7.6 *Habitat and patch use by Choughs feeding in permanent pasture.*

Habitat-patch	Dung-patch	BFOs (*n*)	weighted[a] % of total BFOs in PP
Permanent pasture	-	20	14.5
Permanent pasture	Cow dung	37	28.3
Permanent pasture	Sheep dung	9	6.9
Permanent pasture+bracken	-	2	1.5
Bank	-	6	5.5
Hummocks	-	2	1.2
Fertilised-permanent pasture	-	2	3.2
Moss pasture	Cow dung	1	0.8
Rock/PP	-	45	35.9
Rabbit burrow	-	2	1.5
Roadside	-	1	0.5
TOTAL		127	

[a] Weighted to allow for different number of BFOs made in each month.

Semi-improved permanent pasture (Table 7.7 and Figure 7.6).

Semi-improved pasture was significantly non-preferred in winter and spring, but of the 10 study months it was only totally unused in January. Sand/moss pasture accounted for 71.8% of all BFOs in semi-improved permanent pasture, suggesting that it was preferred over the dominant habitat. Likewise, rock outcrops associated with sand/moss pasture accounted for 25.6% of BFOs, compared to only 9.4% associated with semi-improved pasture. Cow-dung feeding was only recorded in sand/moss pasture (17.2% of BFOs), whereas sheep-dung feeding was only recorded in the dominant habitat (5.5% of BFOs).

Improved pasture (table 7.8 and Figure 7.7

This was the single most-used habitat on the Rhinns, accounting for 32-78% of BFOs and being significantly preferred in all seasons. It was most-used in winter, then its use declined through to the summer before increasing again in the autumn. Improved pasture comprised 5 pasture sub-habitats. Habitat use and selection in these as a percentage of all improved pasture BFOs in each season are presented in Table 7.8 and Figure 7.7a. Habitat use on a monthly basis is shown in Figure 7.7b. Reseeded pastures were significantly preferred in winter and spring, and were avoided in summer (when they would have been silage crops). Recently

Figure 7.5 Patch use by feeding Choughs in Permanent pasture and Coastal Grassland, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

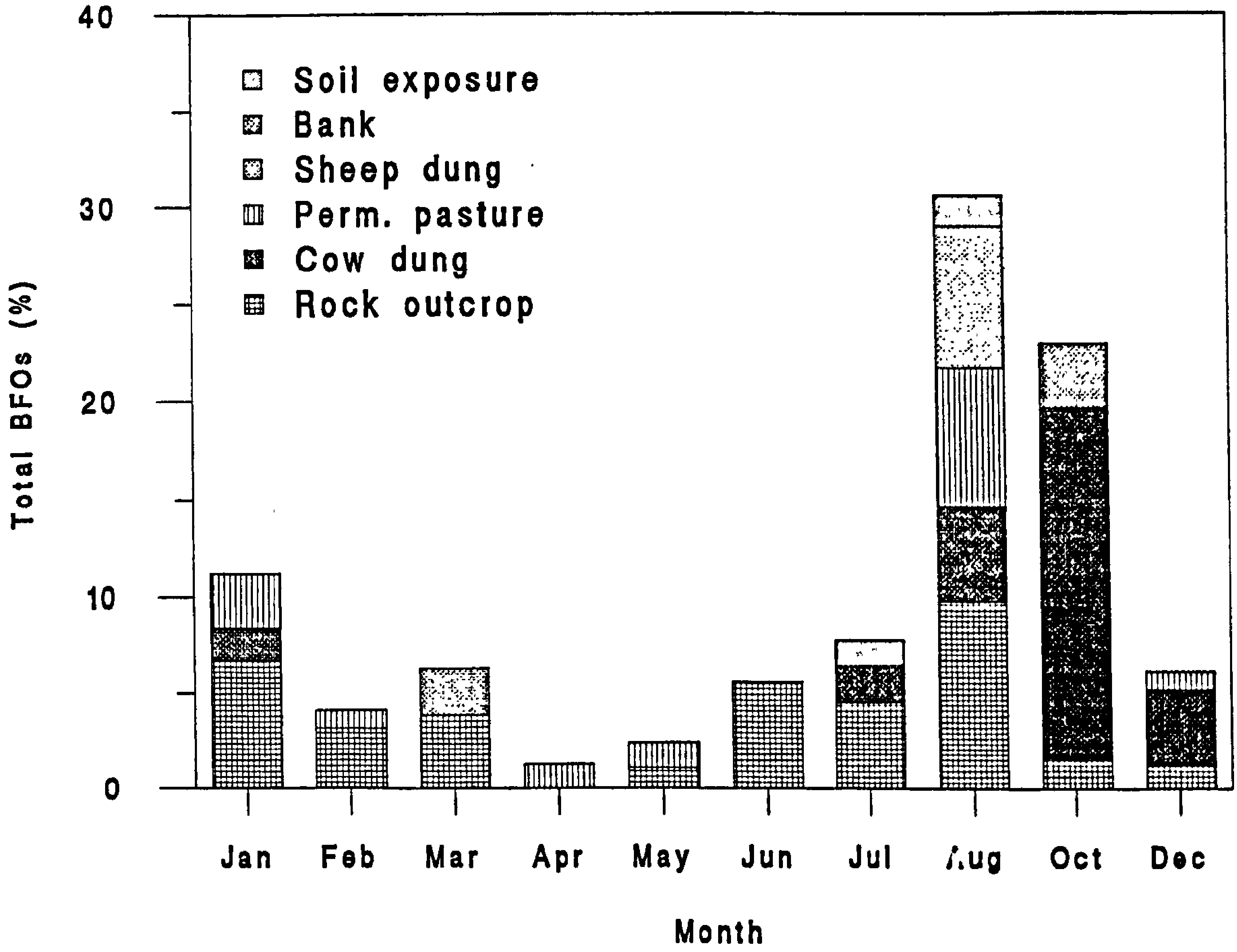
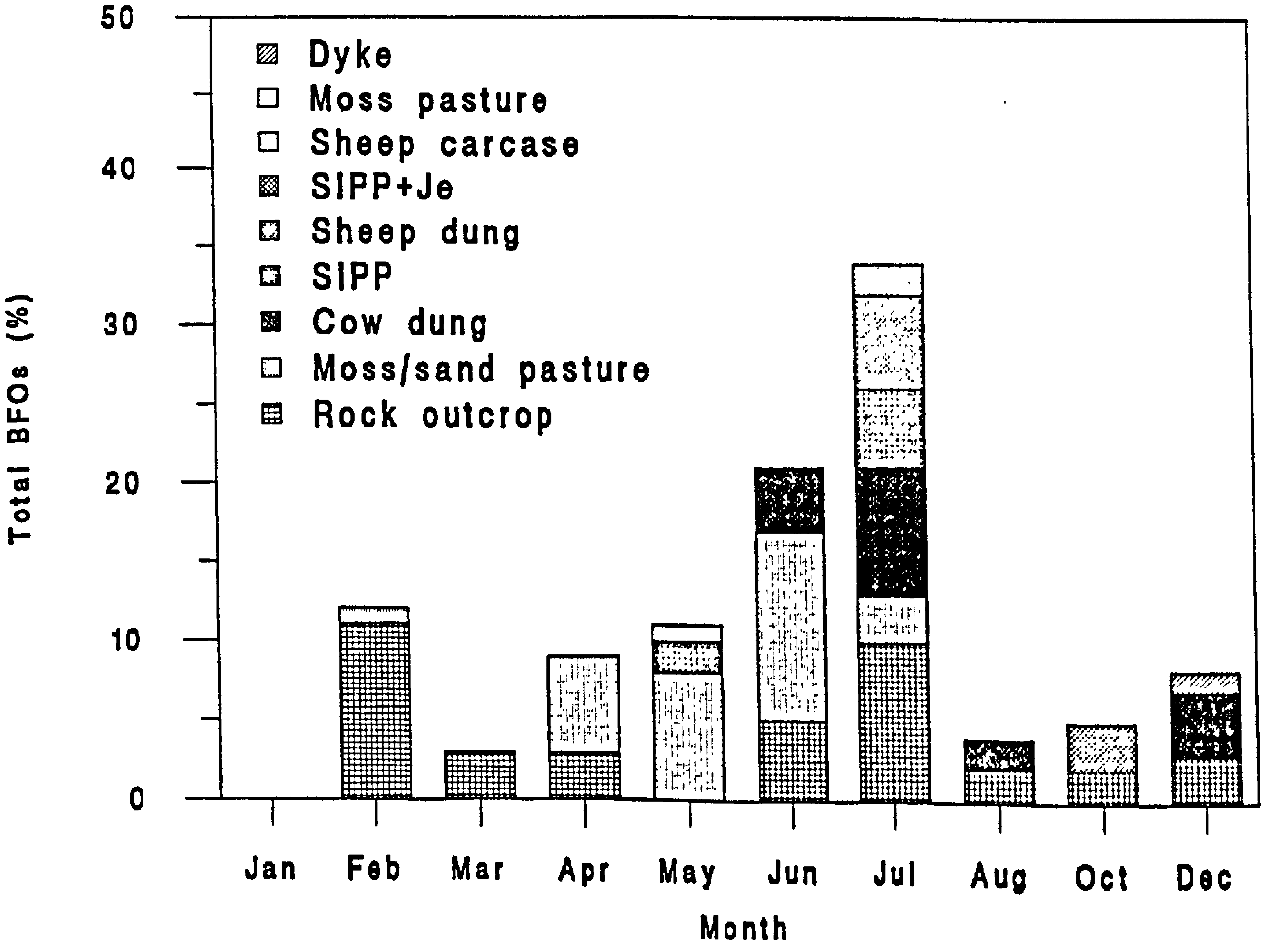


Figure 7.6 Patch use by Choughs feeding in Semi-improved Permanent pasture, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.



improved pasture (RIP) was significantly preferred in spring, summer and autumn, but significantly non-preferred in winter.

Table 7.7 *Habitat and patch use by Choughs feeding in semi-improved permanent pasture.*

Sub-habitat	Habitat-patch	Dung-patch	BFOs (*n*)	weighted[a]% of total BFOs in PP
Semi-imp. PP	Semi-imp. PP	-	12	7.0
	Semi-imp. PP	Sheep dung	7	4.3
	Semi-imp. PP+Juncus	-	4	3.1
	Dyke	-	2	1.2
	Rock/PP	-	13	9.4
	Rock/PP	Sheep dung	2	1.2
	Sheep carcase	-	3	1.8
Sand/moss pasture	Sand/moss pasture	-	43	28.2
	Sand/moss pasture	Cow dung	26	17.2
	Rock/PP	-	42	25.6
	Ruts	-	1	0.8
TOTAL			155	

[a] Weighted to allow for different number of BFOs made in each month.

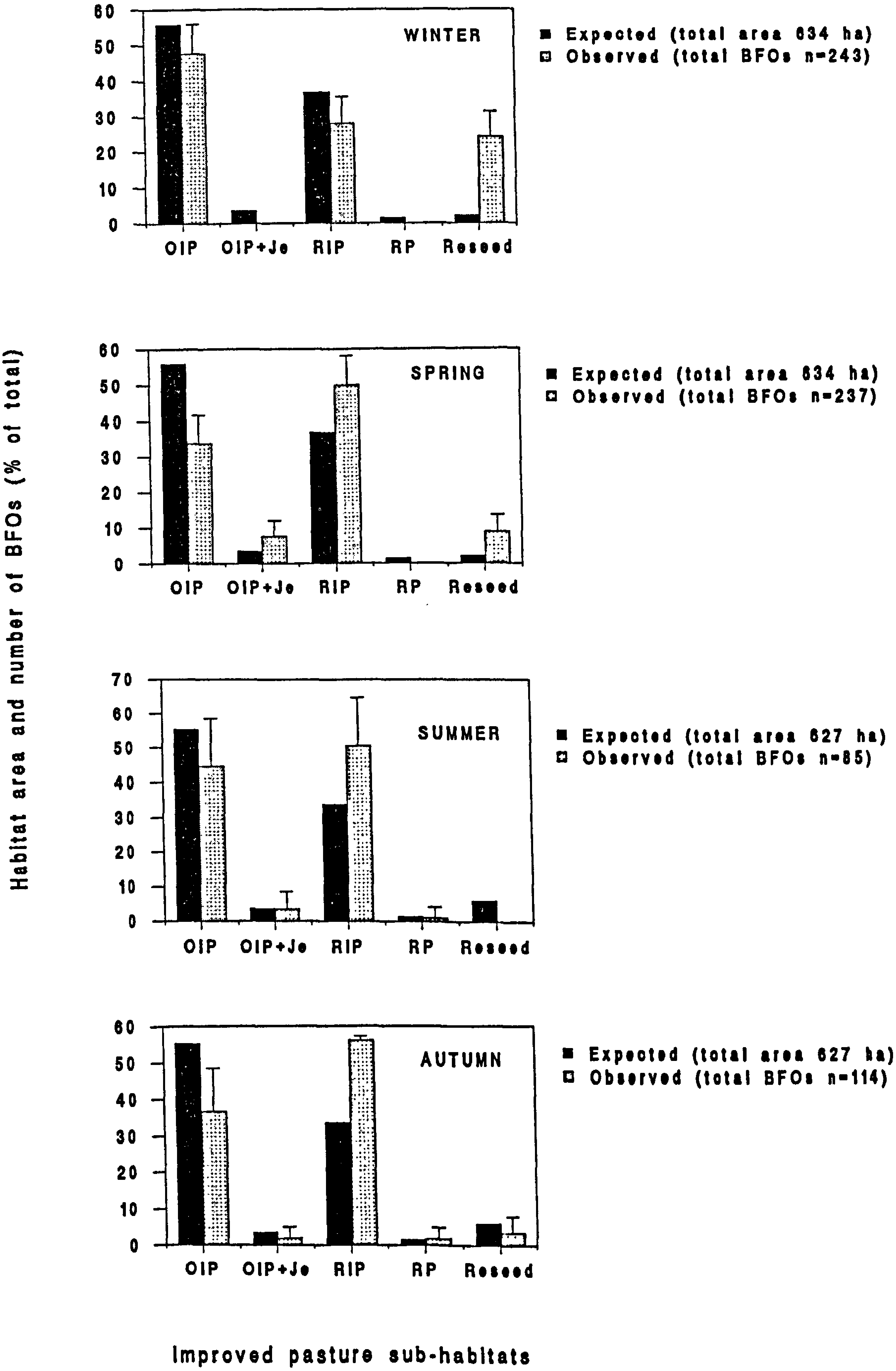
Table 7.8 *Comparison of the area of different Improved Pasture sub-habitats in the study area and the number of Bird Feeding Observations (BFOs) within these sub-habitats. Sub-habitats are described in Table 7.1*

Sub-habitat	Area (ha)	Area (%)	BFOs (*n*)	BFOs[a] (%)	95% Conf. limits of % BFOs lower	upper
a) **Winter** BFOs (*n*=243), total area = 634 ha						
Old improved pasture	354.5	55.9	116	47.7	39.5	56.0
Old imp. past. + Juncus	22.8	3.6	0	0	0	0
Recently imp. pasture	233.3	36.8	68	28.0*	20.6	35.4
Rank Pasture	9.5	1.5	0	0	0	0
Re-seed	14.3	2.2	59	24.3*	17.2	31.4
b) **Spring** BFOs (*n*=237), total area = 634 ha						
Old improved pasture	354.5	55.9	80	33.8*	25.8	41.7
Old imp. past. + Juncus	22.8	3.6	18	7.6	3.2	12.0
Recently imp. past.	233.3	36.8	118	49.8*	41.4	58.2
Rank pasture	9.5	1.5	0	0	0	0
Re-seed	14.3	2.2	21	8.9*	4.1	13.6
c) **Summer** BFOs (*n*=85), total area = 627 ha						
Old improved pasture	346.8	55.3	38	44.7	30.8	58.6
Old imp. past. + Juncus	22.8	3.6	3	3.5	-1.6	8.7
Recently imp. past.	211.0	33.6	43	50.6*	36.6	64.6
Rank pasture	9.5	1.5	1	1.2	-1.8	4.2
Re-seed	37.3	5.9	0	0	0	0
d) **Autumn** BFOs (*n*=114), total area = 627 ha						
Old improved pasture	346.8	55.3	42	36.8*	25.2	48.5
Old imp. past. + Juncus	22.8	3.6	2	1.8	-1.4	4.9
Recently imp. past.	211.0	33.6	64	56.1*	44.1	68.1
Rank pasture	9.5	1.5	2	1.8	-1.4	4.9
Re-seed	37.3	5.9	4	3.5	-.9	8.0

[a] Asterisks indicate habitats for which the % of BFOs, differs significantly from habitat %.

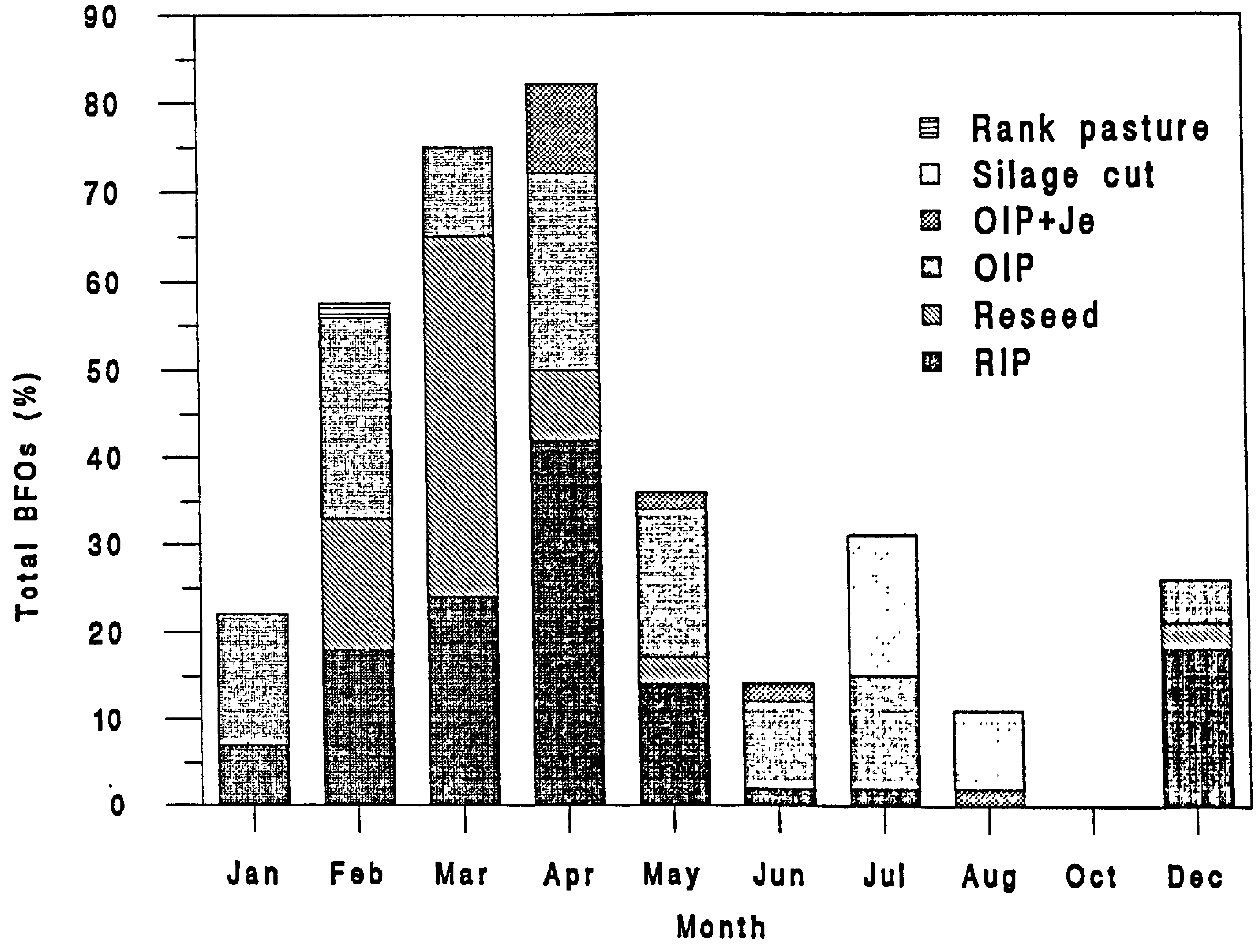
Old improved pasture (OIP) was used less than its availability in all seasons, significantly so in spring and autumn. However, it still accounted for 30-50% of improved pasture BFOs in all seasons. OIP+*Juncus* was avoided in winter, and used in proportion to its avail-

Figure 7.7a Seasonal distribution of Bird Feeding Observations (BFOs) in relation to distribution of Improved Pasture sub- habitats. The habitat areas are labelled "Expected" and the BFOs are labelled "Observed".



Sub-habitats are described in Table 7.1. The 95% confidence limits for the observed values were calculated according to Neu et al. (1974).

Figure 7.7b Use of Improved pasture sub-habitats by feeding Choughs, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.



ability from spring to autumn. Rank pasture had limited extent, and was only used in summer and autumn.

Data on patch use in improved pasture are given in Table 7.9 and Figure 7.8. In all improved pasture types other than rank pasture, the majority of BFOs were recorded in the dominant habitat, ie. pasture, rather than in patches within it. This is in striking contrast to all the fore-going habitats, in which patches were utilised more than the dominant habitat. Consequently, feeding in rock outcrops, dung and other patches formed a much smaller component of total BFOs in improved pasture, although rock outcrops accounted for 29.2% of BFOs in OIP, and in absolute terms dung-feeding was not unimportant, with a total of 48 BFOs; of these, 94% were associated with cow dung. There was only 1 BFO in a silage crop, whereas once the silage was cut it became a favoured feeding site (11.1% of RIP BFOs). There were only 3 BFOs in rank pasture, and these all referred to dung-feeding, so this sub-habitat is evidently not preferred in itself.

Dune and beach habitats (Figure 7.9)

Dune habitats were significantly preferred in all seasons except spring, when they were used in proportion to their availability. Sub-habitat and patch use are shown in Figure 7.9. Fore-dune was not used, and yellow dune was used only in October. Usage of grey dune and dune pasture fluctuated markedly throughout the year, being unused in March and April. It is possible that the fluctuations were due to the fact that most dune BFOs were of non-breeding flock birds - and since these flocks were usually quite cohesive the whole flock tended to be recorded in one or other of the habitats, rather than being spread evenly across them all.

The only patch used by Choughs in dune habitats was cow-dung, in October and December, comprising 6% of 83 BFOs in dune pasture, 16.7% of 36 BFOs in grey dune [feeding behaviour in 26 other BFOs in grey dune could not be seen, therefore these were excluded from the calculation] and 77.8% of 18 BFOs in yellow dune.

Choughs used beach habitats in proportion to their availability in winter and autumn, but they were avoided in spring and summer. Only 3-4 BFOs were recorded in any one month (see Figure 7.10).

Table 7.9 *Habitat and patch use by Choughs feeding in improved pasture sub-habitats Rhinns of Islay, 1988.*

Sub-habitat[a]	Habitat-patch	Dung-patch	BFOs (*n*)	Weighted[b] % of total BFOs in each sub-habitat
Reseed	Reseed	-	75	89.0
	Bare	-	2	3.4
	Moss pasture	Cow dung	5	5.4
	Rock/PP	-	2	2.2
TOTAL			**84**	
RIP	RIP	-	167	57.6
	RIP	Cow dung	22	7.8
	RIP	Sheep dung	1	.4
	Silage cut	-	35	11.1
	Silage crop	-	1	.3
	Bank	Cow dung	2	.6
	Bare	-	3	1.1
	Dyke	-	7	4.4
	Manure spread	-	32	8.2
	Rock/PP	-	21	8.1
	Track	-	2	.6
TOTAL			**293**	
OIP	OIP	-	149	50.8
	OIP	Cow dung	10	4.1
	OIP+Juncus	-	2	.8
	OIP+Juncus	Cow dung	4	1.5
	Dyke	-	8	3.7
	Headland	-	4	2.2
	Permanent pasture	-	2	.5
	Permanent pasture	Cow dung	2	.6
	Rock/PP	-	82	29.2
	RP	-	3	.7
	Reseed	-	2	.6
	Sheep carcase	-	6	2.9
	Track	-	2	.6
	Feed trough (Oats)	-	3	1.8
TOTAL			**279**	
OIP+Juncus	OIP+Juncus	-	18	78.4
	OIP	-	2	9.3
	Rock/PP	-	2	7.6
	Rock/PP	Sheep dung	1	4.7
TOTAL			**23**	
Rank pasture	Rank pasture	Cow dung	2	67.0
	Rank pasture	Sheep dung	1	33.0

[a] RIP = Recently improved pasture; OIP = Old improved pasture.
[b] Weighted to allow for different number of BFOs made in each month.

Figure 7.8 Patch use by Choughs feeding in Improved pasture , Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

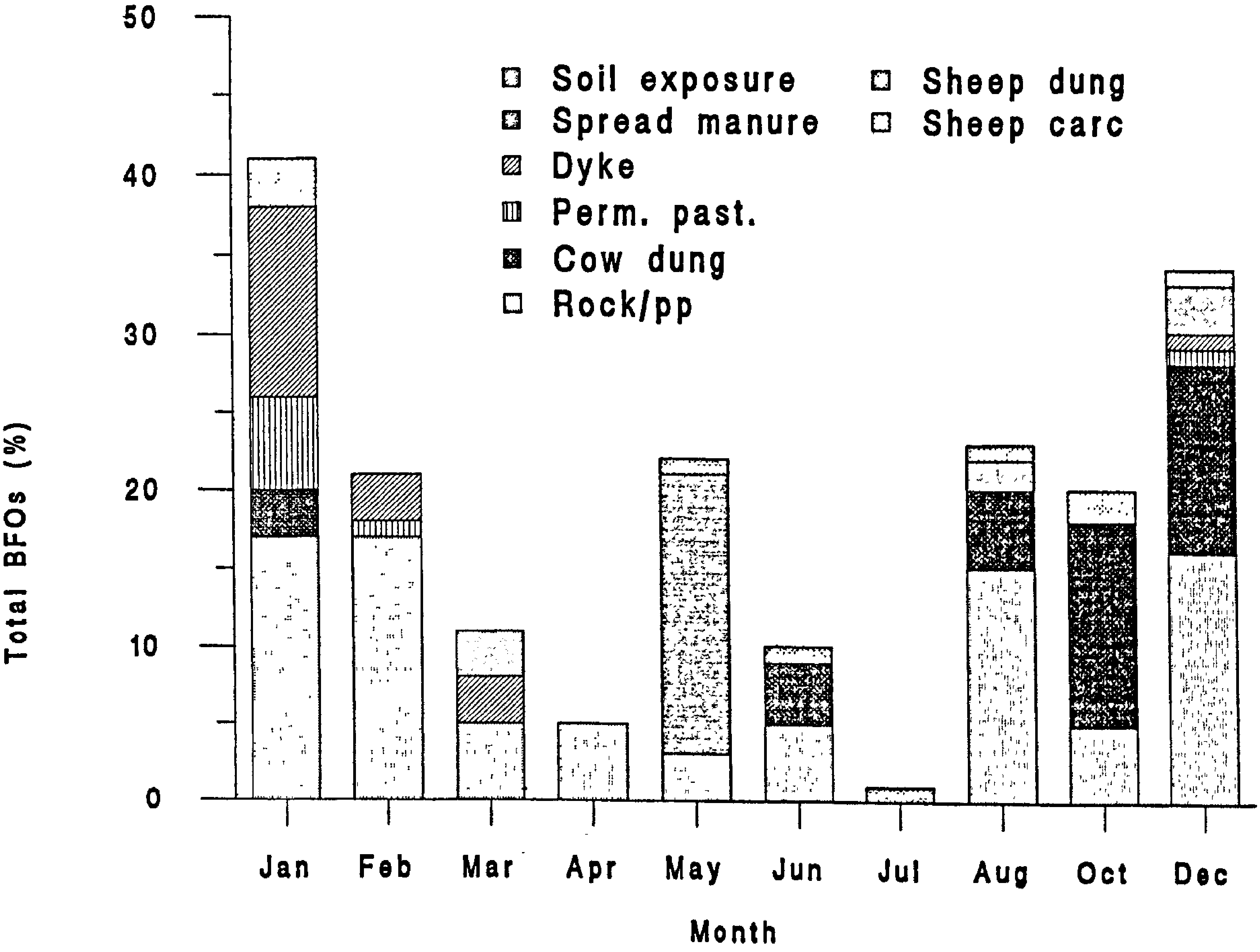


Figure 7.9 Sub-habitat and patch use by Choughs feeding in Dune habitats, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

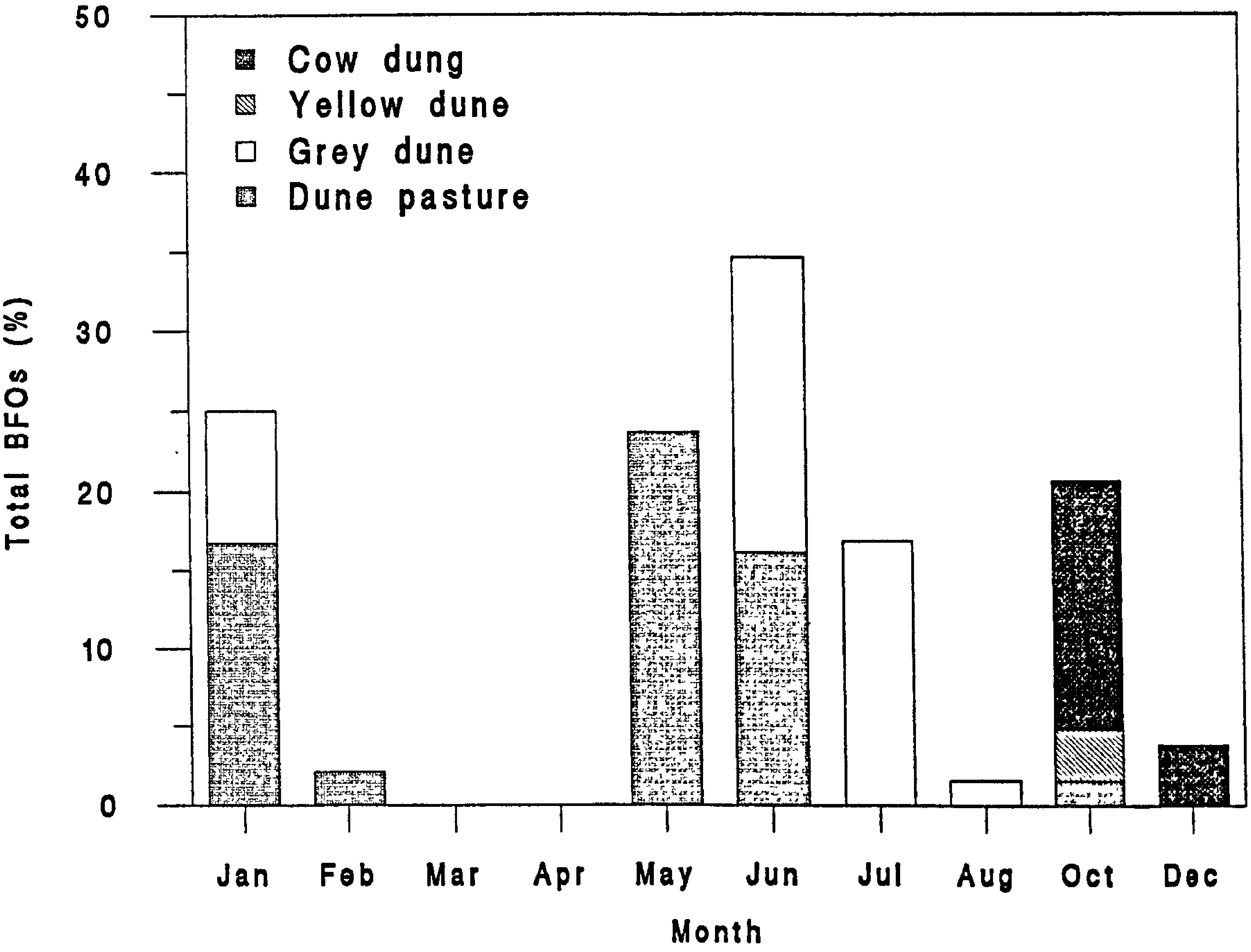
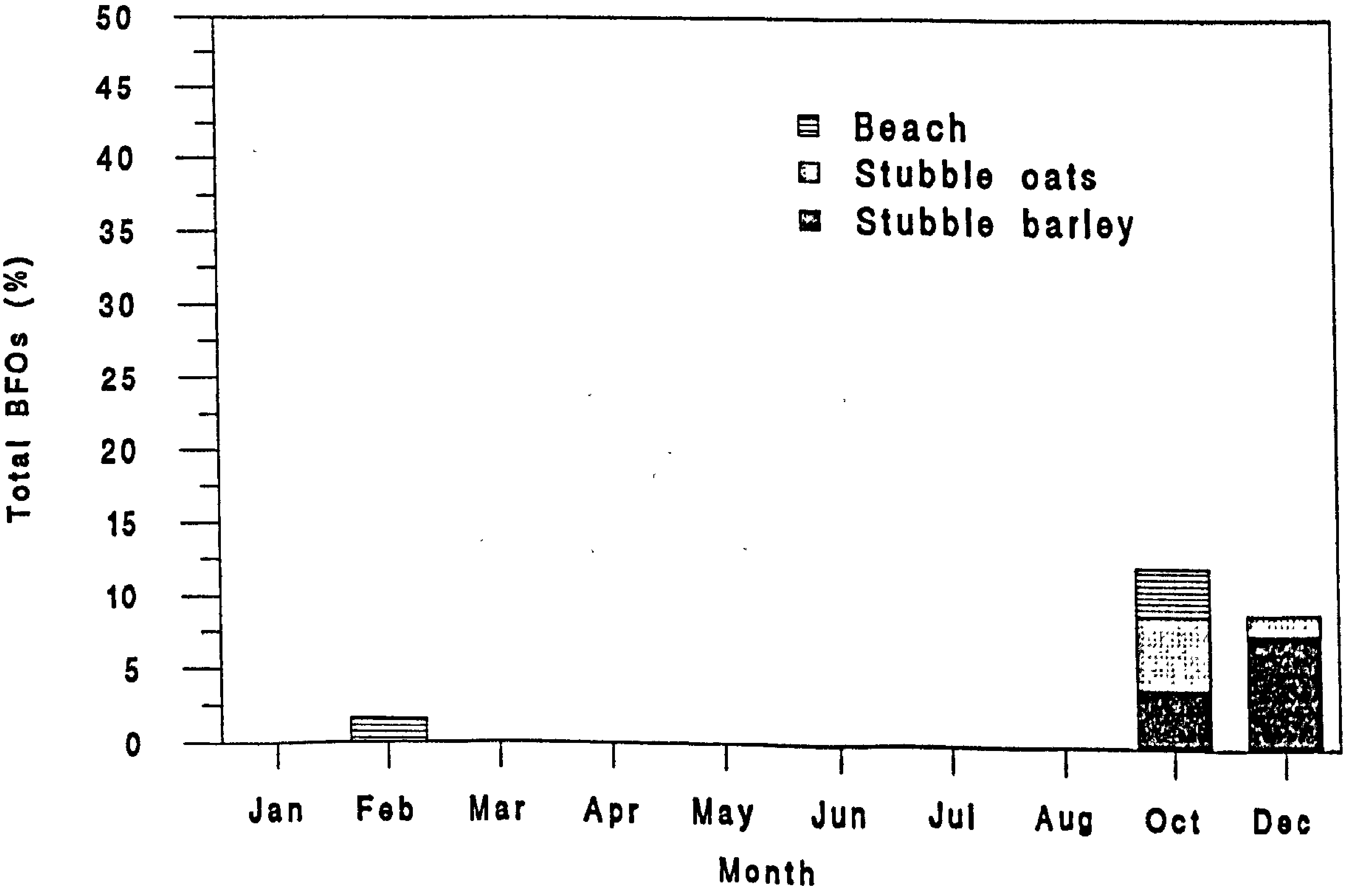


Figure 7.10 Use of Arable and Beach habitats by feeding Choughs, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.



inary sampling showed that a minimum of 40 cores was needed to reduce standard errors to less than the mean. Ten cores were taken at random distances (between 0-9m) from each other along 4 randomly selected transect lines across the field. Invertebrates were extracted using a heat extraction apparatus (Blasdale 1974).

Feeding-site samples. Many Chough feeding sites were too restricted in extent to enable large-scale sampling described above to be undertaken. At these sites a smaller sample of 10-15 soil cores was taken in the immediate vicinity of the feeding site. In habitats too shallow for use of the coring equipment (eg. rock outcrops) a 6.5 cm diameter circle was cut into the vegetation using a stout knife. Both types of sample were sorted by hand on site. Invertebrates were counted and saved for later identification and weighing.

Invertebrates were identified using standard texts, including Brindle (1960) for Tipulid larvae, Brian (1977) for ants and Skidmore (1987) for dung fauna. Some larval Tipulids were kept in rearing cages and hatched out to confirm identification to species level.

Arable habitats (Figure 7.10)

Arable land was significantly preferred in Autumn (when it was in the form of cereal stubbles), and was used in proportion to its availability in winter. It was totally unused in spring and summer. Only cereal crops (barley and oats) were used, with root crops (stubble turnips [a variety of small turnip used as winter fodder for sheep] and potatoes) being completely avoided. Oat and barley stubbles supported 9-10% of BFOs in October and December, but newly sown and growing cereal crops were unused.

Rock outcrops and field boundaries (Figure 7.11).

It is clear from the above analyses that rock outcrops and field boundaries are important patches within a range of habitats. Monthly use of these patches is presented as percentages of total monthly BFOs in Figure 7.11. Bird feeding observations in rock outcrops were divided into four broad categories based on the dominant habitat within which the rock outcrop occurred: 1) coastal rock outcrops - associated with coastal grassland or other coastal habitats; 2) permanent pasture rock outcrops - in permanent and semi-improved pasture and dry heath/acid grassland (where most rock outcrop BFOs were associated with patches of permanent pasture, see above); 3) improved pasture rock outcrops and 4) wet heath/bog rock outcrops (including wet heath/acid grassland mosaic). Boundaries were not subdivided according to habitat and included earth dykes, walls and fences but not hedges.

Despite their limited availability it is clear that rock outcrops in permanent pasture and improved pasture were much-used throughout the year (when combined, accounting for up to 33% of total monthly BFOs), and were particularly important in January, February, August and December when they supported over 20% of monthly BFOs. Outcrops in coastal grassland however were only used in October, despite the abundance of rock outcrops just behind the seacliffs along much of the Rhinns coastline. Field boundaries were most-used when they occurred in improved pasture habitats, and were used from December through to March, with 13.3% of January BFOs in this patch-type.

Herbivore dung (Figure 7.12a)

The above analyses show that the dung of cows and sheep was an important feeding "patch" for Choughs on the Rhinns from summer through to early winter. Cow dung was used more frequently than sheep dung; its use peaked in October with the very high proportion of 60.7% of all BFOs in that month. Both cow and sheep dung featured as an important feeding patch within non-preferred habitats such as bog, marshy grassland, wet heath and wet heath/acid grassland mosaic, and were important components in the use of semi-improved permanent pasture and permanent pasture. It was impossible to quantify availability of dung, and its availability may have differed between habitats. However, to give an approximate estimate of which habitats were most-used for dung-feeding Jacobs Preference Indices (1974) that are presented for all dung feeding BFOs in each habitat in relation to the total availability of habitat (Table 7.10). "Preferred" dung-feeding habitats were all basically some type of permanent pasture - dunes, dry heath/acid grassland mosaic, permanent pasture and semi-improved permanent pasture. Improved pasture was used only in proportion to its extent, and coastal grassland and the "wetter" habitats (wet heath/ acid grass, bog and marshy grassland) were "non-preferred". These results may reflect differences in the amount of dung available in each habitat, or they may indicate that dung in certain habitats is more productive than in others. Without quantifying dung availability in each habitat it is impossible to tell which is the most important factor.

Figure 7.11 Monthly proportion of feeding Choughs in rock outcrops and field dykes/boundaries, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

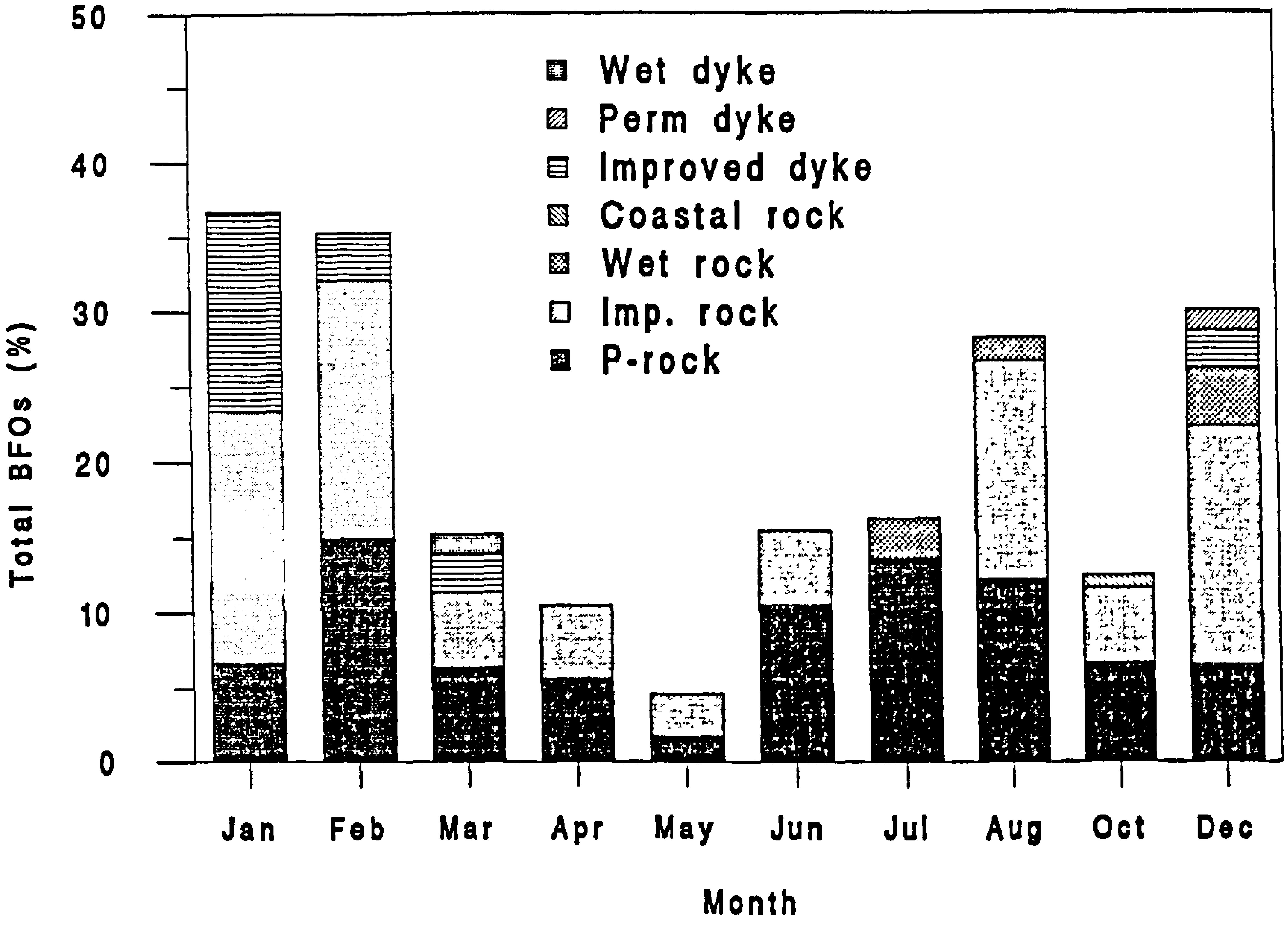


Figure 7.12a Use of Cow dung and Sheep dung by feeding Choughs, Rhinns of Islay, 1988. Total number of monthly BFOs is given in Table 7.3.

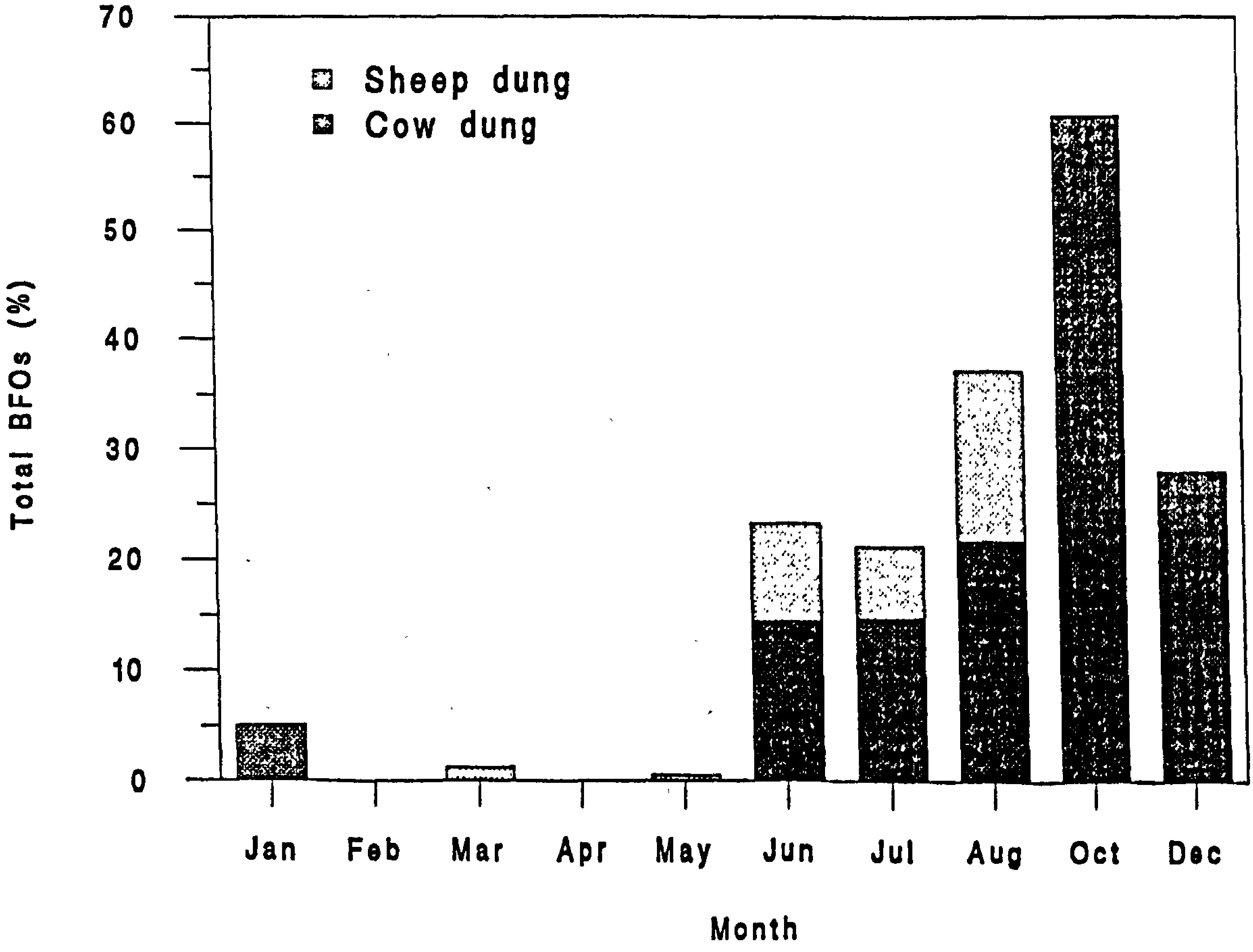


Table 7.10 *Habitat selection by dung-feeding Choughs, Rhinns of Islay, 1988 (total area 3239 ha).*

Habitat[a]	Per cent cover	Per cent of total dung-feeding BFOs (*n*=230)	Jacobs Preference Index (1974)
Bog	16.3	4.4	-.62
Coastal grassland	2.1	1.3	-.24
Dry heath/acid grass	5.1	18.3	.61
Dunes	1.9	10.9	.73
Improved pasture	19.6	22.2	.08
Marshy grassland	6.8	2.6	-.46
Permanent pasture	8.9	20.4	.45
Semi-imp'd perm. past.	5.8	15.2	.49
Wet heath/acid grass	6.0	4.8	-.12

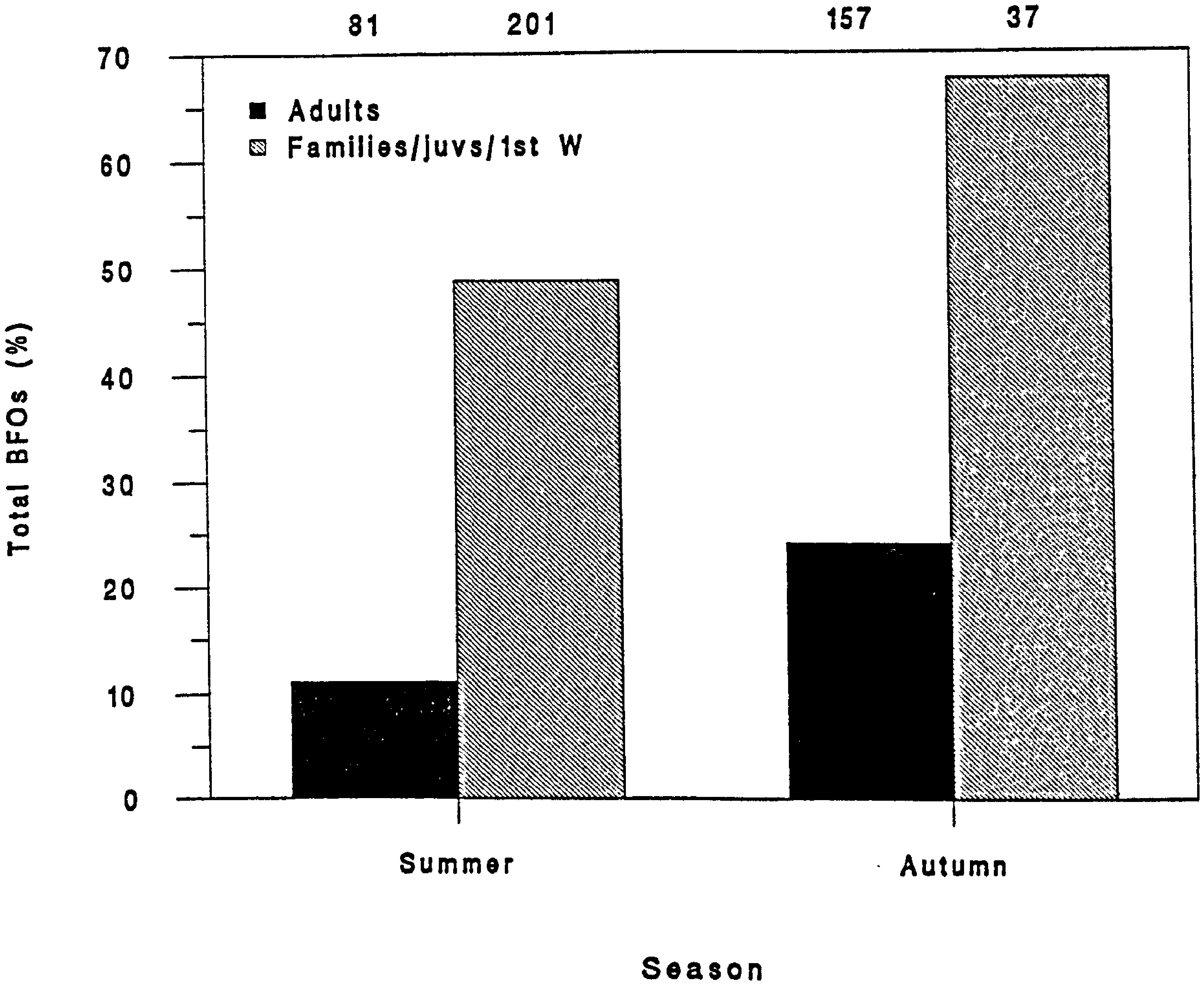
[a] Habitats not listed were not used at all for dung-feeding, therefore they would have a preference index of -1.00.

The number of dung-feeding BFOs as a proportion of all BFOs is presented in relation to bird age in Figure 7.12b for summer and autumn (the seasons in which both age classes (see below) were recorded dung-feeding). Bird age was identified from colour rings, and was divided into two categories - first-year birds and older. To the first-year category were added records of family parties where adults were still feeding juveniles. During summer and autumn 49-68% of BFOs for first-year birds were associated with dung-feeding, compared to only 11-24% for birds more than 1 year old. The differences in each season were statistically significant (summer: *Chi*^{2} 34.7, *d.f.* 1, *P* <.001; autumn: *Chi*^{2} 25.7, *d.f.* 1, *P* <.001).

7.3.2 Vegetation height at feeding sites on the Rhinns

Vegetation height at feeding sites was estimated for a total of 1266 BFOs. Frequency distribution of vegetation height over the whole year is shown in Figure 7.13, and median height on a monthly basis in Figure 7.14. 89.5% of all BFOs were in vegetation <= 5 cm, and 67.9% at <= 3 cm. Median height for the whole year was 3.0 cm, as it was for 7 of the 10 study months, with median values of 2.0 for February and 4.0 for April and October. These results can be compared with changes in field use by pair C in relation to changes in sward height in improved pasture fields under differing grazing regimes (section 7.3.3).

Figure 7.12b Dung-feeding BFOs as a proportion of seasonal BFOs (summer and autumn only). Adult pairs compared with families/juveniles/1st winter birds.



Figures at top of graph indicate sample size for each age-class in each season. Data are not presented for winter and spring due to small number of dung-feeding observations in those seasons.

Figure 7.13 Vegetation height at chough feeding sites, Rhinns of Islay, 1988. Total BFOs n = 1266.

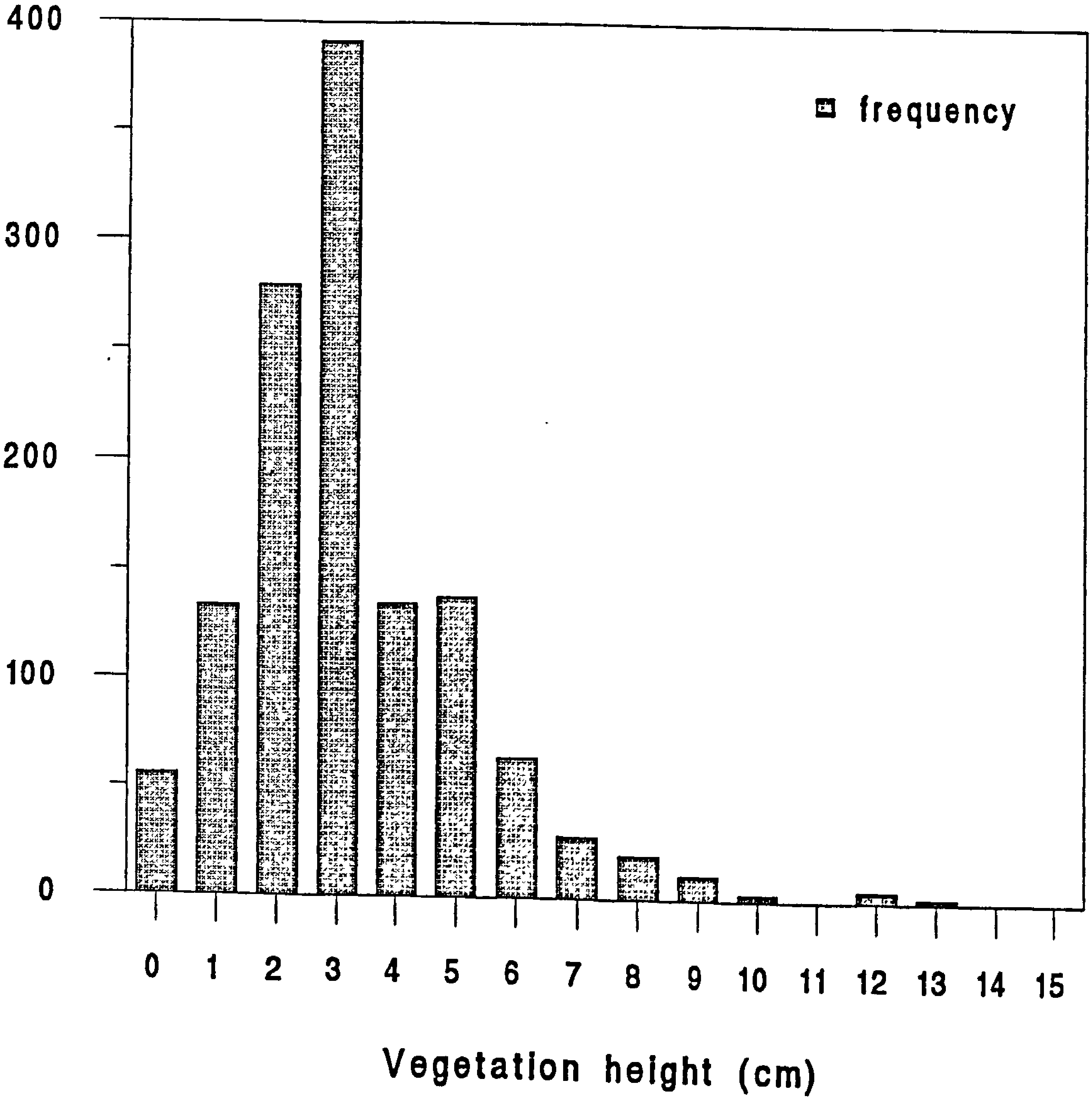
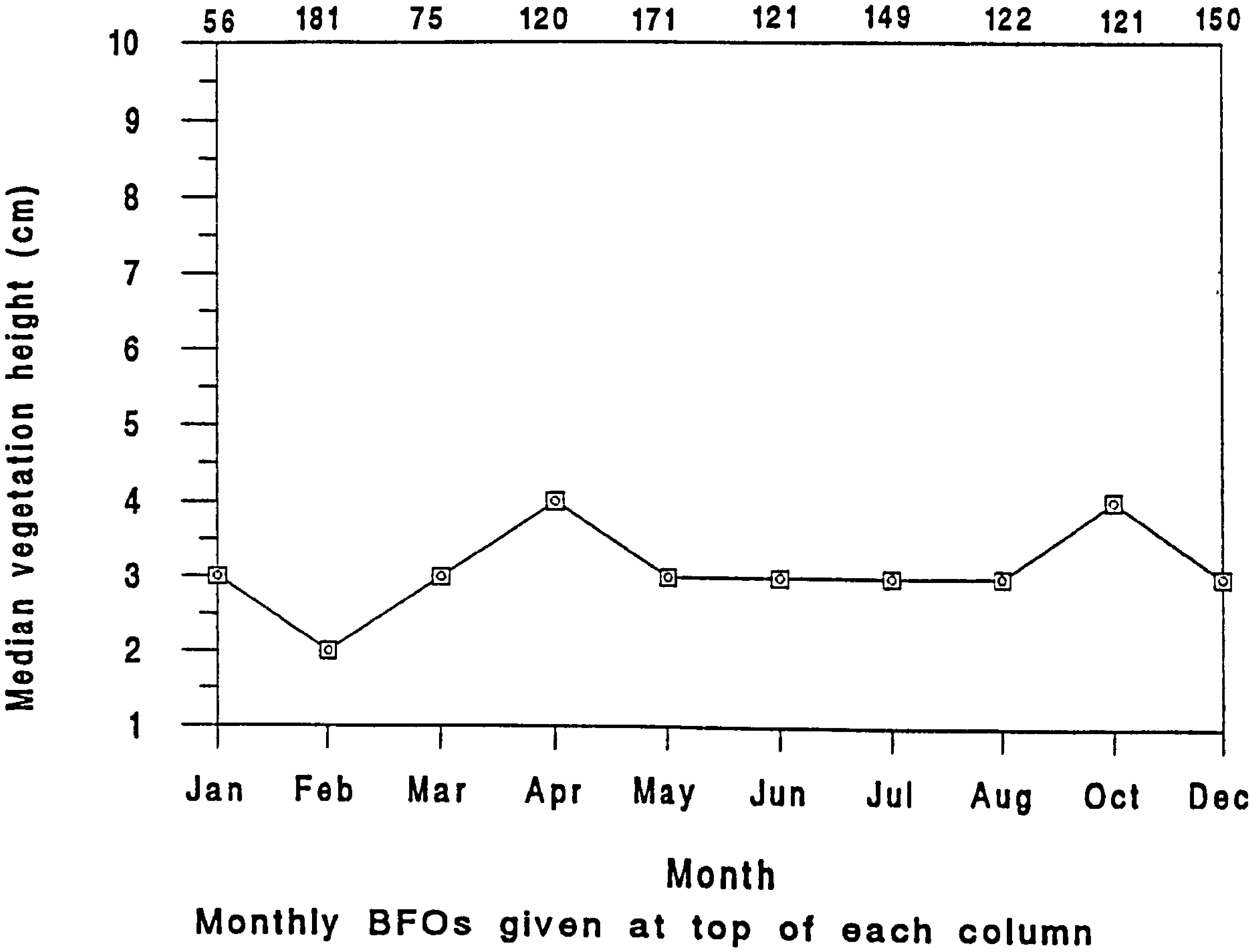


Figure 7.14 Monthly median vegetation heights at Chough feeding sites, Rhinns of Islay, 1988. Total BFOs n = 1266.



7.3.3 Habitat use and habitat selection by study pairs

Breeding parameters and details of duration of total observation times for the 5 study pairs are summarised in Table 7.11. Pairs feeding in dune habitats (mostly pairs D and E) proved more difficult to follow than those foraging in agricultural areas (pairs B and C) due to the presence of other Choughs in the dune habitats. Pair A's breeding attempt failed when the chicks were small, so observations on this pair were discontinued. Habitat availability was assessed for each pair within 1 km of the nest-site (see Methods), though this area did not necessarily include all foraging trips. Habitat use for main-habitats by each pair is given by the percentage of "foraging trip habitats", with confidence limits based on Neu *et al.* (1974). For pairs A and E the sample size of foraging trip habitats was too small to make the calculation of confidence limits worthwhile, so habitat selection is presented simply as a preference index (Jacobs 1974). When habitat preferences were assessed for all combinations of habitats, sub-habitats and grazing regimes, sample sizes were also too small to make calculation of confidence limits worthwhile, so the results of these analyses are also expressed as preference indices.

Table 7.11 *Summary of foraging observations and breeding parameters for 5 study pairs, Islay 1988. Times are in minutes.*

Study pair	Clutch size[a]	No. of fledged young	Total obs time	No. of foraging trips	Foraging trip habitats	Feeding range[b] (ha)	Distance to mature dunes (km)
A	4	0	930	16	17	155	4.5
B	5	3	2880	111	210	102	8.5
C	6	2	3150	108	173	535	7.0
D	5	3	1770	20	49	163	2.5
E	5	3	570	16	22	75	1.3

[a] Data supplied by the Scottish Chough Study Group.

[b] Feeding range calculated using Kenward's (1987) convex polygon method. Areas of fresh water and sea excluded from calculation of total area.

Pair A

Pair A nested in an area dominated by permanent pasture and bog (Table 7.12). There was virtually no improved pasture or agricultural habitat within 1 km of the nest; the small area of improved pasture present was very old. A total of 930 minutes of observations were made on this pair during 19th April - 19th May, though 180 of these were made before incubation had begun. The female's total feeding range was 155 ha. The breeding attempt of this pair was unsuccessful; a brief account of the events leading up to nest failure is given below. The female was observed nest-building (accompanied by her mate) on 19th April, and both birds were observed feeding together within 0.5 km of the nest-site. On 25th April the female was seen making short foraging trips away from the nest, but spent most of her time at the nest, presumably incubating eggs. The male was not seen during the 2 hour observation period. On 2nd May the female made a long foraging trip to a dune system 4.7 km from the nest-site; again the male was not seen. During 5-13th May the female continued incubation/brooding, but it was evident by then that she had been deserted by her mate. Again she was observed making short foraging trips close to the nest-site, presumably feeding herself, and perhaps young chicks. On 19th May, a different (colour-ringed) male was seen "consorting" with the female, and though she was still apparently incubating/brooding on this date, she was also seen carrying a dead 2-3 day-old chick from the nest site and placing it on a wall. When the wall was inspected later that day, a second dead chick and a partly hatched egg were also found. By 24th May there was no sign of the female at the nest-site and the breeding attempt had evidently been abandoned: once the chicks had hatched she was presumably unable to continue the breeding attempt unaided.

The nature of this breeding attempt means that habitat selection by the foraging female is severely biassed because in order to incubate the eggs successfully she was constrained to feeding close to the nest. The female spent most of her time at the nest, presumably incubating/brooding. Only 17 foraging trips were recorded (Table 7.12), comprising a total of 276 minutes (38.3% of the total observation period). The female mostly foraged close to the nest in permanent pasture and improved pasture, with some suggestion of a greater preference for improved pasture. The one long distance foraging trip that she made (4.7 km from the nest) was to a heavily grazed mature dune system, apparently in preference to an immature dune system present within 1 km of the nest-site, which was unused.

Table 7.12 *Habitat preferences of the female of pair A, as indicated by the number of foraging trips to habitats within 1 km of the nest. Foraging trips outwith a 1 km radius are also indicated.*

Habitat	Habitat area (ha)	Habitat area (%)	Foraging trip habitats (*n*)	Foraging trip habitats (%)	Jacobs Preference Index (1974)
Bog	158.4	50.2	0	0	-1.00
Fore dunes	3.4	1.1	0	0	-1.00
Dunes > 1 km	-	-	1	5.8	-
Imp'd pasture	7.6	2.4	3	17.6	.75
Perm. pasture (PP)	47.0	14.9	13	76.6	.45
PP + bracken	27.4	8.6	0	0	-1.00
Wet heath	70.4	22.8	0	0	-1.00
TOTAL	314.2		17		

Pair B

A total of 2880 minutes of observations were made on pair B, during 15th April - 14th June. The feeding range of pair B was 102 ha. All foraging trips were to fields within 1 km of the nest-site. This female laid 5 eggs and 3 young fledged. Habitat availability (within 1 km of the nest) and habitat selection are shown in Table 7.13 (main habitats) and Table 7.14 (main habitats, sub-habitats and dykes). The whole area was extensively grazed by sheep (several hundred) and beef cattle (c.75), only 6.7% being ungrazed (ie. fenced off). There were three main habitats, bog, heath and pasture, each covering approximately one third of the area. There were no arable crops, although 5.3% of the area was given over to silage. Of the main habitats (Table 7.13), grazed improved pastures were significantly preferred. Wet heath, bog and ungrazed improved pasture were significantly non-preferred. Semi-improved permanent pasture and wet heath/acid grassland mosaic were used in proportion to their availability. Marshy grassland and wood were avoided.

Improved pasture comprised 19.8% of the area, of which 14.4% was permanently grazed throughout the study period by sheep and beef cattle. Considering preference of habitats and sub-habitats (Table 7.14) the three pasture sub-habitats, reseed, RIP and OIP, were highly preferred, except when ungrazed (ie. RIP fields saved for silage), when they were avoided. There was a suggestion that preference decreased with increasing age of pasture: Jacobs indices - reseed 0.95, RIP 0.70 and OIP 0.63.

Table 7.13 *Habitat selection by pair B for all fields within 1 km of the nest-site (total area 337.1 ha). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974). The number of Foraging trips >1 km from the nest-site is also given.*

Habitat	Grazed/ ungrazed[a]	Habitat area (%)	Foraging trip habitats (n)	Foraging trip habitats[b] (%)	95% Confidence limits of % trips	
					lower	upper
Bog	G	35.7	18	8.6*	3.49	13.65
Improved pasture	G	14.7	142	67.6*	59.11	76.13
Improved pasture	U	5.3	2	1.0*	-0.72	2.62
Marshy grassland	G	4.6	0	0	0	0
Semi-imp'd perm.past.	G	6.2	9	4.3	-0.56	8.02
Wet heath	G	18.8	13	6.2*	1.77	10.61
Wet heath/acid grass	G	13.6	26	12.4	6.36	18.4
Woodland	G	1.2	0	0	0	0

[a] G = grazed, DU = grazed by dairy cattle or ungrazed, LG = lightly grazed, rabbits, U = ungrazed.

[b] Figures marked with an asterisk are significantly different from expected ($p < .05$).

Table 7.14 *Habitat/sub-habitat preference of Pair B (based on habitat availability within 1 km of nest-site). Total area of all fields falling within 1 km of nest = 337.1 ha*

Habitat	Grazing regime	% area within 1 km of nest	% of all foraging trip habitats (*n* = 210)	Jacobs index (1974)
Bog	Sheep/Beef C[a]	32.6	1.0	-.96
Dry bog	Sheep/Beef C	2.5	6.2	.44
Dyke (IP)		0.3	0.5	.23
Marshy grassland	Sheep	3.2	0.0	- 1.00
Marshy grassland	Ungrazed	1.4	0.0	- 1.00
Moss pasture	Sheep/Beef C	0.5	1.4	.49
OIP	Sheep/Beef C	8.6	29.0	.63
Dyke (PP)		0.1	0.0	- 1.00
RIP	Sheep	4.2	20.0	.70
RIP	Ungrazed	5.3	1.0	-.71
Rank pasture	Sheep	1.0	0.0	- 1.00
Reseed	Sheep	0.6	18.1	.95
Semi-imp. PP	Sheep/Beef C	6.1	4.3	-.18
Dyke (wet habs)		0.4	0.0	- 1.00
Wet heath	Sheep/Beef C	18.8	6.2	-.56
Wet heath/acid grass	Sheep/Beef C	13.2	12.4	-.04
Wood	Sheep/Beef C	1.2	0.0	- 1.00

[a] Beef C = Beef cattle

Pair C

A total of 3150 minutes of observations were made on pair C during 15th April - 16th June. The total feeding range (excluding sea) of pair C was 535 ha, resulting primarily from the birds' foraging trips to the heavily grazed dune system 7 km from the nest-site. The female laid 6 eggs and 2 young fledged. Habitat availability (within 1 km of the nest) and habitat selection by pair C are shown in Table 7.15 (main habitats) and Table 7.16 (main/sub-habitats). Pair C's nest was situated close to the centre of a dairy and arable farming unit, and there was a strong separation within the feeding territory between highly improved pastures/arable land, and semi-natural bog and heath. Only half the area was grazed, of which 11.1% was by dairy cattle (which only graze fields intermittently) and 27.1% was rough grazing (including bog, wet heath, wet heath/acid grassland and saltmarsh) with a very low density of livestock.

Approximately 40% of the area comprised bog and heath, 38% improved pasture, and 11.7% arable crops. Although 38% of the total area was improved pasture, only 4.4% of the total area was permanently grazed (ie. not silage or dairy grazing)

Table 7.15 *Habitat selection by pair C for all fields within 1 km of the nest-site (total area 357.3 ha). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974). The number of Foraging trips >1 km from the nest-site is also given.*

Habitat	Grazed/ ungrazed[a]	Habitat area (%)	Foraging trip habitats (n)	Foraging trip habitats[b] (%)	95% Confidence limits of % trips lower	upper
Arable	U	11.7	4	1.5*	-1.61	4.55
Bog	G	23.0	7	2.6*	-1.44	6.56
Dunes >1 km	G	0	16	5.9	-0.12	11.84
Improved pasture	DU	33.6	40	14.7*	5.98	23.32
Improved pasture	G	6.2	76	27.8*	17.67	38.01
Marshy grassland	U	1.6	0	0	0	0
Permanent Pasture	G	1.5	6	2.2	-1.52	5.92
Salt marsh	U	2.4	0	0	0	0
Wet heath/acid grass	G	19.0	24	8.8*	1.7	15.88
Woodland	U	0.2	0	0	0	0

[a] G = grazed, DU = grazed by dairy cattle or ungrazed, LG = lightly grazed, rabbits, U = ungrazed.

[b] Figures with an asterisk are significantly different from expected (p <.05).

Table 7.16 *Habitat/sub-habitat preference of Pair C (based on habitat availability within 1 km of nest-site). Total area of all fields falling within 1 km of nest = 357.3 ha.*

Habitat/sub-habitat	Grazing regime	% area within 1 km of nest	% of all foraging trip habitats (*n*=173)	Jacobs index (1974)
Barley	Ungrazed	10.4	2.3	-.66
Bog	Sheep/mixed	4.2	0.0	-1.00
Bog	Ungrazed	17.4	0.0	-1.00
Dyke	-	1.7	4.0	.42
Dunes >1 km	Sheep/Beef C.[a]	0.0	9.2	-
Marshy grassland	Ungrazed	1.6	0.0	-1.00
Moss pasture	Sheep/Beef C.	1.5	4.0	.47
New reseed	Dairy	0.3	0.6	.32
New reseed	Ungrazed	8.2	1.2	-.77
OIP	Sheep/Beef C.	1.4	5.8	.62
OIP + *Juncus*	Sheep	1.6	0.0	-1.00
Permanent pasture	Sheep	1.5	2.3	.22
Raised beach pasture >1 km	Sheep/Beef C.	0.0	1.2	-
Rape	Ungrazed	1.3	0.0	-1.00
RIP	Dairy	10.8	4.6	-.43
RIP	Sheep	1.1	19.7	.91
RIP	Ungrazed	14.3	16.8	.09
Wet heath/acid grassl'd	Sheep	19.0	13.9	-.19
Reseed	Sheep	0.3	14.5	.96
Saltmarsh	Sheep	2.4	0.0	-1.00
Wood	Ungrazed	0.2	0.0	-1.00

[a] Beef C. = Beef cattle

Nine per cent of pair C's foraging trips were to dune systems 7 km distant from the nest-site. This probably under-represents the total amount of time spent feeding in this habitat since most of the trips to dunes were of longer duration (1 - 1.5 hrs) than trips to habitats nearer the nest-site. The raised beach pasture used outwith the 1 km nest radius appeared to be used as a stop off point on the way to and from the dune system.

Of the main habitats used by this pair grazed improved pasture was significantly preferred, whilst ungrazed/dairy cattle grazed improved pasture, arable, bog and wet heath/acid grassland mosaic were significantly non-preferred. Marsh grassland, salt-marsh and wood were avoided.

Habitat/sub-habitat preferences (Table 7.16) followed the same general pattern as for main habitats. Within grazed pastures there was a suggestion of increasing preference for younger aged pastures (Jacobs indices: reseed 0.95, RIP 0.91, OIP 0.62, PP 0.22). Preferred sub-habitats included dykes (within improved pasture) and moss pasture (within bog). Non-preferred sub-habitats included RIP grazed by dairy cattle. OIP+*Juncus* was avoided.

Recently improved pasture (RIP) had the highest availability of all pasture types within 1 km of the nest (26.2% of total area), but its utilisation by feeding Choughs was strongly influenced by land-use. Mixed sheep/beef cattle-grazed RIP was highly preferred, pasture saved for silage was used approximately in proportion to its availability, and pasture used for grazing by dairy cattle was non-preferred. In Figure 7.15 the use of recently improved pasture in relation to grazing regime is shown during the breeding period (April - June). Pastures managed for dairy cattle grazing were used very little. Silage pastures were used early in the season (prior to growth of the crop) and after the silage was harvested in July. Sheep/beef cattle-grazed RIP was used throughout the season, particularly from mid-May to the end of June during the peak period of chick growth. Figure 7.16 shows variation in sward height in 3 RIP fields under each land-use. Each field was the most-used of its type by Pair C within their territory. Sward height was not measured in the silage field once it exceeded 15 cm, in order to avoid damage to the crop - but it continued growing after this time, and was probably 50-60 cm when harvested in early July. Sward height was similar in all fields early in the season. Sward-height in the dairy and silage fields exceeded 4 cm by the end of April, and fluctuated between 5-11 cm for the rest of the season in relation to the cycle of introduction and removal of the dairy herd. Sward height increased consistently in the ungrazed silage field. The sward in the mixed grazing field remained below 4 cm throughout the Chough's breeding season.

Sward height in the non-goose grazed field at Octofad Farm was 4-6 cm higher than in the goose grazed silage field in pair C's territory Figure 7.17. Mean sward heights were 5.24 cm (SD 1.98) on 5th April, 7.85 cm (SD=2.13) on 28th April and 12.47 cm (SD 4.81) on 14th May.

Figure 7.15 Proportion of time spent feeding in recently improved and reseed pastures in relation to grazing regime, Pair C.

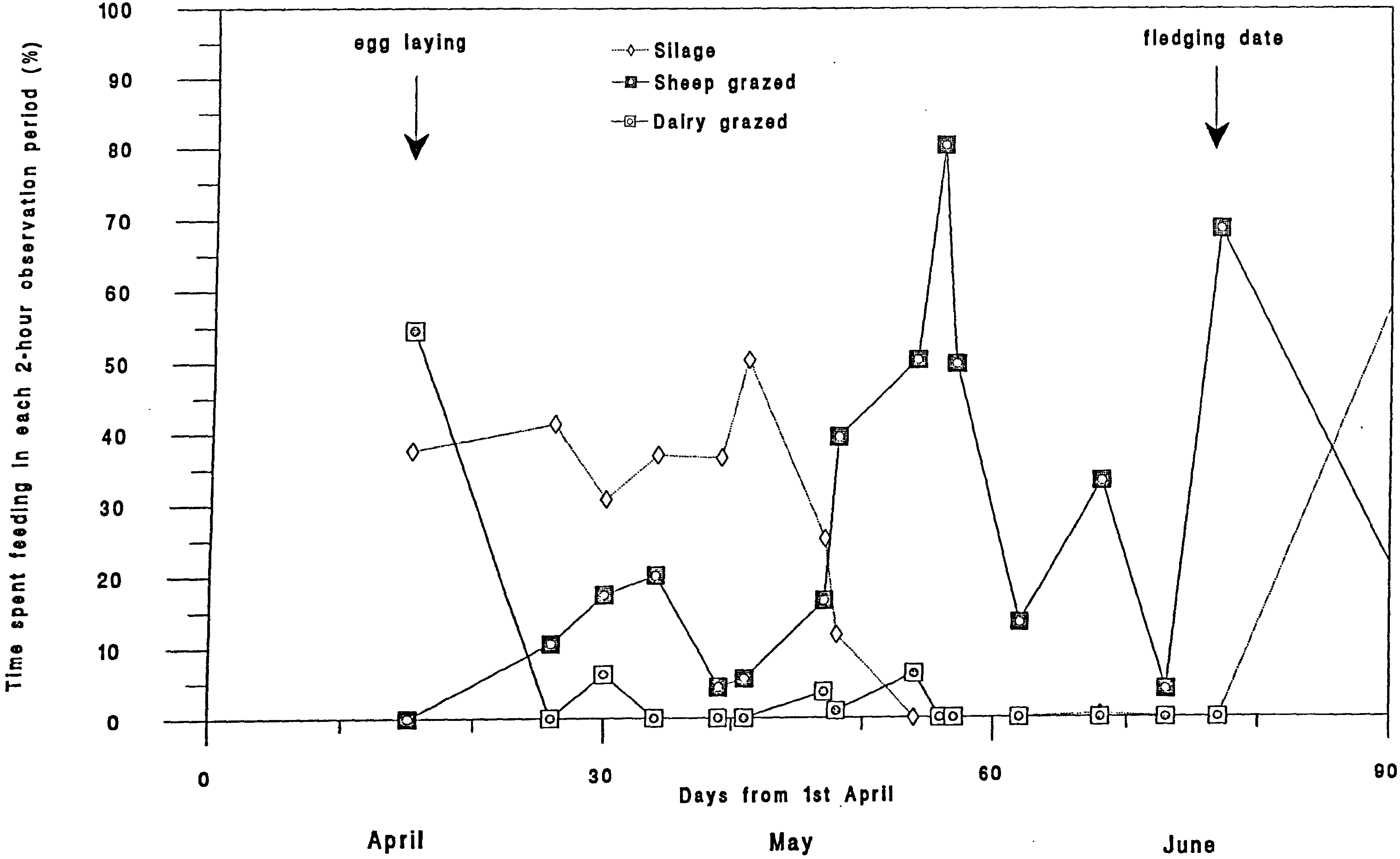
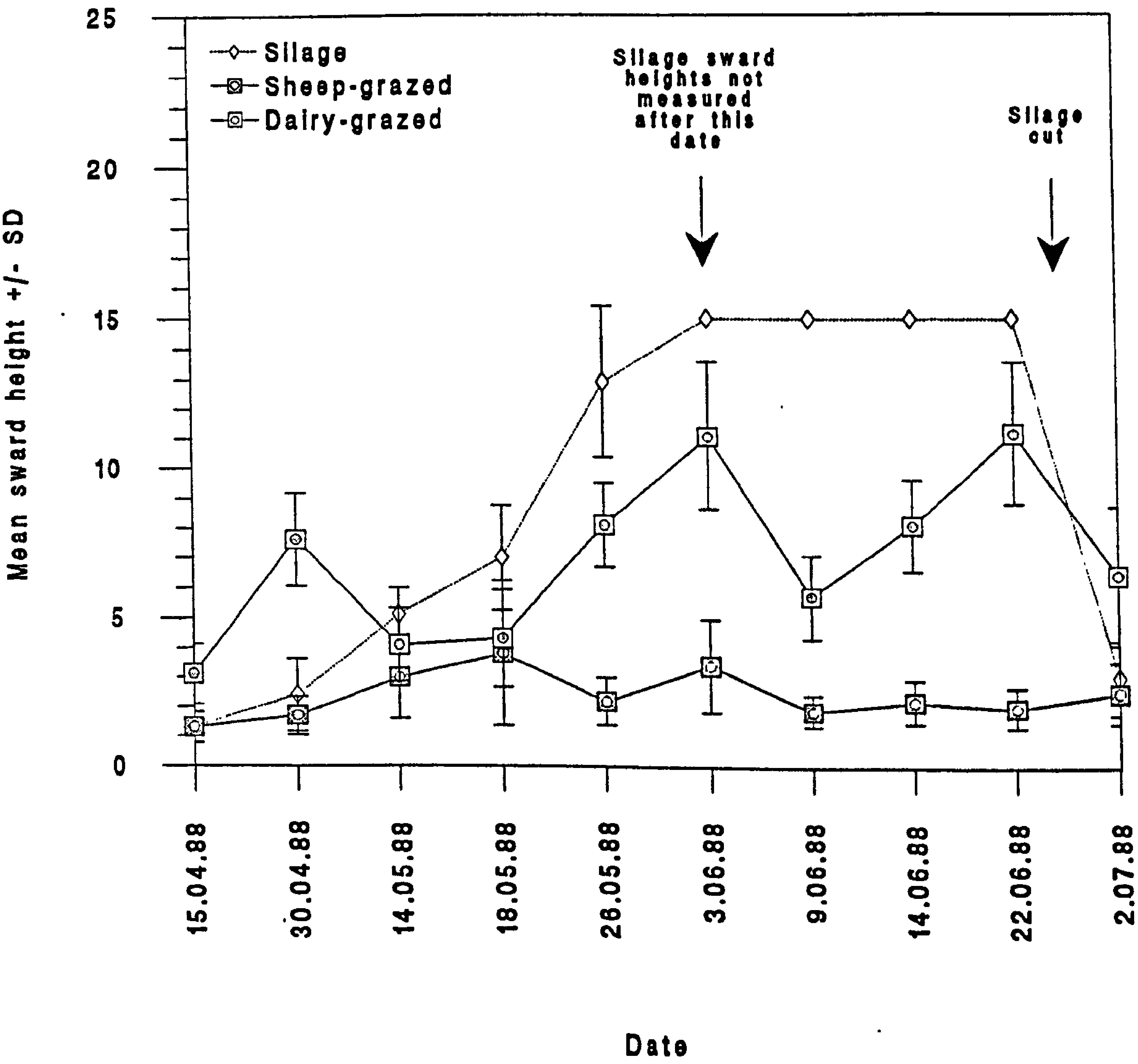


Figure 7.16 Mean sward height in 3 recently improved pasture fields with different grazing regimes within the feeding range of pair C.



Pair D

A total of 1770 minutes of observations were made on pair D during 23rd April - 24th June, comprising 20 foraging trips. The total feeding range (excluding sea) was 163 ha. The female laid 5 eggs and 3 fledglings were reared. Habitat selection data are presented in Table 7.17. Due to the small number of foraging trip habitats (*n*=49) the error margins are large. The main habitats within 1 km of the nest-site were bog (38.6%), an immature dune system (24.9%) and permanent pasture (12.9%). There was slightly more grazed improved pasture (7.7% of the total area) than ungrazed improved pasture (6.1%). Only one habitat showed a significant difference from expected, this being a significant preference for grazed improved pasture fields. Other habitats were used in proportion to their availability except bog, wet heath, marshy grassland and sea/inter-tidal, which were avoided. 42.9% of pair D's foraging trip habitats were in a heavily grazed mature dune system *c.* 2.5 km from the nest-site.

Table 7.17 *Habitat selection by pair D within 1 km of the nest-site (total area 314.2 ha). Habitats are described in Table 7.1. The 95% confidence limits were calculated according to Neu* et al. *(1974). The number of Foraging trips >1 km from the nest-site is also given.*

Habitat	Grazed/ ungrazed[a]	Habitat area (%)	Foraging trip habitats (n)	Foraging trip habitats[b] (%)	95% Confidence limits of % trips lower	upper
Bog	G	38.6	0	0	0	0
Dunes (mature) >1 km	G	-	21	42.9	-	-
Dunes (imm.) ≤1 km	LG	24.9	11	22.4	7.0	37.8
Improved pasture	G	7.7	12	24.5*	8.7	40.3
Improved pasture	U	6.1	1	2.0	-3.2	7.2
Permanent pasture	G	12.9	4	8.2	-1.9	18.3
Marshy grassland	G	0.7	0	0	0	0
Sea/inter-tidal		6.8	0	0	0	0
Wet heath	G	2.2	0	0	0	0

[a] G = grazed, DU = grazed by dairy cattle or ungrazed, LG = lightly grazed, rabbits, U = ungrazed.

[b] Figures marked with an asterisk are significantly different from expected ($p < .05$).

Pair E

Only 570 minutes of observations were made on Pair E, comprising 16 foraging trips. The total feeding range (excluding sea) was 75 ha. the female laid 5 eggs and 3 fledglings were reared. This pair foraged mostly in a mature dune system >1 km from the nest-site, in which it was impossible to track the birds' movements. Habitat preference within 1 km of the nest-site is shown in Table 7.18. The area within 1 km of the nest was dominated by bog (38.4%), sea/inter-tidal zone (28.3%) and a variety of pasture habitats. The only habitat used within 1 km of the nest was grazed, improved, pasture, this being preferred (Jacobs Index 0.65). All other habitats were avoided. Over 70% of foraging trip habitats were in a mature dune system *c.* 1.5 km from the nest.

Table 7.18 *Habitat selection by pair E within 1 km of the nest-site (total area 314.2 ha). Habitats are described in Table 7.1. The number of foraging trips >1 km from the nest-site is also given.*

Habitat	Grazed/ ungrazed[a]	Habitat area (%)	Foraging trip habitats (n)	Foraging trip habitats[b] (%)	Jacobs Preference Index (1974)
Bog	G	38.4	0	0	-1.0
Coastal grassland	G	4.9	0	0	-1.0
Coastal grassland	U	2.5	0	0	-1.0
Dunes (mature) >1 km	G	-	16	72.7	-
Improved pasture	G	7.3	6	27.3	0.65
Improved pasture	U	10.7	0	0	-1.0
Permanent pasture	G	0.7	0	0	-1.0
Permanent pasture	U	1.6	0	0	-1.0
Road	U	0.2	0	0	-1.0
Sea/inter-tidal		28.3	0	0	-1.0
Wet heath/acid grass	G	5.4	0	0	-1.0

[a] G = grazed, DU = grazed by dairy cattle or ungrazed, LG = lightly grazed, rabbits, U = ungrazed.

[b] Figures marked with an asterisk are significantly different from expected (p <.05).

Prey density in most-used improved pasture fields of pairs B and C.

In Table 7.19 the role of food availability in influencing the amount of time spent feeding in improved pasture by Pairs B and C is shown. Invertebrate sampling methods are described in Chapter 8; only the abundance of Tipulid larvae is considered here since this was the main prey item taken in improved pastures (see Chapter 8). Tipulid density is relatively low by May, so the error around the mean estimates is high due to the large number of cores containing no Tipulids. Even so, the density estimates for fields sampled more than once did not vary greatly, and it is thought that the methods used provide a reasonable estimate of Tipulid density; a similar sampling effort was used by Tinbergen (1986) to assess Tipulid availability in pastures used by foraging Starlings.

Tipulid densities were roughly similar in the three pasture sub-habitats in pair B's territory, 17-24/m^2, whereas there was a three-fold variation in field usage, with the OIP field being least-used, and the reseed field being most-used.

Table 7.19 *Density of* Tipula paludosa *larvae recovered from soil core samples taken in the most-used improved pasture feeding fields of Pairs B and C.*

Date	Field	Habitat/ Land-use	% of all imp'd past. feeding obs.[a]	Number of soil cores in sample	Number of Tipulid larvae	Density per m^2	Stand. error
PAIR B							
17.05.88	B02	OIP-gzd[b]	10.4	52	3	17.39	9.84
19.05.88	B15	RIP-gzd[c]	23.7	50	3	18.08	10.22
11.05.88	B17	RS-gzd[d]	32.9	70	4	17.22	8.42
09.06.88			32.9	50	4	24.11	11.75
PAIR C							
15.05.88	C04	RIP-DG[e]	9.0	48	5	31.3	13.41
15.06.88			9.0	44	4	27.3	13.20
18.05.88	C11	RIP-sil[f]	18.6	52	8	45.2	14.76
5.07.88			18.6	45	9	60.3	18.17
10.05.88	C21	OIP-gzd	7.9	29	6	62.3	27.42
16.06.88			7.9	44	7	47.9	16.82
17.05.88	C24	RIP-gzd	32.5	50	2	12.1	8.44
18.06.88			32.5	48	1	6.2	6.28
15.06.88	C06	RS-gzd	23.6	25	1	12.0	12.05

[a] Total number of feeding minutes: pair B = 1085, pair C = 1216.
[b] Old improved pasture - sheep/beef cattle grazed
[c] Recently improved pasture - sheep/beef cattle grazed
[d] Reseed - sheep grazed
[e] Recently improved pasture - Dairy cattle grazed
[f] Recently improved pasture - silage crop

A similar pattern was shown in the permanently grazed fields in Pair C's territory, but here Tipulid density was approximately five times greater in the (least-used) OIP field as compared to the reseed and RIP fields in which the pair spent 300-500% more of their foraging time. Clearly, the amount of time spent foraging in fields cannot be explained simply in terms of prey abundance.

In the dairy cattle-grazed and silage fields in pair C's territory, Tipulid density was relatively high (27-60/m^2) throughout the breeding season. This suggests that the non-use of these fields by pair C once the sward exceeded 4 cm was not due to concomitant changes in invertebrate abundance.

Sward characteristics of grazed pasture fields

The sward characteristics, distance from nest and Jacobs preference indices for the 3 most-used fields within the territories of pairs B and C are shown in Table 7.20. There was no consistent pattern in usage in relation to distance from nest, and sward heights in all fields were almost identical (range 1.62-1.92 cm). However, there was a simple positive relationship between field usage and sward bareness - the barer fields were used more than those with a tight sward, and field bareness showed a negative correlation with number of years since reseeding. The comparison is particularly valid for fields C21 and C24 which were equidistant from the nest, and were part of the same grazing unit (stock could wander freely between fields).

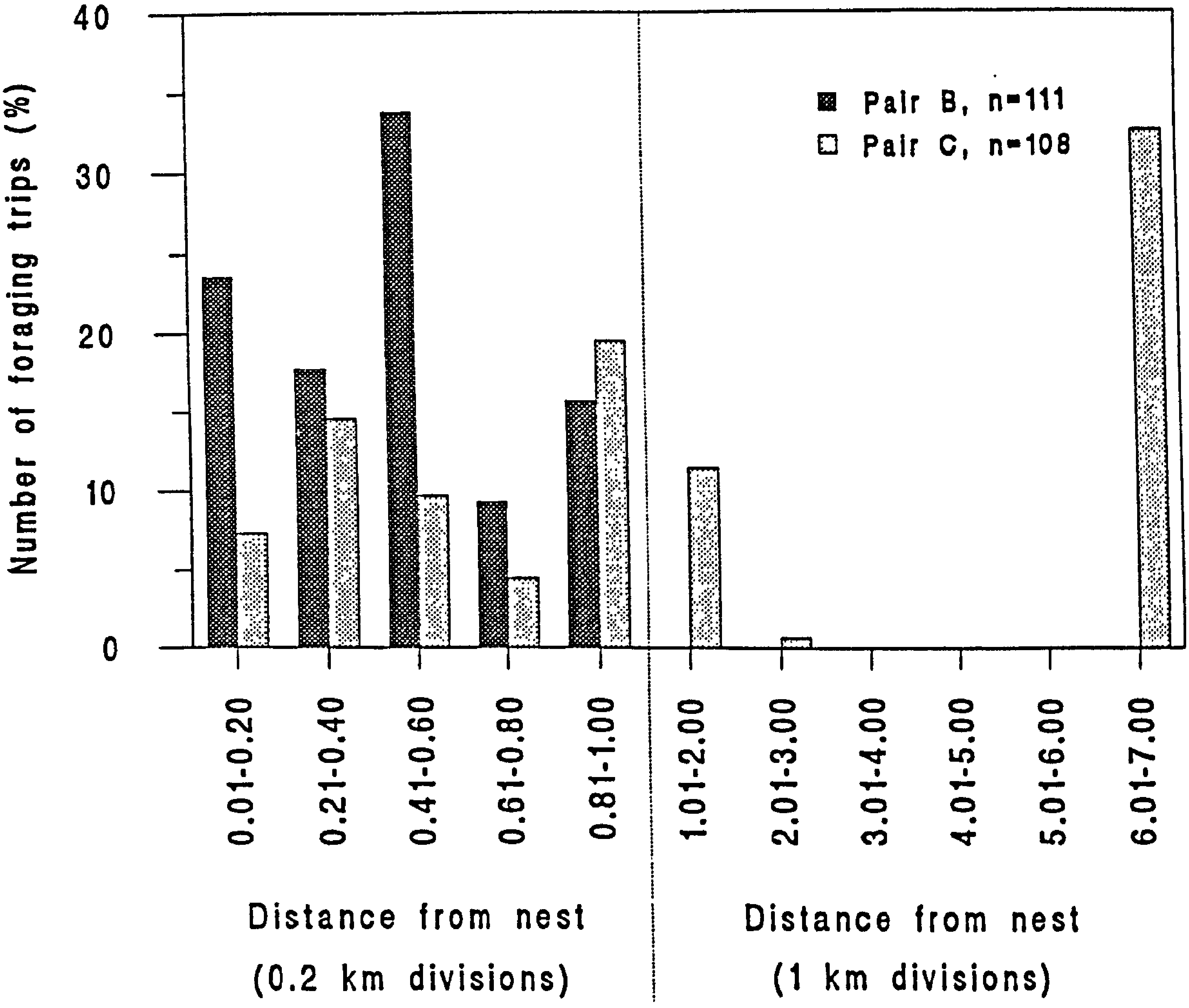
Table 7.20 *Comparison of vegetation characteristics of the most-used permanently grazed improved pasture fields in the feeding territories of Pairs B and C, 27-28th May, 1988.*

Field	Sub-habitat	Jacobs Preference index	Distance from nest (km)	*n*	Mean sward height (SE) cm	Mean sward bareness (SE)
PAIR B						
B02	OIP	.54	0.1	25	1.62 (.11)	.04 (.04)
B15	RIP	.65	0.9	25	1.85 (.20)	.78 (.10)
B17	Reseed	.94	0.6	27	1.89 (.15)	1.33 (.21)
PAIR C						
C21	OIP	.51	0.7	25	1.72 (.15)	.08 (.06)
C24	RIP	.86	0.8	31	1.77 (.11)	.55 (.12)
C06	Reseed	.95	0.2	26	1.92 (.16)	1.15 (.19)

Foraging distance

Figure 7.18 shows the number of foraging trips to fields at different distances from the nest by Pairs B and C during the breeding season (mid-April to late June). To avoid difficulties over

Figure 7.18 Distance from nest of foraging trips, pairs B and C



what constitutes an independent feeding incident fields were only included once for each foraging trip. The median field distance for pair B was 0.38 km (*n*=111), and for pair C, 0.75 km (*n*=108). The difference was significant (U = 2825.5; z = -6.79; *2-tailed* P = < .001, Mann-Whitney *U*-test).

7.3.4 Land-use on the Rhinns of Islay and the Rhinns of Galloway

The Kilchoman parish covers a total of c.138 km^2, compared to 28.3 km^2 for the parish of Portpatrick. Rough grazing comprised c.75% of all land at Kilchoman, but only 30% at Portpatrick. Habitat composition within the remaining improved land for both parishes is presented in Figures 7.19 and 7.20. There were no great differences between parishes in the proportions of improved land-types. Both comprised approximately 60% improved pasture, with Portpatrick having proportionally more cereals (7-24%) and Kilchoman proportionally more hay/silage (14-41%). The proportion of hay/silage increased in both areas from 1965 onwards as silage production increased in popularity as a means of saving winter fodder.

In contrast, there were marked differences in the proportions of the different types of livestock in the two parishes. In Portpatrick 55-82% of livestock units were dairy cattle, compared to 21-51% at Kilchoman, whereas sheep represented 25-36% of livestock units at Kilchoman compared to 9-16% at Portpatrick. In both areas, horses declined from c.10% in 1915 to <1% in 1985.

Figure 7.19 Composition of improved farmland, Kilchoman parish Islay, 1915-85

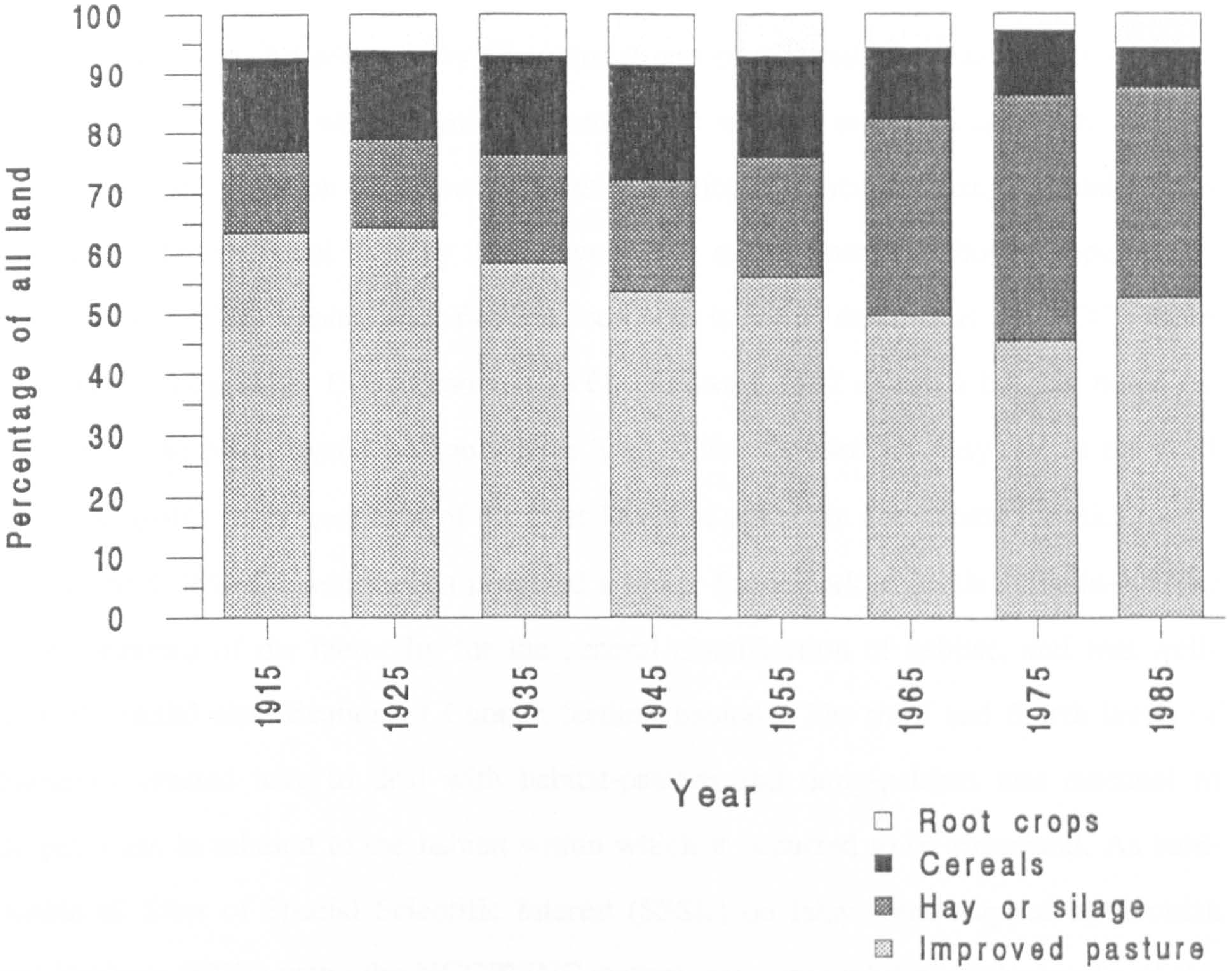
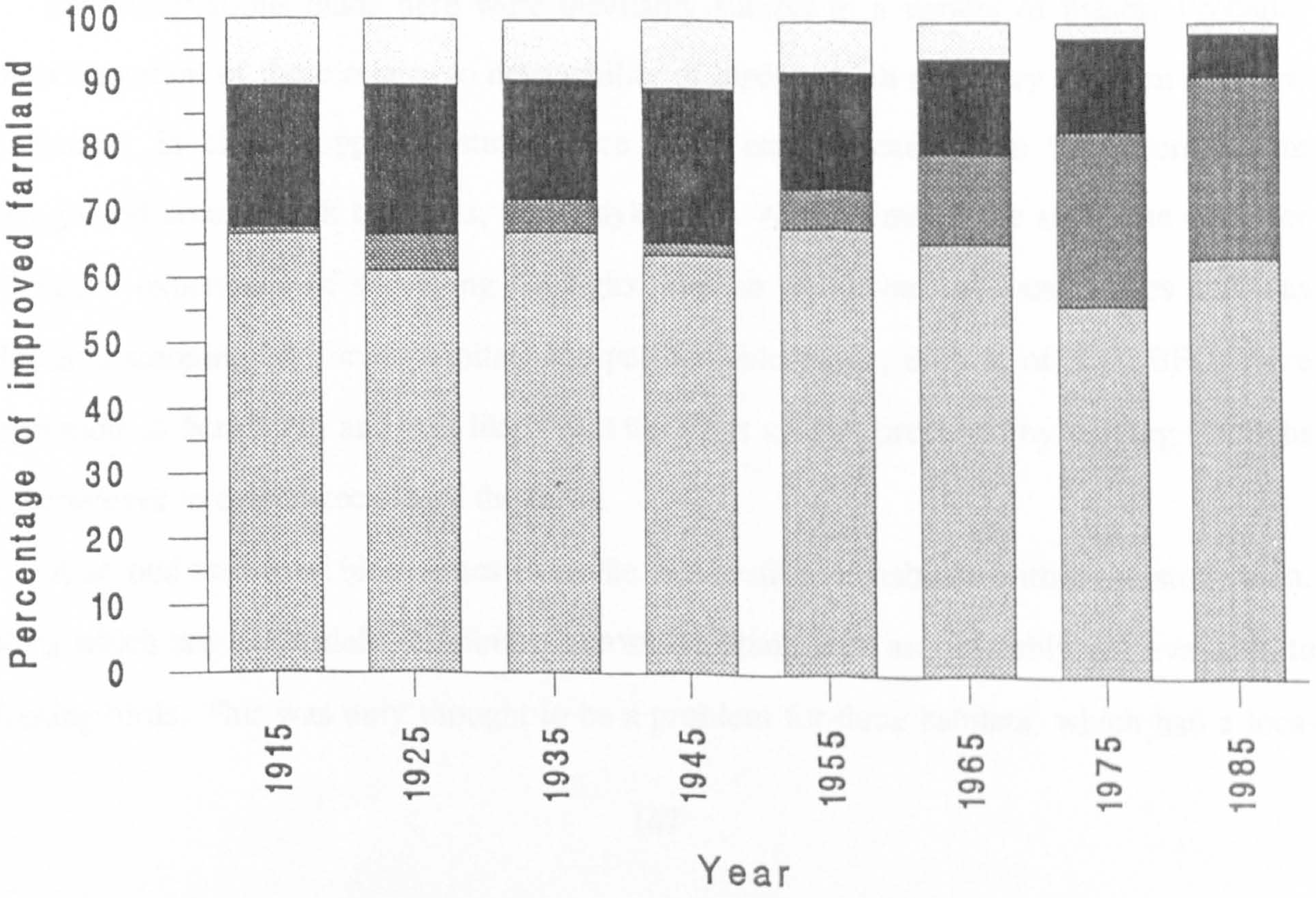


Figure 7.20 Composition of improved farmland, Portpatrick parish Wigtonshire, 1915-85



7.4 DISCUSSION

In studying habitat use and selection by Choughs, it was considered important in this study to use a habitat classification which would be compatible with an existing classification. This would facilitate interpretation of the results within a national habitat context, and make them easily understood at the local level by those involved in management of Chough populations. The NCC/RSNC (1986) habitat classification used here is not as detailed as the NCC's more recent National Vegetation Classification (NVC) (Rodwell 1982 *et seq.*) but, as noted by Meyer (1991), the NVC would probably have been a) too detailed for easy use in the field and b) too inflexible in its treatment of the finer levels of patch use and habitat mosaics.

The NCC/RSNC classification provided a broad framework at levels 1 (main-habitat) and 2 (sub-habitat) of the hierarchy for the general classification of habitat, and was well-suited to the initial classification of Chough feeding habitats. The third and fourth levels of the hierarchy created here to deal with habitat-patches and dung-patches was essential to enable patch use in relation to the habitat within which it occurred to be examined. As habitats within all Sites of Special Scientific Interest (SSSIs) on Islay were mapped by Scottish Natural Heritage (SNH) using the NCC/RSNC system, the compatibility of the results of this study should greatly facilitate their interpretation and implementation by local SNH staff in relation to their own Chough monitoring and management programmes within Islay SSSIs.

The observations made here were inevitably subject to a variety of biases. Probably the most important of these relates to detectability of birds, which may vary between habitats. Birds feeding in close-cropped pastures were more easily located than birds foraging in broken ground around rock outcrops, along dykes etc. At the time of the study the observer had 2 years' experience of surveying Choughs, and so was aware of these biases and was assiduous in scanning "difficult" habitats and patches. Moreover, 89.5 % of 1266 BFOs were in vegetation $\leq$ 5cm high, and it is likely that the short swards preferred by feeding Choughs lend themselves to easy detection of the birds.

A second source of bias comes from the distribution of habitats within the study area. Habitats which are not widely distributed across the study area are probably not available to all feeding birds. This was only thought to be a problem for dune habitats, which had a localised distribution in two areas within the study area. I considered leaving these squares out of the analysis, but they were used extensively by non-breeding birds and breeding pairs. For these reasons the squares were retained, but it should be borne in mind that the results on dune habitat use form the Rhinns transect data are probably conservative. An analysis of the influence of habitat on nest-site occupancy on the entire Rhinns peninsula (Appendix 4) showed that nest-sites in areas with dunes had high occupancy rates by breeding Choughs. The importance of dunes was also shown by studies on individual breeding pairs (see below).

There were fewer biases inherent in the observations made on the study pairs. These observations provide a useful comparison with the Rhinns transects, although they were restricted to the breeding season only. Attempts were made to observe habitat use by the study pairs outwith the breeding season, but the data collected were not evenly spread across the year, and there were obvious biases involved in the initial location of these pairs (there were many occasions when pairs were not found, which would invalidate conclusions drawn only from occasions when birds were found). Clearly, the only way to make unbiased observations on individual pairs outwith the breeding season is by the use of radio-tracking equipment, but at the time of the study this was considered to be inadvisable, due to the sensitivities of the local human population to conservationists (see Chapter 2).

7.4.1 Seasonal Habitat use on the Rhinns.

When interpreting the results on habitat preference and habitat use it is important to appreciate the difference between preference and use (as indicated by the total monthly percentage of BFOs). Only those habitats with no BFOs were totally avoided by feeding Choughs. Non-preferred habitats may still support a significant proportion of feeding birds in absolute terms. Moreover, when considering the habitat composition of a hypothetical ideal Chough territory, relatively small areas of the most preferred habitats should satisfy the Chough's feeding requirements, whereas proportionally larger areas of less-preferred habitats are likely to be needed.

Analysis of habitat selection by feeding Choughs at the first level of the habitat classification (main-habitat) reveals a simple pattern of habitat use. Habitats with a tall vegetation structure were avoided completely (wood, tall fen and bracken). "Wet" or wet-peat based habitats (bog, flush, marshy grassland, wet heath and wet heath/acid grassland mosaic) were non-preferred. [It should be noted that wet heath is not literally a wet habitat, the wet prefix indicates dominance of plants with a preference for moist rather than dry peat eg. Cross-leaved Heath *Erica tetralix* rather than Bell Heather *Erica cinerea*; in the summer months, such habitats may be completely dry on the surface]. Most of these "wet" habitats also have a relatively high vegetation structure (> 10 cm), especially marshy grassland. In contrast, dry heath/acid grassland mosaic was used more than wet heath habitats despite its more limited extent, and was significantly preferred in the summer. Pasture and dune habitats were much used throughout the year, and were significantly preferred in most seasons. When combined they accounted for more than 50% of BFOs in all seasons.

Improved pasture was generally used more than permanent pasture and semi-improved permanent pasture. Use of dunes fluctuated through the year, possibly resulting from the chance presence/absence of flocks of non-breeders in the dune system during the short time window (c. 1 hour) needed to survey this habitat. However, the presence of large flocks of non-breeders (up to 45 birds) in the dune system in several months of the year, plus high nesting densities adjacent to dunes suggests that this is a very important feeding habitat. This is supported by the fact that 4 of the 5 study pairs spent a large proportion of their time foraging in a mature dune system, despite the fact that this was distant from most nest-sites (see below). This suggests that dunes must provide high quality and/or a high quantity of food to offset the energetic costs involved in commuting further from the nest. Within dune systems, grey dune and dune pasture were the most-used sub-habitats, these having the most highly stabilised substrates.

Bearing in mind its proximity to many nest-sites on the Rhinns transect, it is surprising to note the low usage of coastal grassland and cliffs by foraging Choughs. This finding conflicts with the results of the analysis on nest-site occupancy described in Appendix 4 which showed a significant positive relationship between nest-site occupancy and area of coastal grassland. It is possible that birds foraging on coastal cliffs/coastal grassland may have been more difficult to detect that birds in inland areas. Arable and beach habitats were used primarily in the autumn. This may suggest that this is a period of low invertebrate availability in the pastoral habitats used throughout the rest of the year. There was a large proportion of arable habitat within 1 km of the nest of pair C, but it was rarely used (April - June). When the arable fields were used it was notable that the birds fed in the unploughed headlands at the edges of the fields rather than in the arable crops themselves.

Within improved pastures Choughs generally fed within the habitat itself, rather than within patches of other habitats, suggesting that these are preferred habitats in their own right. Improved pasture was least-used in summer. This probably reflects the fact that many improved pastures would have been used as silage at that time of year, and would therefore have unfavourable sward heights for foraging Choughs from May onwards (see below). Old improved pastures may be more important at this time of year since they are more likely to be grazed throughout the summer than recently improved pastures/reseeds. Reseeds were highly preferred in the early months of the year on the Rhinns, and by the two study pairs whose feeding territories each contained permanently grazed reseeded fields which were grazed throughout the summer.

The improved pasture sub-habitats described here are evidently closely related to each other. It is possible therefore that in the absence of any one of these sub-habitats in a particular area, another closely related sub-habitat could just as easily be used by foraging Choughs. Whether this is so could only be addressed by making similar observations in a different study area which contained different proportions of these sub-habitats.

7.4.2 Seasonal Patch use on the Rhinns.

The habitat analysis described above gives no clue as to whether Choughs are utilising the dominant habitat itself, or a patch within it. Analysis of patch use showed that in some habitats Choughs <u>only</u> used patches of some other kind of habitat. The general pattern was for patch use to be low in preferred habitats, but high in non-preferred habitats. There was also a general tendency for patch-types located within preferred habitats to be preferred over the <u>same</u> patch-types within non-preferred habitats.

For some patch types the habitat within which they occur appears to be important in determining their use. For example, rock outcrops and dykes within improved and permanent pastures were preferred to those within coastal grassland, bog and wet heath. This highlights the subtlety of the relationship between habitat and patch use, and the importance to feeding

Choughs of mosaics or juxtapositions of patches within other habitats. The very high selection indices for patches such as rock outcrops within permanent and improved pastures suggests that this is the result of a positive preference for these patch-types, rather than the chance occurrence of birds within these patches due to their associating with the dominant habitat. A clear example of this is provided by the high preference indices for rock outcrops in improved pasture in June, August and October, at a time when use of improved pasture itself reached its lowest levels.

The most frequently used habitat-patches were rock outcrops and dykes (earth banks with or without walls) or other types of field boundaries (excluding hedges, which were unused); these accounted for over 30% of monthly BFOs in December, January and February. There was a tendency for these patches to be used more when they occurred within permanent or improved pasture rather than in heath, bog or coastal grassland. They were used most in the winter months and in late summer.

A more nebulous patch-type was that of soil exposures. It was not always possible to classify feeding observations as belonging to this type, but clear-cut examples included birds feeding along tractor ruts through fields, along track-sides, steep banks, at rabbit burrow entrances and in bare areas within fields. It is probable that a proportion of dyke and rock outcrop BFOs related to birds feeding at soil exposures within these habitat features.

Feeding at or near sheep carcases accounted for a relatively small overall percentage of BFOs, but could have been important feeding sites to individual pairs. 4% of all feeding observations for study pair C where patch use was known (ie. excluding the observations from the dune system where the birds were out of sight) were at a single sheep carcase in an area of rough pasture. This was the only carcase that I could find on a thorough search of the whole territory, so it is possible that had there been more carcases available to this pair, carcase-use would have been greater. Some carcase-feeding incidents on the Rhinns were recorded from "carcase dumps", areas where farmers dump or bury carcases - usually situated well away from farm buildings and in a soft substrate (peat/bog) which facilitates easy burying. Although all recorded carcase feeding incidents were associated with sheep carcases, I have also seen Choughs feeding at cow, deer and goat carcases in other parts of Islay, and at all times of year. In January 1987, during an unusually cold spell which lasted for 7 days (lowest overnight temperature -7°C), I attempted to follow one pair of Choughs on the Oa throughout each day. Up to 22.5% of 27 feeding events recorded for this pair were at either a carcase dump or at 4 sheep/goat carcases in their feeding territory. It is possible that carcases provide important feeding opportunities during such cold periods, when sub-surface prey are unavailable due to the frozen ground.

Dung

Another important patch type was herbivore dung, mostly cow dung, used between June and December, and mostly associated with permanent pasture (including semi-improved permanent pasture and permanent pasture patches within dry heath/acid grassland) and dunes, rather than with improved pasture or "wet" habitats. This habitat association may be related to substrate preferences of the adult Scarabaeid beetles. The main dung beetle associated with cow-pats in autumn on Islay is *Aphodius rufipes* (*pers. obs.*). This species lays its eggs in the substrate below the dung, the larvae develop in the pat and once mature, burrow into the soil below the pat to hibernate as prepupae until pupation in the following summer (Holter 1979). It is possible that permanent pasture and dry heath provide the right substrate for the egg-laying female and/or the burrowing/hibernating larvae.

The low occurrence of sheep dung-feeding observations was unexpected, since sheep dung is generally abundant and widely dispersed over most habitats, and supports its own dung fauna. It is possible that sheep-dung feeding incidents were under-recorded due to the difficulty of spotting the smaller dung at a distance, and due to the short time spent by birds at individual droppings. In contrast, cow-dung feeding is readily identified due to the flicking away of large quantities of faecal matter by feeding birds, and by their spending more time at individual cow-pats than at sheep droppings.

Dung-feeding accounted for a significantly greater proportion of summer and autumn feeding incidents of first-year birds than of older birds. This difference may be related to the lack of feeding experience of the younger birds, for which dung provides an easily recognised feeding site, and a "habitat" which requires little "skill" to obtain food from compared to, for example, probing in pastures. Age-related differences in foraging success have been demonstrated in many bird species. Stevens (1984) showed a similar scenario in juvenile Starlings which fed on cultivated cherries (*Prunus sp.*) in the summer and autumn because these required less skill to find than Tipulid larvae which were fed on primarily by adults.

The lower preference for dung-feeding amongst adult birds suggests that dung may not be a "preferred" feeding habitat for this age group. The physical nature of dung (especially cow dung) varies with age - being semi-liquid when fresh, but drying (in favourable weather conditions) as it matures. There can be little doubt that a moist/dry mature pat containing abundant dung beetle larvae represents a rich feeding site for Choughs of all ages. However, from November onwards most cow pats contain only the larvae of the Yellow Dung Fly *Scathophaga stercoraria* (*pers. obs.*), which mature rapidly (Laurence 1954) and thus can be found in semi-liquid dung. Adults were rarely seen feeding in this "immature" dung, but first-year birds fed in it through until January, when the *Scathophaga* larvae become scarce (Gibbons 1987). Perhaps the wetness of the dung or possibly a lower profitability when containing only *Scathophaga* larvae makes this type of dung non-preferred by adults. Inexperienced first winter birds may have little choice but to continue feeding in dung until they become efficient feeders in other habitats.

The greater importance of dung-feeding to first winter Choughs has important conservation implications. From June through to mid-winter dung appears to be an important source of easily obtained food for inexperienced birds. It may act as a "buffer" until such time as these birds learn to feed in habitats which require more specialised feeding techniques. First-year Choughs suffer high levels of mortality (25% die within 4 months of fledging, and 29% within their first year (Bignal *et al.* 1987b). The presence of cow dung may be particularly important to their over-winter survival.

7.4.3 Study pairs

Although the 5 study pairs nested in areas of contrasting habitat and land-use, their habitat selection shared several common features. Firstly, most pairs showed a significant preference for grazed improved pasture, but not for ungrazed improved pasture. Dune habitats were also very important, despite the fact that they were found mostly at distances >1 km from the nest-site. For pair D and the female of pair A there was a suggestion that mature dunes were preferred to immature dunes, as both flew further to feed in the former. This may have been due to the fact that the mature dunes were heavily grazed by sheep and cattle, whereas only rabbits *Oryctolagus cuniculus* were present in the immature dunes in question. It is notable that the pair A female was prepared to fly 5 km to feed in mature dunes, despite the constraints imposed on her by her need to incubate. Pair C flew 7 km from the nest-site to feed in the same mature dune system, particularly later in the breeding cycle when most of the improved pasture habitats within 1 km of their nest-site had been ungrazed for several weeks.

The mature dune system in question was heavily grazed throughout the year by cattle and sheep, and comprised several sub-habitats, mostly the more stable dune grassland and grey dune, which can withstand heavy grazing pressure better than the more immature yellow dune and fore dune sub-habitats. The "catchment" area of this dune system for foraging Choughs during the breeding season extended to 7 km from the nest, including (unexpectedly) 4 of the 5 study pairs. Clearly, heavily grazed mature dunes are extremely important to foraging Choughs in the breeding season. However, non-systematic observations of other pairs nesting within this 7 km radius suggested that not all pairs used these dunes during the breeding season. Excluding "pair" A, the pairs which made "normal" breeding attempts (pairs C, D and E) and which used the dunes all successfully reared young. Pairs D and E nested <3 km from the dunes and reared 3 young each, whilst pair C which nested 7 km from the dunes reared only 2 young. The pair with the smallest feeding range (pair E) nested closest to the dune system of all study pairs (though still >1 km distant from it).

Pair B nested 8.5 km from the mature dune system and made no use of this habitat. This pair foraged entirely within 1 km of the nest-site. Their feeding range was extensively grazed by beef cattle and sheep. The pair foraged mostly in grazed improved pastures, wet heath/acid grassland mosaic and moss pasture (within bog). They successfully reared three young. Most improved pasture feeding occurred in a few fields, whereas birds ranged more widely in other habitats. This suggests that a relatively small proportion of grazed improved pasture (14.7%) within 1 km of the nest-site is sufficient to support breeding Choughs, but that a greater extent of other habitats may be required. Pair B had the second smallest feeding range of all study pairs..

Why then should some pairs fly several kilometres to feed in dunes? In the case of the pair A female, this would appear to have been due to the absence of improved pasture habitat close to the nest (2.4% of all habitats within 1 km of the nest-site). Similarly, there was only a small proportion of grazed improved pasture within a 1 km radius of the nest-sites of pairs C, D and E (<8% in each), compared to 14.7% for pair B. Moreover, the 1 km range of these pairs had a low availability the other habitats used by pair B - grazed heath/acid grassland, permanent pasture and semi-improved permanent pasture, and were dominated by bog (a significantly non-preferred habitat in all cases).

It is difficult to assess the roles of different habitats in the feeding ecology of the study pairs, in particular, the role of grazed improved pasture. Pair B had the largest area of this habitat within their 1 km range (14.7%), and this accounted for 67.6% of all foraging trip habitats. The question is, if there had been more of this habitat available, would it have been used more - perhaps up to 100% of foraging trips? Work by Tinbergen (1986) on the Starling suggests that this is unlikely. In his study, Starlings fed on Tipulid larvae in improved pasture fields. However, Tipulids were used only as a "quantity" prey item, and appeared to lack essential nutrients for chick growth. These were provided by feeding on Lepidopteran larvae in saltmarsh. A similar scenario may apply with Choughs. Invertebrate sampling (see Chapter 8) suggested that Tipulid larvae were the main prey item taken in improved pasture fields during the breeding season. In other habitats a greater diversity of prey is available, including dung fauna, and it is possible that as with the Starling, these other invertebrates are important components of the Chough's diet. Within 1 km of pair B's nest-site a wide range of feeding opportunities existed, since the bog, wet heath/acid grassland and permanent pasture habitats were all continuously grazed by both sheep and cows. Feeding observations showed that birds fed on spiders in moss pasture (when the chicks were young), and cow-dung fauna in wet heath/acid grassland, invertebrate groups which are likely to be high in nutrients (see Chapter 8). Such feeding opportunities were much more limited within 1 km of the nests of pairs C, D and E, and it may be this which caused them to use dune habitats so extensively. Dune habitats support a diverse dung beetle community (Fowles 1994) as well as a variety of Lepidopteran and Tipulid larvae (see Chapter 8). As such they may provide all the necessary components of the Chough's diet. This is supported by the observation that the feeding range of pair E (which nested close to mature dunes) was smaller than that of pair B, despite pair E having to fly 1 km to get to the dunes.

The habitat composition within 1 km of the nests of pairs B and C was broadly similar, but the land-uses contrasted markedly. The dairy farming unit within which the nest of pair C was situated meant that most of the improved pasture habitat was unsuitable for feeding (see section 7.4.4). Moreover, the permanent pasture, heath and bog habitats were only lightly grazed by small numbers of sheep. This contrasted with the 1 km range of pair B in which all habitats were heavily grazed by beef cattle and sheep. The contrast in the foraging behaviour of the two pairs suggests that both dairy farming (in agricultural habitats) and low grazing pressure (in semi-natural habitats) is detrimental to Choughs. The response of pair C to these land-uses was to forage up to 7 km from the nest in the mature dune system. Despite a presumably greater foraging effort, they reared one less chick than pair B, and in the absence of the dune habitat one wonders whether this pair would have been able to breed successfully. Non-systematic observations of pair C in 1987 suggested that the pair did not use the dunes during that year, and the pair's breeding attempt was unsuccessful (the young chicks apparently died of starvation when *c.* 10 days old). Could the pair have learnt that to rear young successfully they had to utilise the dunes?

7.4.4 Habitat structure

Sward height

Short sward height was an important structural feature of Chough feeding sites. Almost 90% of Chough feeding observations on the Rhinns were in swards estimated as being less than 5 cm high. The high vegetation profiles of heath and bog may be one feature which makes these habitats generally non-preferred, and why Choughs mostly used patches of permanent pasture or moss pasture (respectively) within these habitats. With the onset of spring grass growth, swards in improved pastures become too high for feeding Choughs unless they are grazed by stock. Grazed improved pastures were preferred during the breeding season by all study pairs, whereas ungrazed improved pastures were non-preferred. Fields grazed by dairy cattle are only grazed intermittently and were unused by pair C once the sward height exceeded 4 cm (despite the low availability of alternative pasture feeding sites within 1 km of their nest). A similar effect was found in silage fields which were preferred feeding sites of pair C prior to rapid grass growth in mid-May, after which they were unused until the after the crop was harvested (Figure 7.15).

The fact that silage pastures were preferred again once the silage had been harvested strongly suggests that it was changes in vegetation structure rather than food abundance which brought about this switch. This was demonstrated by invertebrate sampling in field C11 in pair C's territory, a silage field which prior to the rapid spring grass growth had been one of the favoured feeding fields of the pair. The abundance of Tipulid larvae in this field remained at roughly the same level once the crop began to grow (see Table 7.16) whereas the pair's use of the field dropped to zero when the sward was at its greatest height. Following harvesting of the crop in July, the pair (plus their 2 juveniles) spent 48-90% of two 2 hour observation periods feeding in this and one other silage cut field. The suggestion is that short vegetation structure makes the prey more available to probing Choughs.

Bareness

Study pairs B and C showed a preference for younger improved pastures, and this was mirrored on the Rhinns transects early in the year. This preference appears to be related to the greater bareness of the swards in younger fields, rather than to field age *per se*, or to invertebrate abundance. Newly reseeded fields have many bare interstices between the grass stalks, but as the pasture matures and the grass stems "tiller out" (produce side-shoots) as a result of grazing (see Spedding 1971), the bare patches are gradually filled in. Consequently old improved pastures typically show a tight-knit fibrous root and stem structure with few bare interstices. Sward bareness can also be produced as a result of poaching or treading by stock. In May 1988 pair C spent much time feeding in a well trodden area close to a gate entrance within silage field C11, at a time when the sward height in the rest of the field prohibited feeding. The importance of sward bareness is emphasised by the fact that pairs B and C continued to feed in reseeded and recently improved fields which had lower levels of Tipulid abundance than adjacent old improved pastures with less-bare swards. Again the suggestion is that prey items such as Tipulids are more available to feeding Choughs in fields with barer swards. This is discussed further in Chapter 8.

Several other species of birds have been shown to be dependent on short vegetation and bare ground for feeding. Two such species are the Woodlark *Lullula arborea* and Stone Curlew *Oedicnemus burhinus*. Both are British "Red Data Birds" (Batten *et al.* 1990) (c.220 and c.160 breeding pairs in 1990 respectively), and a decline in grazing pressure from rabbits following the outbreak of myxomatosis is thought to have been one of the factors responsible for the 20th century decline of both species (Bowden 1990, Green 1988). Galbraith *et al.* (1993) showed that the preferred feeding habitats of Dotterels *Charadrius morinellus*, another "Red Data Bird", not only had the shortest and sparsest vegetation, and that such areas had the highest densities of their main prey *Tipula montana*, but also , possibly "rendered the prey more conspicuous".

7.4.5 Land-use

Afforestation

Afforestation is inimical to Choughs on Islay. No Choughs were observed feeding in afforested habitats on the Rhinns transects, despite their covering 15% of the area surveyed. This result is easily interpretable in terms of the rapid development of rank vegetation within newly planted forestry plantations following the exclusion of grazing animals (Avery & Leslie 1990). Exclusion of grazing animals precludes the possibility of dung or carcase feeding opportunities - even within areas which may remain unplanted.

Marquiss *et al.* (1978) showed that a 45% reduction in the Raven population of the Southern Uplands of Scotland between 1946-75 was associated with large scale afforestation within the area. It is difficult to assess the immediate impact of the afforestation of 950 ha (almost 18%) of the Rhinns peninsula on its Chough population. Assuming that heath ((dry heath, dry heath/acid grassland, wet heath and wet heath/acid grassland) and bog were the main habitats afforested, then 48.8% of the Rhinns transect comprised these habitats prior to afforestation, of which 28.7% was subsequently lost. The monthly proportion of feeding observations for these habitats combined ranged from 0% (January and March) to 26.6% (August). If we assume that these habitats support 26.6% of the Rhinns Chough population in August, and that there are no alternative feeding sites to which these birds could switch, then the loss of 28.7% of bog and heath habitats may have reduced the area's carrying capacity for

Choughs by 7.6% (ie. 28.7% of 26.6%). This figure would be slightly higher for the Rhinns SSSI as a whole, where 35% of all bog and heath habitats were afforested, giving a reduction in carrying capacity of 9.3%. These estimates may be close to maximum estimates since most afforested areas are more than 1 km from the sea, thus not in close proximity to Chough nest-sites.

Analysis of patch use suggests that in August most Choughs in heath and bog habitats are dung-feeding, and that most of the birds involved are probably first-years. The loss of these habitats may therefore have a particular impact on the survival of young Choughs, as it is known that approximately 25% of first years die within four months of fledging (Bignal *et al.* 1987b).

The impact of the loss of heath and bog habitats is likely to be greater where afforestation has impinged on the feeding territories of breeding pairs. On parts of the east coast of the Rhinns, trees have been planted on former heath and rough grazing habitats to within 0.3 km of the coast, well within the foraging range of 6 pairs which nested along this stretch of coast in 1988. Observations of study pair B suggested that individual pairs may spend up to 30% of their feeding time in these habitats when they are extensive within 1 km of the nest (heath and bog *c.* 65% of pair B's territory, (see Tables 7.13 and 7.14)) and 18.2% of foraging trips included these habitats.

The proximity of forestry to the east coast of the Rhinns means that the foraging area of these pairs throughout the year is now confined to a narrow belt 0.3-1.5 km wide comprising mostly improved pasture. It was suggested for pair B that breeding pairs require a balance of grazed improved pasture and grazed semi-natural habitats for successful breeding. One can only speculate as to the role that afforestation may have already played in the observed reduction in the number of breeding pairs along this coastline from 6 pairs in 1988 to 3 pairs in 1993 (*per. obs.*).

Afforestation greatly benefits some bird species in the early years of tree growth, particularly predators of the Short-tailed Field Vole *Microtus agrestis*, which greatly increases in abundance following the removal of grazing animals. Such predators include the Short-eared Owl *Asio flammeus*, Barn Owl *Tyto alba* and Kestrel *Falco tinnunculus* (Avery & Leslie 1990). Evidence was provided in Chapter 4 that Barn Owls may be successful over

Choughs in competition for nest-sites, and Kestrels may also compete for nest-sites. An increase in population size of these species on the Rhinns might lead to their usurping some traditional Chough nest-sites. In 1993 a summering Barn Owl apparently caused the non-use of one such barn nest-site in the immediate vicinity of an afforested area, despite the fact that the resident pair were present early in the season and were observed nest-building (*pers. obs.*).

As the planted forest matures, it may also have "edge effects" on foraging Choughs, particularly on the east side of the Rhinns where the corridor effect described above will be most marked. Will Choughs be able to tolerate this "enclosure" of their environment? Hopefully the effects of tree growth on the number of breeding pairs and their foraging behaviour in this area will be monitored in years to come since, as stated by Avery & Leslie (1990) in relation to moorland birds, "there is little information on the indirect effects [of afforestation] such as might be mediated... by increased predation." In parts of Wales, local ornithologists have become concerned at the proximity of forests supporting Goshawks *Accipiter gentilis* to some inland Chough nest sites, which have recently been deserted (Cross *et al.* 1993).

Further afforestation on Islay seems unlikely in the current economic climate. The designation of the Argyll Islands ESA and the Farm Woodlands grant scheme may however provide financial support for planting of small woodlands/ copses. When mature, these copses could provide nuclei for nesting Rooks *Corvus frugilegus*; if competition between Choughs and Rooks can be demonstrated (see Chapter 4) then such developments should be carefully considered beforehand. The impact of tree planting could be minimised by planting species which are not preferred by nesting Rooks.

Farming systems

Some traditional land-features benefit Choughs on Islay. Many field boundaries on the Rhinns are dykes (walls plus earth banks), which provide feeding sites (primarily soil exposures) which would not be available if the field boundaries comprised simple fences or walls. Likewise small field sizes increase the total availability of dyke-feeding opportunities per unit area. Modern farming trends towards larger field size and the use of fences without dykes are to the detriment of Choughs.

It is clear that the pastoral habitats and land-uses found on Islay are suited to the feeding requirements of Choughs. The island's climate favours pastoral agriculture, particularly through its mild winters which ensure a long growing season for grasses, which in turn provides good conditions for rearing sheep and beef cattle. These animals produce the right habitat structure and habitat components for feeding Choughs. Study pair B nested in a mixed sheep/beef farming unit most of which was permanently grazed throughout the summer. In 1988 they foraged entirely within 1 km of their nest, had a total feeding range of 102 ha and fledged three young. A total of 71.9% of all foraging trip habitats for this pair were in grazed pasture habitats, yet these comprised a total area of only 20.9 ha.

On the other hand, farming systems which reduce the available area of permanently grazed pasture or heath habitats are not favourable to Choughs. In this study, dairy farming represented one such system. It is a high intensity system, characterised by the growth of large areas of silage and arable crops (for winter feed for the cattle), intermittent grazing of pastures in summer (the cattle being dependent on a relatively long sward (>5 cm)), and the in-wintering of cattle. These habitats and grazing regimes provide few feeding opportunities for Choughs. Study pair C nested at the centre of a dairy farming unit and had a feeding range 5 times larger than that of pair B, as a consequence of their feeding in a dune system 7 km from the nest site. This presumably due to the unfavourable vegetation structure of the silage and dairy grazed pastures which comprised most of the improved pasture habitat within 1 km of the nest. The pair foraged up to 7 times further from the nest than pair B, and thus presumably expended more energy in foraging, yet they reared one less young to fledging.

In recent years, silage has become increasingly popular as a source of winter fodder for beef and dairy cattle. Approximately 35% of improved land in the parish of Kilchoman on Islay was given over to silage growth in 1985 (see below and Figure 7.19). It is difficult to assess the overall impact of silage fields on Chough feeding ecology. Between May and June sward-height in silage fields prohibits Chough usage. However, once the crop has been harvested in July silage fields provide a short and bare sward, and an unseasonably high density of Tipulids (due to the fact that the Tipulids are not preyed upon by birds when the crop is tall - thus suspending the seasonal decline in numbers of larvae (see Barbash 1988) by approximately two months). In the post-fledging period silage fields were highly preferred by Chough families, and may have been particularly important in areas where dung was not available. The use of silage fields in the early spring by Choughs on Islay is facilitated by the large goose populations which graze these fields until late April (see below). In areas without geese, silage fields would be suitable for feeding Choughs for a smaller proportion of their breeding season.

However growth of winter fodder is an essential part of beef-rearing farm units. When these cattle are wintered outside (rather than in sheds), their dung provides valuable autumn and winter feeding opportunities for Choughs. In terms of conservation management, the best recommendation for silage growth would be to avoid using fields in the immediate vicinity of nest-sites for silage.

Grazing

The most fundamental land-use in relation to Chough feeding ecology is that of grazing by domestic animals. Grazing produces the short swards and bare areas which are crucial to Chough feeding (see above), as well as preventing field boundaries, rock outcrops etc. from becoming overgrown. Reductions in stocking levels are thus detrimental to the species' feeding ecology. Bullock *et al.* (1983) present three case histories, from Ramsey Island, Bardsey Island and the Calf of Man, where numbers of breeding pairs were inversely correlated with stocking densities. Grazing herbivores also produce dung, a preferred feeding "habitat-patch" in the autumn and winter, and carcases, which provide additional feeding opportunities.

Grazing animals may also produce or maintain suitable feeding habitats for Choughs. Heath/acid grassland mosaics are usually the product of grazing and sometimes burning of heathland habitats (see Cadbury 1993), and these mosaics are preferred to pure heath. Moss pasture, a preferred feeding habitat on Islay is the product of heavy grazing of drained wet heath and bog, habitats characteristic of Islay's mixed grazing systems.

Different types of grazing animals have different effects on the vegetation (see Spedding 1971), the presence of the smaller herbivores (sheep/ rabbits) is probably crucial in providing close-cropped swards. Reduced grazing pressure resulting from reduction in rabbit populations following the outbreak of myxomatosis had many ecological effects (see Sumption & Flowerdew 1985) and has been implicated in the decline of the Woodlark and Stone Curlew in Britain (see above). The loss of rabbits from cliff-top habitats which subsequently "scrubbed over" has been proposed as a contributory factor in the Chough's extinction in Cornwall (Rolfe 1966, Meyer 1991).

Beef cattle are less selective grazers than sheep (Gordon & Iason 1990), and play a valuable role in removing rank vegetation - particularly around field margins, dykes and rock outcrops. Horses may fulfil a similar role, but their numbers are now much reduced. Dairy cattle on the other hand prefer only the most nutritious grasses, and prefer to graze pastures with a sward >5 cm high. One consequence of this is that habitat features such as rock outcrops and dykes within dairy farm units rapidly become overgrown with coarse grasses and weeds, and are thus lost to Choughs as potential feeding sites.

On Islay there are two wild/feral species of larger herbivores: Red Deer *Cervus elaphus* and feral goats. The deer are found primarily in the upland areas, whilst the goats occur along the sea cliffs. Both probably contribute to the maintenance of the small Chough populations in these semi-natural habitats by maintaining close-cropped swards and by providing dung and carcase feeding opportunities.

On Islay geese are important grazing animals, especially on improved pastures. Up to 25,000 Barnacle Geese and 10,000 Greenland White-fronted Geese *Anser albifrons flavirostris* winter on the island. Percival & Houston (1992) found that the geese had a dramatic effect on yield of silage pastures. Part of this effect is brought about by the fact that several weeks of spring grass growth are lost to grazing geese prior to their departure in late April. The occurrence of large numbers of Barnacle Geese in the territory of pair C undoubtedly facilitated the pair's nesting attempt by maintaining a very short sward in silage fields until late April. Sward heights in silage fields ungrazed by geese at Octofad on the Rhinns were 4-6 cm higher at this time of year. Geese may also cause sward bareness through "puddling and treading" of wet pastures, and by pulling out certain grass species and clover *Trifolium repens* to feed on subterranean organs (White-fronts only, *pers. obs.*).

Relatively low numbers of geese occur on the Rhinns; their beneficial effect is probably limited to the more intensively farmed areas of Islay where geese (particularly Barnacles) concentrate. Ironically, it is the very fields which farmers reserve for silage which are most preferred by the geese since in these fields there is no competition from domestic stock (see McKay 1992). Naturally this infuriates the farmers, but from the Chough view-point it means that the most intensively managed and fertilised pastures (which would normally have maximum sward heights) retain a short sward until at least late April.

Outwintering of cattle & slurry/manure production

On Islay, there are still many farms where beef cattle are wintered out of doors, thus providing the dung essential to first-winter Choughs. The cattle usually require supplementary feeding, formerly hay but now mostly silage, but also including "draff", the remnants of the malted barley from the local whisky industry, a relatively cheap supplementary feed. Cattle are usually wintered on dunes, permanent pasture or heath/acid grassland habitats, to avoid poaching of improved pastures. The presence of well-drained dune systems on Islay, such as those at Machir Bay and Ardnave, have probably always favoured the out-wintering of beef cattle. These sites are not subject to poaching and support large numbers of beef and sheep throughout the year, ensuring the presence of large amounts of cow dung. The importance of these areas to Choughs is indicated by the large flocks of first-winter and sub-adult birds which use these sites (see above and Still 1989). In contrast to beef cattle, dairy herds are usually wintered indoors, thus providing no dung-feeding opportunities for Choughs. Moreover, current trends in farming practise are moving increasingly towards the in-wintering of beef cattle and even sheep, and Choughs may have suffered indirectly from the Agricultural Development Programme which grant-aided the building of sheds for in-wintering cattle (some within the Rhinns study area itself).

Unprocessed cattle manure and bedding (straw) collected from cattle shed floors and spread on improved fields was a favoured feeding patch of Choughs in May on the Rhinns, the birds feeding on the abundant Dipteran larvae which had developed in the manure prior to spreading. This is a traditional farming practice which is now becoming increasingly rare: dung is more usually efficiently scavenged from modern in-wintering sheds, and stored as liquid slurry, in which virtually no macro-invertebrates develop. Manure heaps were comparatively rare on the Rhinns, and no Choughs were observed feeding at them. However, elsewhere on the island Choughs were frequently observed feeding at manure heaps, including a sightings on Islay in relation to a multivariate classification of land-types. On a national scale, observers involved in the 1982 national Chough breeding survey recorded habitat on a 1 km square basis and recorded feeding incidents of Choughs located on the survey (Bullock *et al.* 1983). However, all the above studies except Curtis *et al.* have looked at habitat <u>use</u> rather than habitat <u>selection</u>.

The findings of the current study highlight the importance of grazed improved pasture, grazed semi-natural habitats such as permanent pasture and heath/acid grassland mosaics, and perhaps most importantly, grazed mature dune systems, to Choughs on Islay. A variety of patches within these habitats are also important. Some are associated with grazing herbivores (dung and carcases), some are habitats in their own right (soil exposures) and some are artificial sites created by man (earth banks/dykes, other field boundaries, manure heaps). The permanent presence of grazing animals was important in producing a short sward and a bare substrate. In the absence of dunes it is perhaps particularly important that a mosaic of improved pasture and unimproved semi-natural habitats occurs within a small area.

These results concur in general terms with those from other studies of Choughs on Islay (Warnes 1982, Curtis *et al.* 1989), and with the results of the national breeding survey in 1982 (Bullock *et al.* 1983) in which most feeding incidents were associated with pasture. However, it is difficult to make direct comparisons with the results of Curtis *et al. (1989)* due to the multivariate habitat classification they employed. They recorded a general preference for a variety of "grassland" or "moorland grassland" habitats, but also found a preference for "marsh/*Juncus*/rushy fields" which contrasts with the current findings, and they make no mention of the use of dung and other patches within the dominant habitats surveyed.

The results from the Islay studies and the national survey contrast with those from Welsh study areas. In Dyfed Meyer (1991) recorded most Chough feeding incidents on coastal cliffs and associated unimproved cliff-top pastures. On South Stack Bullock (1981) found that Choughs fed for most of the year in maritime heathland, apart from in July and August when they fed on sea cliffs. On Bardsey Roberts (1983) also recorded Choughs feeding in heathland for most of the year, but here the birds fed in patches of permanent pasture within the heath (as in the current study). Improved pastures were used relatively infrequently in all the Welsh studies (though they were present in all), but the national survey suggested that they were more widely used at inland sites in Wales (Bullock *et al.* 1983). Dung-feeding was recorded by Roberts (1983) in sheep and horse dung, and by Meyer (1991) mostly in cow dung. In contrast to Bardsey and the Isle of Man, Choughs on Islay rarely used beaches for feeding, despite the close proximity of one beach to the communal roost.

It is difficult to interpret the basis of the differences between studies. As noted in section 7.1, the studies away from Islay may have suffered to some extent from small population sizes - especially Meyer's (1991) (7 breeding pairs on 100 km of coastline). The low breeding density in his study area may suggest that habitat conditions were not ideal for Choughs. Even so, the dominant feeding habitats in all Welsh studies were semi-natural habitats (heath and sea-cliff) whereas in this study, use of semi-natural habitats was low.

There are obvious climatic differences between these study areas, the Welsh sites all having much warmer summers and higher levels of accumulated temperature (Islay 1441 day°C above 5.6°C (Birse and Dry 1970), coastal Wales range 1650-1925 day°C above 5.6°C (Bendelow & Hartnup 1980)). It is possible that the higher levels of insolation in Wales result in greater invertebrate diversity and/or productivity in unimproved habitats; certainly there are species associated with unimproved habitats in Wales which are not found further north (eg. the Cockchafer *Melolontha melolontha*) or which are less abundant further north (eg. the Yellow Mound Ant *Lasius flavus*) (see Discussion Chapter 5). The higher breeding success of Choughs in Wales compared to Scotland (Bullock *et al.* 1983, Bignal *et al.* 1987b) suggests that in Wales these unimproved habitats provide high quality feeding.

Whilst there were differences between study areas in the habitat types used by Choughs, the structural characteristics of preferred habitats were broadly similar. All studies identified short swards as being crucial to feeding Choughs. Bullock (1980) and Meyer (1991) also highlighted the importance of bare substrate (in heathland and cliff-top habitats).

Are the habitats used by Choughs on Islay unique?

Islay possesses some habitats and land-uses which may be considered particularly favourable to Choughs. Of these the heavily grazed dune systems are probably the most important. Dunes supported large flocks of Choughs throughout the year, and were the focus of long-range foraging movements by 4 of the 5 study pairs. Grazed dunes show all the characteristics of the preferred feeding sites of Choughs - they have a short sward which is also relatively bare; the sandy substrate is friable and easy for Choughs to probe in; large numbers of sheep and beef cattle graze the dunes throughout the year providing abundant dung and some carcases. It is possible that the presence of the dune systems on Islay was one factor which facilitated the survival of the Chough population here when the species became extinct in other areas of Scotland.

Even so, many pairs of Choughs on Islay spend their whole year within their territories away from dune habitats. In these areas the only slightly unusual habitat is perhaps the abundance of rock outcrops, especially within improved fields. However, these and most of the other habitats on the Rhinns, can be found in many other areas of Britain in which Choughs are absent (as suggested by Ratcliffe 1990). Based on this study it would be difficult to attribute the Chough's westerly distribution in Britain to any unique habitats which occur in these areas only. The characteristics of heavily grazed improved pasture mixed with rougher hill grazings along with the rearing of sheep and beef cattle can be found throughout many parts of inland and coastal Britain such as the flanks of the Pennines, the Lake District and the Southern Uplands, and in the Scottish islands as far north as Shetland. These findings lend weight to the hypothesis proposed in Chapter 5 that climate is the ultimate factor controlling Chough distribution in Britain.

Choughs use a range of habitats throughout the year, with some little-used habitats nevertheless being important in certain months, eg. arable land and heath. This emphasises the importance of diversity within a small area; the juxtaposition of a range of habitats throughout Islay probably contributes to its status as the Chough's Scottish stronghold. Even unfavourable habitats/land-uses such as dairy and arable farms are usually relatively small units lying close to more "Chough-friendly" land-uses. It is clear that monocultures would be non-beneficial, even if these were of preferred habitats. Choughs use a range of habitats whose relative importance varies from month to month. The loss of any one of the main habitat components could have a detrimental effect upon a Chough population in a given area, and this effect may be experienced by different components of the population itself. For example, first-year birds may be affected more by the absence of herbivore dung than the adult population.

Comparison of land-use on the Rhinns of Islay and the Rhinns of Galloway

In Chapter 5 I identified the Rhinns of Galloway as being climatically identical to Islay, thus constituting a climatic control area in which comparisons between habitat and land-use between areas could be made to shed light on the possible causes of the Chough's extinction on the south-west mainland of Scotland. The main habitat difference between the two parishes compared was that Kilchoman on the Rhinns of Islay had a higher proportion (75%) of rough grazing land compared to Portpatrick (30%) on the Rhinns of Galloway. It is difficult to be specific about what habitats "rough grazing" (as defined in the agricultural censuses) actually represent, but on Islay these include heath, bog, semi-improved permanent pastures and permanent pastures, habitats which are particularly important for feeding in dung, carcases and rock outcrops. However the proportions of the different types of improved habitats were roughly similar in both areas throughout 1915 to 1985.

The two areas differed markedly in the composition of the three main types of grazing animals - beef and dairy cattle and sheep. In Portpatrick in 1935, dairy cattle constituted 72.3% of all livestock units, with 10.9% of both beef cattle and sheep (presumably similar proportions of the two types of cattle were present in 1915-25, but were not separated on the return forms for these years). At this time 40% of land was given over to hay, cereal or arable crops. This general pattern of land-use is broadly similar to that which prevailed in the territory of study pair C on Islay in 1988 - basically a mixed dairy/arable unit.

In contrast, sheep comprised 26.7-35.6% of all livestock units at Kilchoman between 1915 and 1935, which added to the 7.7-9.6% horse livestock units would have ensured the presence of short-grazed pastures in improved and rough grazed pastures. Even so, during 1935-45 (and presumably before) dairy cattle constituted over 50% of livestock units. This proportion had declined to 21.3% in 1985, with a concurrent increase in beef cattle livestock units from 6.1% in 1935 to 44.4% in 1985. Given that the grazing regimes associated with beef cattle are more Chough-friendly than those of dairy cattle, this suggests that land-use on the Rhinns of Islay has become increasingly favourable for Choughs in the latter part of this century. The same is true of Portpatrick, where the total number of livestock units increased from 1608 in 1915 to 3649 in 1985, with the proportion of sheep and beef cattle livestock units increasing by 5% and 13% respectively. The overall number of livestock units remained much the same at Kilchoman (3997 in 1915, 4115 in 1985). In both areas the number of horse livestock units fell from 9.5% in 1915 to less than 3.5% by 1955, and to less than 1% by 1985, which suggests an on-going decline from earlier times.

It is unfortunate that the data set commence at approximately the same time as the Chough became extinct around Portpatrick, thus making it difficult to assess the role of land-use change in the extinction. The data suggest that Portpatrick parish may not have been ideal for Choughs even as early as 1915. However, of the variables considered, only the decline in horse numbers correlates with the decline of the Chough. Horses are often grazed on rough pasture, produce a shorter sward than dairy cattle and would probably have been wintered out of doors, and as such represent much more "Chough-friendly" grazers than dairy cattle. It is possible that their loss was the last straw for Choughs in an already deficient environment.

Though this numerical analysis points to an increasingly favourable environment for Choughs in both areas in recent decades, differences in modern farming methods may cancel out these positive trends. These include the in-wintering of cattle, production of slurry and growth of silage crops (see above). Field sizes in Portpatrick are large, and bounded by fences rather than dykes, many of which are overgrown with weeds. Discussions with local farmers suggested that sheep were bought in as lambs for fattening, thus there are few areas grazed permanently by sheep. The doubling of livestock units in Portpatrick between 1915 and 1985 probably indicates intensification of land management rather than a simple increase in grazing pressure. The Rhinns of Galloway also lacks the "benefits" associated with the presence of large numbers of geese on Islay. There is little rough grazing ground, and perhaps most crucial of all, the cliff-tops are totally ungrazed by domestic stock, and in the absence of goats or free-ranging sheep, are covered in a rank growth of bracken, gorse *Ulex europea* or heather.

The above scenario has a parallel in Cornwall, where fencing off of the cliff-tops is thought to have been one of the processes which led to the extinction of the Chough in Cornwall (Rolfe 1966, Meyer 1991). Whilst coastal cliffs were rarely used by feeding Choughs on Islay, the birds here had a wide range of alternative semi-natural habitats to choose from. On the Rhinns of Galloway, as in parts of Wales, and perhaps coastal Cornwall (Meyer 1991), coastal clifftops may be the only semi-natural habitat available to foraging Choughs. When grazing stock are excluded from this habitat, the Chough's fate is probably sealed.

CHAPTER 8

DIET, FEEDING BEHAVIOUR and FOOD AVAILABILITY

8.1 INTRODUCTION

Unlike other British corvids, the Chough has a specialised invertebrate diet (Holyoak 1968). The slender down-curved bill is well adapted for the extraction of invertebrates from pastures and soil exposures, and for breaking open a variety of substrates, such as dung, moss, loose soil and sand, to reveal invertebrates. The diet of the Chough has been examined by several authors (Bullock 1980, Warnes 1982, Roberts 1982, Meyer 1991, McCracken *et al.* 1992) by faecal and pellet analysis. All studies have shown that invertebrates predominate, with some cereal grain taken in the autumn and winter months. There is no substantiated evidence of carrion, vertebrates or household scraps being eaten in Britain, except perhaps in very severe weather, but the last two have been recorded more frequently elsewhere in the range (see Goodwin 1986). Compared to other British corvids, Choughs are less dependent on grain, but on the continent cereals are taken more frequently (Goodwin 1986, Soler 1989). Worms (Oligochaeta) are rarely taken in the British Isles (though see below).

Studies within Britain indicate that there are dietary differences between study areas. These may be associated with climatic or habitat differences between areas (see Chapters 5 & 7), or to the different methodologies used in diet analysis. On Islay, cereal grains appear more frequently in the diet than in Wales (Warnes 1982, McCracken *et al.* 1992a) (though see Discussion). Beach-feeding resulted in more coastal species in the diet on Bardsey (Roberts 1982), and in south-west Wales Meyer (1991) found much evidence of worms in the diet, in contrast to other studies.

However, there are many methodological problems associated with assessment of diet by faecal and pellet analysis (see Green & Tyler 1989), and these can make comparisons between studies and areas difficult. For example, Meyer (1991) suggested that the low occurrence of worms in studies other than his own may have been due to other workers not having specifically looked for worm chaetae in Chough faecal samples. He also noted the under-representation of ants (Formicidae) in his own study. He found that presence of ants was a major influence on habitat selection in the breeding season, yet their remains were not found in a single faecal sample from that period ($n=105$).

There is a clear need for feeding experiments with Choughs to calibrate the findings of faecal analysis. Attempts to carry out such experiments as part of this study were unsuccessful (see below). The Chough's diet has been described in broad terms by the above studies. However, only McCracken *et al.* (1992a) attempted to quantify the composition of the diet in terms of abundance of food items per faeces/pellet, rather than simply noting presence/absence within faeces. The former method provides a much clearer picture of the importance of different food items within the diet, but is much more time consuming and tends to reduce the number of samples that can be analysed. However even this method still only deals with frequency of prey, not the actual fresh weight of prey consumed. This is important because for example, one large moth larva may be equivalent in terms of fresh weight of prey ingested to 50 small Dipteran larvae (e.g. Bibionids or 2nd instar Tipulids).

The aim of this chapter is not to provide an exhaustive description of the Chough's diet throughout the year, but to focus on the characteristics of the favoured food items, and to identify the limitations of faecal and pellet analysis in quantifying the Chough's diet. I investigate the Chough's diet by adopting a rigorous methodology to the collection of fresh faecal samples, and by using a conversion factor to transform number of prey fragments in faeces to the fresh weights of food items at the time of ingestion. The composition of faecal samples is compared with that of pellets (i.e. undigested remains ejected through the bill rather than as faeces). This analysis was carried out to facilitate interpretation of results from other studies which included pellets. In the absence of experimental studies, the only way to investigate biases inherent in faecal sampling is by direct observation of food intake by feeding birds. In this chapter I compare feeding behaviours, invertebrate densities at feeding sites and their relationships with the results of faecal analysis.

8.2 METHODS

8.2.1. Diet

Chough diet was assessed by faecal analysis, and compared with pellet analysis (see Section 8.2.2 below). Fresh faeces were collected from the Rhinns study area or from study pairs. These included specimens collected in the field during the day, and fresh over-night faeces collected from roost sites soon after the birds had left the roost in the morning (freshness was ensured by clearing away all old faeces from roost sites on the previous day). Thus no samples were more than twelve hours old. Faeces were only used in the analysis if it was 100% certain that they were from Choughs. This was easily ensured at roost sites of individual pairs, but required extreme care when samples were taken from birds in the field. Correct identification in the field was ensured by making careful observations on foraging Choughs using a telescope, and after a faecal deposit had been made a) only collecting faecal deposits when it was easy to mark and locate them, and b) by carefully searching a wide area (up to 5m) around that where the fresh faecal deposit had been made; if any other fresh bird faeces were found within this area, then the presumed Chough faecal sample was rejected. It was surprising how often a second faecal deposit was present in such areas, even though no other species of bird had been seen in the area during the observation period. Field samples were collected on pursuit days when pairs or flocks were followed until a sample of around 5g of faeces had been collected.

After collection, faeces were stored in glass jars in a freezer at -15°C. Sorting methods followed those of Green & Tyler (1989) who describe a standardised procedure for faecal analysis. Their procedure is described below, along with my own adaptations of it. Sub-samples of *c.* 0.5g were taken from individual faeces and amalgamated prior to taking a 1g sub-sample from the whole to ensure greater representation of each sample. The 1g Samples were not washed in a sieve prior to sorting (contra Green & Tyler 1989 and McCracken *et al.* 1992) as this could have resulted in the loss of smaller fragments, especially worm chaetae; nor were samples washed in 20% potassium hydroxide. An 85-mm transparent Petri dish was adapted (as in Green & Tyler 1989) by the addition of a central perspex disc which created an annular 5-mm channel around the edge of the dish. The underside of the Petri dish was marked with radial lines at 10° intervals so that the annulus was divided into 36 equal sectors. Small amounts of faecal material were placed in this channel, and teased apart aided by the addition of alternate drops of 70% alcohol and detergent, and scanned under incident light using a 6.25-250 x binocular microscope. The channel was narrow enough for its entire contents to come under the field of view of the microscope up to 30x magnification, and by rotating the dish through 360° one could be confident that its entire contents had been searched. Located prey fragments were identified then removed for storage in alcohol. The dish was rotated through 360° at least twice or until no more prey fragments could be found. Finally, a sample of ten 10° sectors were scanned under high magnification and the number of worm chaetae (if present) counted. Worm chaetae are virtually transparent, but can be "illuminated" with transmitted light at certain critical angles, which can be found by changing the angle of incident light until transparent material in the sample shows up clearly.

A reference collection of prey fragments was built up from invertebrates collected at Chough feeding sites and pitfall traps placed in a range of different habitats. Identified fragments were fixed to index cards or stored in alcohol for reference. Faecal fragment identification was based on these specimens, and on illustrations in Tatner (1983) and Moreby (1987). Only discrete and identifiable prey fragments were counted (Table 8.1). I concentrated on using those items that were carried in fewest number by the animals concerned, and which were least likely to be broken down during digestion. Mandibles, jaws and fangs (from spiders) were the most useful items, since they are possessed by the majority of taxa, are robust, are usually easily identifiable to family (both adults and larvae), and small enough not to be fragmented during digestion. The uniformly small size of mandibles across groups helps to overcome biases associated with differences in conspicuousness of prey fragments. For example, earwig mandibles were counted in this study rather than their much larger and therefore more conspicuous cerci (the pincer-like anal appendages). All taxa were identified from their mandibles/jaws/fangs except adult Scarabaeidae and Curculionidae (head capsules), Cyclorrhaphan fly larvae (mouthparts), Diplopoda (head capsules) and Oligochaets (chaetae). Unfragmented head capsules were dissected to confirm that they carried two mandibles. The mouthparts and spiracular discs of Cyclorrhaphan fly larvae proved particularly difficult to identify to family level; most were thought to be Muscidae or Scathophagidae. Fragments of spider fangs were difficult to separate from the claws of some beetles, and may have been under-estimated. Seeds and fragments of cereal grains were simply counted.

The absolute number of individuals was calculated from the number of fragments: 5 mandibles would be recorded as 2.5 individuals. These numbers were not rounded up to the nearest "whole individual" since these data were subsequently used to convert faecal fragments to live prey weights. For larger invertebrates (eg. Lepidopteran larvae) such rounding up could produce a large bias. It was not possible to quantify invertebrate groups which possess variable numbers of identifiable parts (eg. worm chaetae) or no quantifiable parts (snails). For these groups it was only possible to record presence/absence in each sample. The same applied to fragments of cereal grains.

During the course of this study 2 attempts were made to obtain calibrations of faecal fragments in relation to prey ingestion. The first was with a wild bird from Islay which was kept in captivity whilst it recovered from a wing injury. A large amount of time was spent getting the bird habituated to feeding on provided prey, and on collecting prey to feed to it. Unfortunately the bird escaped on the first day of the experiment as I entered the aviary to collect its faeces. A second experiment was planned in conjunction with Richard Meyer on captive birds in Cornwall, but we had great difficulty in getting the birds to accept "natural" food, so the experiment was abandoned. Meyer (1991) later succeeded in conducting one small-scale feeding experiment using worms, but he was unable to quantify the relationship between number of worms ingested and number of chaetae produced.

The number of individual prey items was converted to an estimate of fresh weight of ingested animal prey by allocating a standard mass to each taxon and age-class (adult/larval), based on the fresh mass of live invertebrates collected from feeding sites (see Table 8.1). *Tipula paludosa*-type larvae were differentiated from the smaller *T. marmorata* group (based on differences in mandible shape). Allowance was made for seasonal variation in body size in *Tipula paludosa*-type larvae, which show a marked annual growth curve. Taxa were categorised according to whether they were hard- or soft-bodied (see Table 8.1). Those which were intermediate between these two categories (Dermaptera and Formicidae) were allocated to the hard-bodied category. Worms, snails and cereal grains could not be quantified in this way and were excluded from biomass analyses.

8.2.2 Comparison of composition of faeces and pellets

To compare the differences in proportions of different types of prey item in faeces and pellets, a sample of 5 pellets and 5 faeces, 1 each from the months of August, October, November, December and January were compared. The pellets and faeces were collected fresh from below roost sites that had been cleared of old faeces/pellets the previous afternoon. Thus the faeces and pellets came from the same pair of birds on the same dates. Whole pellets and whole faeces were dissected for analysis. Two comparisons were made, one between the frequency of hard and soft prey items in the different types of sample, the other between the frequency of animal and vegetable items. Vegetable items were counted as individual fragments (husks of cereal grains or complete seeds).

8.2.3 Feeding behaviour

Feeding behaviours were recorded for all *Bird Feeding Observations* ($n=1307$) made on the Rhinns transect (see Chapter 7). Although some of these data are closely related to the habitat-use data presented in Chapter 7 they are presented here separately since the habitat-use data give no impression of the feeding methods used within each habitat. Categories are exclusive, and are self-explanatory - eg. dung-feeding, soil-exposure-feeding etc. In each case the term implies that the birds were feeding at or in the habitat, but not on it, eg. dung- and carcase-feeding birds were not feeding on the dung or carcase itself. Pasture-feeding here refers only to the specific behaviour described below, and does not include other feeding behaviours within pasture habitats. In pasture-feeding, the bird walks slowly across the pasture scanning the ground intently. As it progresses regular exploratory probes or pecks are made. When prey is found the bird rapidly probes and digs until the prey item is extricated or the feeding attempt aborted. Pasture-feeding Choughs often turn over stones or dung as they move across a pasture; these behaviours are almost instantaneous and are rarely employed exclusively, so they have been aggregated under pasture-feeding here. I have seen birds employing these techniques exclusively, but not on formal Rhinns transects.

"Digging" refers to birds digging concertedly, usually in a friable substrate (such as sand or peat), which is visibly excavated or removed. It does not include the short bursts of digging which occur when pasture-feeding birds expose prey items (described above). In "surface-feeding" the bird is obviously searching the habitat surface for food items, and is typified by a plover-like (Charadriidae) progression (most unlike other Chough feeding behaviours): the bird makes a short run, then halts with its head craned upwards, makes another short run and so on, until it finally "dips" down to retrieve prey from the surface without any digging or probing. Ant-feeding is associated with mounds of the Yellow Mound Ant *Lasius flavus* (Hymenoptera:Formicidae) and is characterised by rapid digging and swallowing. Some distant observations of birds rock outcrop-feeding probably included a proportion of misclassified ant-feeding observations.

Dyke- (stone-wall), rock outcrop-, and soil exposure-feeding were similar to each other. Birds search the respective habitats with exploratory probes followed by rapid digging or flicking/tearing away of surface vegetation, moss or loose soil. These 3-dimensional habitats were explored thoroughly. Stubble-feeding refers only to birds judged to be feeding on spilt grain as evidenced by birds gleaning food items from the surface or by digging, rather than any other feeding method (e.g. birds were often observed dung-feeding within stubble fields).

8.2.4 Food availability and feeding site sampling

The quantification of invertebrate abundance at Chough feeding sites is complicated by the variety of sites and substrates used - eg. dune systems, pastures, dung, ant-hills, rock outcrops, earth banks etc. Several previous studies have used pitfall trapping to assess food availability (Warnes 1982, McCracken & Foster 1992c). The limitations of pitfall trapping are well-known (Greenslade 1964), and this method seems inappropriate for a bird which feeds primarily on immobile sub-surface invertebrates (see Results). For these reasons my sampling technique was based entirely on the use of soil cores (see Barbash 1988). Samples were taken using a 6.5 cm diameter soil corer (area 132.7 cm^2) made from a 15 cm section of cylindrical, durable, drain-pipe plastic.

Two types of sample were collected: field samples and feeding-site samples:

Field samples. In open pasture fields, a random sample of 40+ soil cores was taken. Prelim-

8.3 RESULTS

8.3.1 Faecal analysis

A total of 60 faecal samples (15 from each season) collected during 1988 were analysed. Prey taxa recorded in faecal analysis are presented in Table 8.1. The table shows which type of body fragment was used to quantify occurrence of each prey type, whether taxa are hard- or soft-bodied, and the standardised fresh weight accorded to prey items. Faecal analysis revealed fragments from a total of 1873 individual prey items belonging to 18 taxa. The Number of individual prey items taken (except worms and snails) in each season are presented in Table 8.2.

A comparison of the composition of the diet in terms of a) number of individual prey items and b) the total calculated fresh weight of these prey items is shown in Figure 8.1. Only those taxa contributing ≥ 5% of the total seasonal calculated fresh weight of prey are shown. If one considers only number of individual prey items in the diet then it is clear that the importance of small-bodied prey (e.g. Bibionids) is over-estimated, and large-bodied prey (e.g. Lepidoptera) is under-estimated. The most important taxa over the whole year in terms of weight of prey ingested were Tipulid larvae, Aphodius larvae, Carabid larvae, and Lepidopteran larvae. During winter, spring and summer these groups accounted for 75-86% of the total seasonal biomass.

It was not possible to quantify the number of worms and cereal grains in the diet based on faecal analysis. Frequency of presence/absence of these groups in faecal samples is presented in Figure 8.2. Worms were recorded in less than 25% of samples in all seasons,

Table 8.1 *Invertebrate prey taxa recorded in Chough faeces (n = 60), Islay 1988. The types of prey fragment used in identification are given, along with classification of prey items into hard- or soft-bodied categories, and the standard mass estimate accorded to each type of prey item.*

Prey taxon	Age	Identified prey fragment[1]	Hard-(H) or Soft-(S) bodied	Standard mass estimate of live prey (g)
COLEOPTERA				
Carabidae	Adult	M	H	.08
Carabidae	Larva	M	S	.08
Curculionidae	Adult	HC	H	.02
Elateridae	Adult	M	H	.10
Elateridae	Larva	M	S	.10
Scarabaeidae				
Aphodius	Adult	FT	H	.06
Aphodius	Larva	M	S	.10
Staphylinidae	Adult	M	H	.08
Staphylinidae	Larva	M	S	.08
DIPTERA				
Unidentified	Adult	W	S	.02
Bibionidae	Larva	M	S	.02
Muscidae	Larva	MP	S	.06
Muscidae	Pupa		H	.03
Scathophagidae	Larva	MP	S	.04
Scathophagidae	Pupa		H	.04
Tipula paludosa	Adult	W	S	.08
Tipula paludosa	Larva winter	M	S	.15
	spring	M	S	.45
	summer	M	S	.50
	autumn	M	S	.03
T. marmorata group	Larva	M	S	.15
OTHER				
Araneae (spiders)		M	S	.02
Diplopoda (millipedes)		RF	H	.02
Dermaptera (earwigs)		M	H	.08
Formicidae (ants)	Adult	M	H	.01
Gastropoda (slug)		Skin	S	-
Lepidoptera (moths)	Larva	M	S	.30
Oligochaeta (worms)		Chaetae	S	-
Opilionid (harvestmen)		M	S	.02
Orthoptera (crickets)		M	H	.04

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[1] FT = first tibia (2 per animal); HC = head capsule (1 per animal); M = mandible, jaw or fang (2 per animal); MP = mouthparts (1 set per animal); RF = ring fragment (many per animal); W = wing (2 per animal)

Table 8.2 *Number of individual prey items in Chough faeces collected on Islay, 1988 (n=15 in all seasons).*

		Total number of individuals in each season				
Prey taxon	Age	Winter	Spring	Summer	Autumn	Year Total
COLEOPTERA						
Unidentified	Adult	3.5	7.0	4.5	1.0	16.0
Carabidae	Adult	39.0	4.0	1.5	17.0	61.5
Carabidae	Larva	144.0	12.5	4.5	37.5	198.5
Curculionidae	Adult	0.0	36.0	27.0	0.0	63.0
Elateridae	Adult	0.0	7.5	10.5	0.0	18.0
Elateridae	Larva	5.5	8.0	12.0	3.0	28.5
Scarabaeidae						
Aphodius	Adult	2.0	66.5	36.0	22.5	127.0
Aphodius	Larva	31.5	50.0	118.5	30.0	230.0
Staphylinidae	Adult	2.0	2.5	4.0	6.0	14.5
Staphylinidae	Larva	10.5	4.5	6.0	24.0	45.0
DIPTERA						
Unidentified	Adult	2.0	6.5	12.0	4.0	24.5
Bibionidae	Larva	183.0	22.0	0.0	109.0	314.0
Muscidae	Larva	5.0	3.0	12.5	25.0	45.5
Muscidae	Pupa	2.0	0.0	0.0	3.0	5.0
Scathophagidae	Larva	11.0	8.0	8.0	81.5	108.5
Scathophagidae	Pupa	3.0	0.0	0.0	5.0	8.0
Tipula paludosa	Adult	0.0	0.0	5.0	3.0	8.0
Tipula paludosa	Larva	122.0	65.5	11.0	45.5	244.0
T. marmorata group	Larva	32.5	9.5	18.5	28.0	88.5
OTHER						
Araneae (spiders)		5.0	6.5	10.0	2.0	23.5
Dermaptera (earwigs)		52.5	5.0	13.5	37.5	108.5
Diplopoda (millipedes)		0.0	1.0	0.0	0.0	1.0
Formicidae (ants)	Adult	0.0	2.0	3.5	3.0	8.5
Gastropoda[1] (snails)		-	+	-	-	
Lepidoptera (moths)	Larva	10.5	16.5	4.5	11.0	42.5
Oligochaeta[1] (worms)		+	-	+	+	
Opilionid (harvestmen)		0.0	0.0	32.5	4.5	37.0
Orthoptera (crickets)		0.0	0.0	4.0	0.0	4.0
TOTAL INDIVIDUALS		666.5	344.0	359.5	503.0	1873.0
TOTAL CALCULATED WEIGHT[2] (g)		55.0	51.2	31.9	31.1	169.2

[1] Presence (+) or absence (-).

[2] See Table 8.1 for weights accorded to each taxon/age-class.

Figure 8.1 Comparison of total number of individual animal prey items and total calculated fresh weight of these prey items (see Table 8.1) in 60 Chough Faecal samples, Islay 1988.

Only those groups comprising more than 5% of total fresh weight of live prey ingested in any one season are included. Calculations exclude worms. Fresh weights have been multiplied by 5 for graphing purposes.

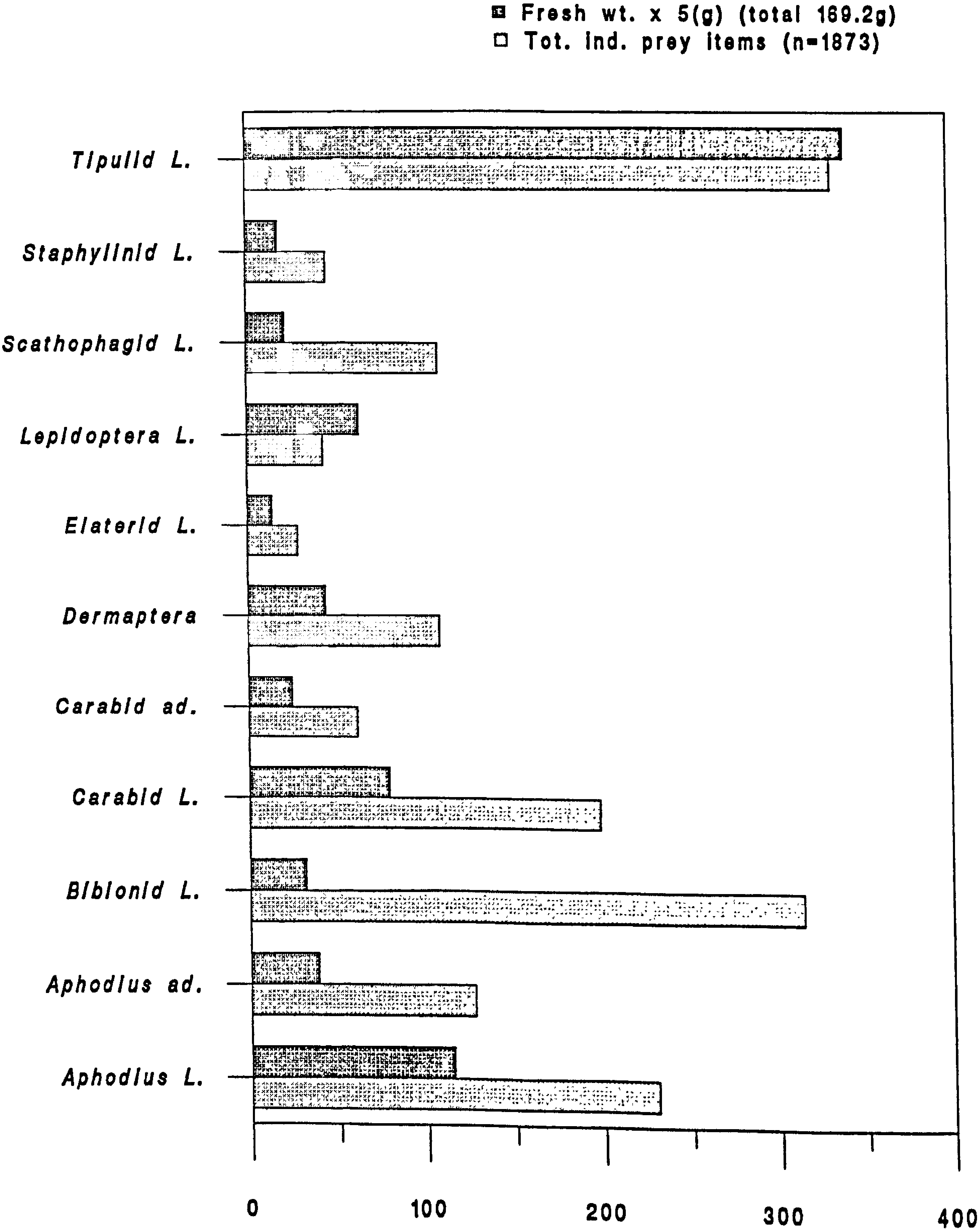
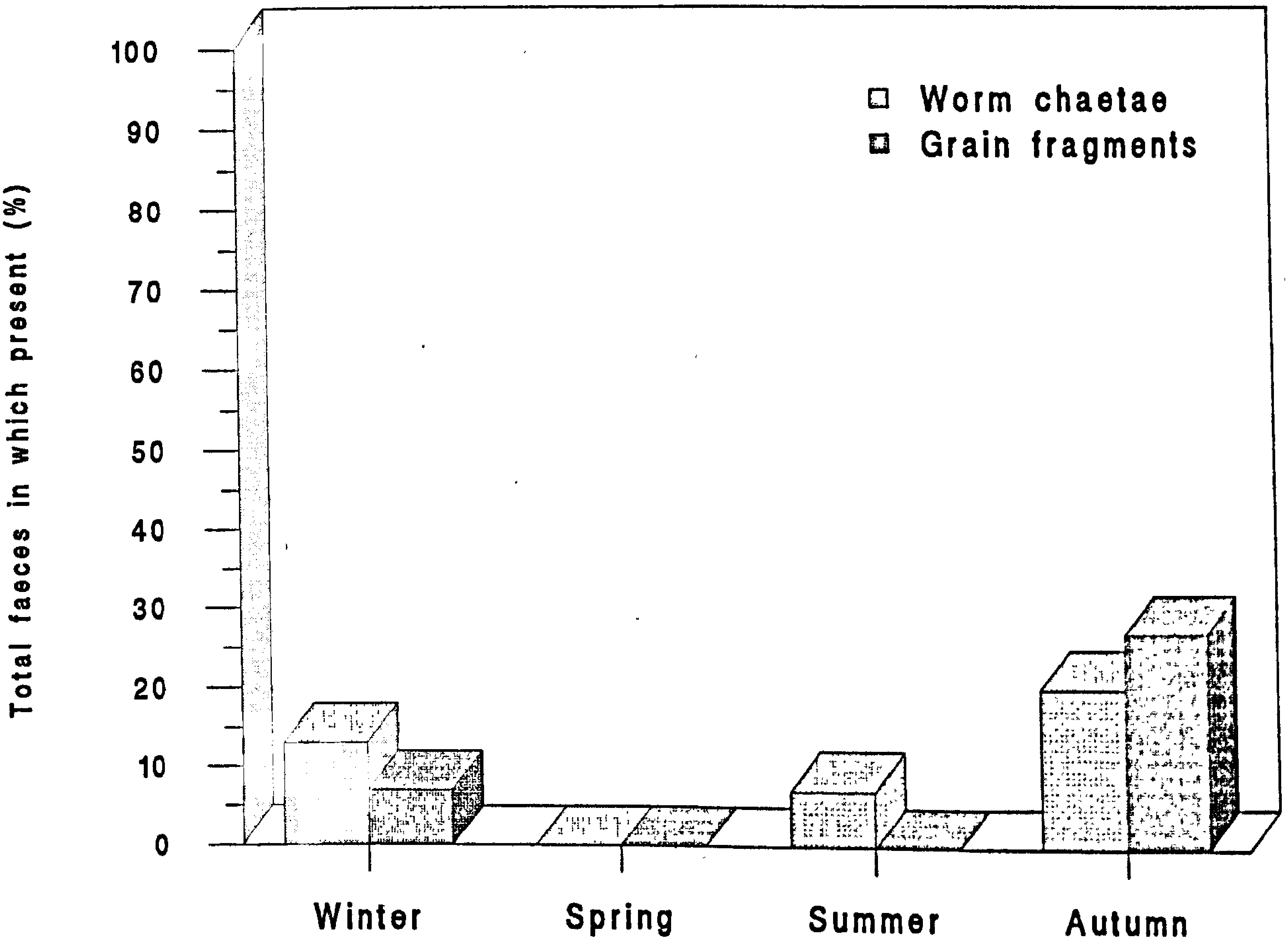


Figure 8.2 Seasonal frequency of worm chaetae and grain fragments in Chough faeces, Islay 1988, as represented by presence/absence (n=15 for all seasons).



and were completely absent in the summer. Cereal fragments were present only in autumn and winter, being most frequent in autumn when they were present in 27% of faecal samples.

The total weight of animal prey ingested based on prey fragments in the 60 faecal samples was 169.2g. There was much seasonal variation in the composition of the diet. Figure 8.3 shows the composition of the diet for all taxa contributing >5% by weight in any one season. Only 4 taxa contributed more than 5% by weight to the diet, in spring and summer, with Tipulid larvae and Aphodius larvae being the dominant groups. The diet in winter and autumn was much more diverse, with 6 and 8 taxa present respectively, and with less dominance by any one taxon. Most of the main prey groups were larval forms, and soft-bodied prey accounted for 82-96% (by weight) of the animal diet in each season (Figure 8.4).

8.3.2 Comparison of composition of faeces and pellets

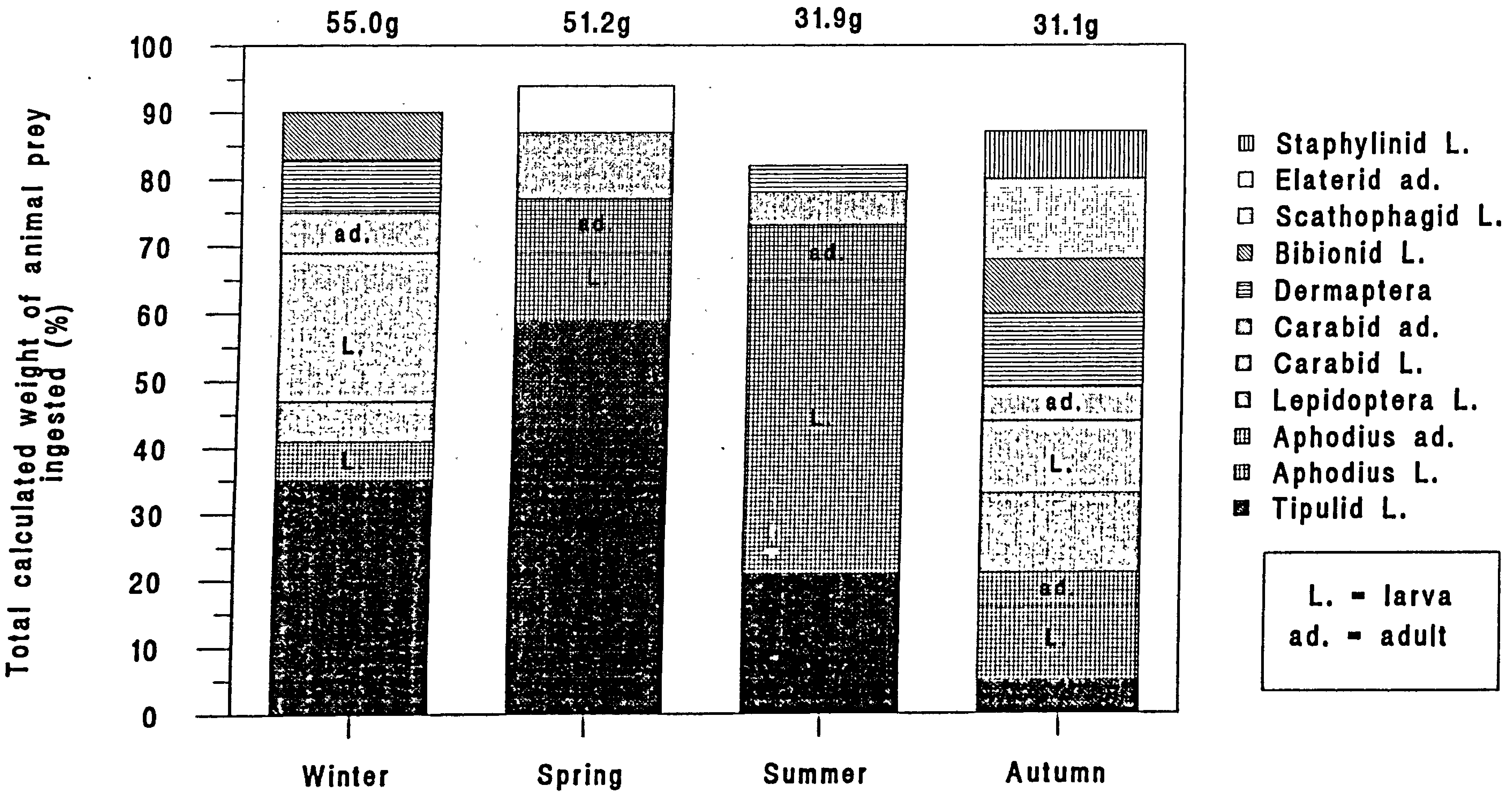
Analysis of 5 faecal and 5 pellet samples revealed totals of 251 individual animal prey items (excluding worms) and 135 whole seeds or cereal fragments (Table 8.3). When the proportions of hard- and soft-bodied prey faeces and pellets were compared, the proportion of hard-bodied animal prey was significantly greater in pellets (*Chi*^{2} = 32.4, *df* = 1, *P* <.001). When the proportion of individual animal prey items *vs.* vegetable fragments was compared, a significantly higher proportion of vegetable fragments was found in pellets than in faeces (*Chi*^{2} = 39.7, *df* = 1, *P* <.001).

Table 8.3 *Comparison of the composition of different food/prey items in fresh faeces and pellets collected from Chough roosts, August 1988 - January 1989.*

	Total individual animal prey items[1]		Total animal prey	Total vegetable fragments
	Hard-bodied	Soft-bodied		
Faecal samples (*n*=5)	10	145	155	38
Pellets (*n*=5)	34	62	96	97

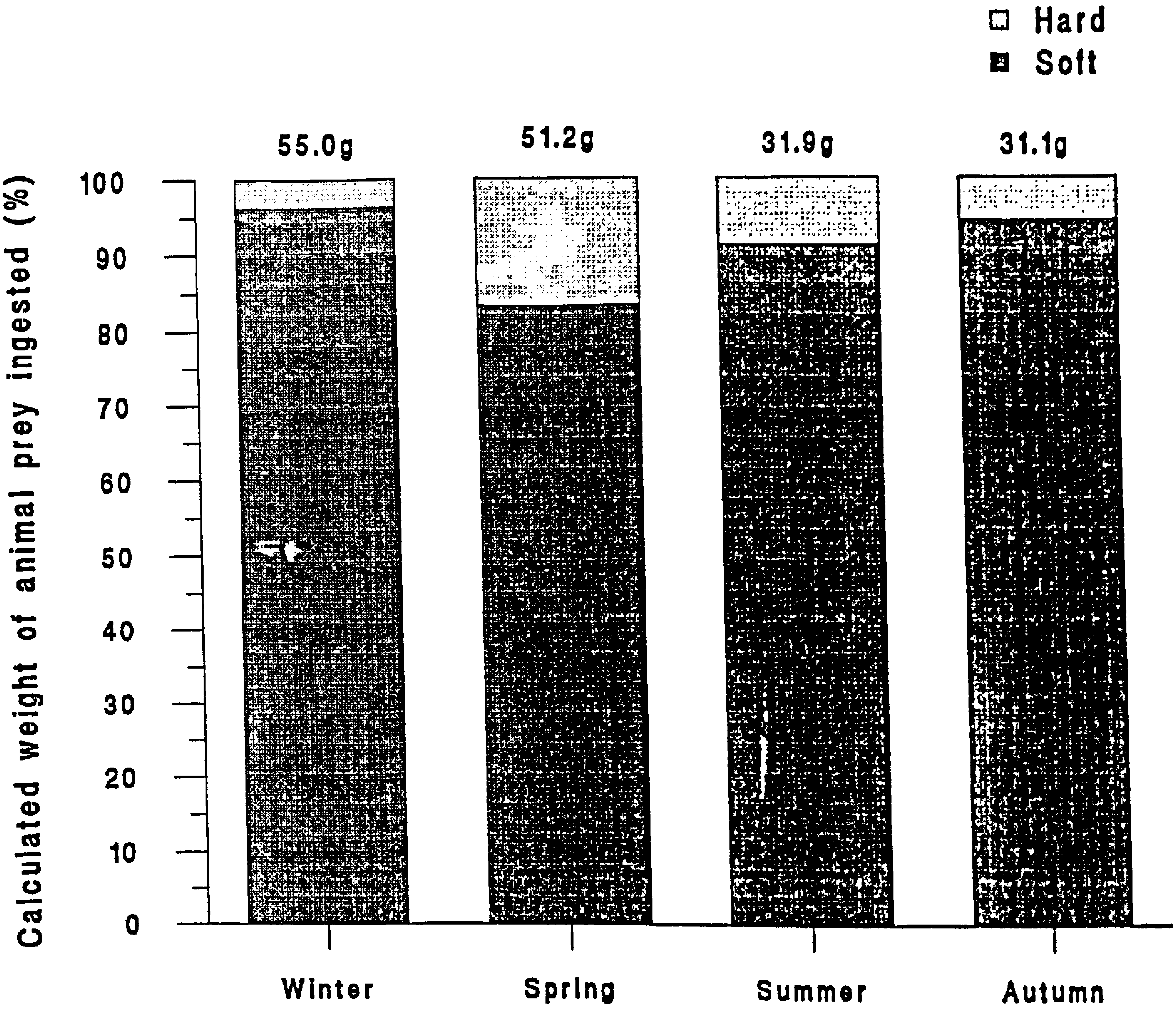
[1] calculated number of individuals computed from number of identifiable prey fragments per animal (see Table 8.1).

Figure 8.3 Seasonal composition of the Chough's animal prey diet (excluding worms), as indicated by faecal analysis (n = 15 in each season). See text for further details.



Total calculated weight of ingested animal prey is given at the top of each column. Conversion factors from prey fragments in faeces to fresh weights of live prey ingested are given in Table 8.1.

Figure 8.4 The proportion (by weight of ingested animal prey, excluding worms) of soft-bodied and hard-bodied prey in the diet of the Chough as indicated by faecal analysis (n=15 in each season). See text for details.



Total calculated weight of ingested animal prey is given at the top of each column. Conversion factors from prey fragments in faeces to fresh weights of live prey ingested are given in Table 8.1.

8.3.3 Feeding behaviour

Feeding behaviour was recorded for 1307 Bird Feeding Observations made on the Rhinns transects. Seasonal percentages of the main feeding behaviours were weighted (to allow for seasonal differences in number of BFOs) and are presented as yearly totals in Table 8.4. Pasture-feeding accounted for over 50% of all feeding observations, with dung- and rock outcrop-feeding the next most frequent behaviours at c.17% each. The remaining categories each comprised less than 4% of all feeding observations, however, their importance should not be under-estimated since, as shown for habitat and patch-use in Chapter 7, averages for the whole year may under-estimate feeding behaviours which are important over shorter time periods (eg. seasons or months).

Table 8.4 *Proportion of feeding behaviours of Choughs recorded on the Rhinns transects, Islay, 1988 (n = 1307).*

Feeding behaviour	% of total annual feeding obs.[a]
Unclassified	1.7
Ant	1.1
Beach	.5
Carcase	1.1
Dung	17.7
Digging	2.0
Dyke	1.8
Animal feeding station	.4
Pasture	51.4
Rock outcrop	16.7
Surface	.3
Soil exposure	3.5
Stubble	1.8

[a] Percentages weighted by season, to allow for differences between seasons in number of feeding observations.

8.3.4 Field sampling and Feeding-site sampling

The results of invertebrate sampling in feeding habitats are presented in Appendix 3. Due to the small number of sample cores taken (10-15 in some habitats), and the high variation in invertebrate densities, no error estimates are given. Instead the maximum biomass value (grams of live prey (fresh weight) per m^2) for each taxon in each habitat/patch is given. It was not possible to weigh all the invertebrates in all samples, the weight of unweighed individuals was estimated using the standardised weights for animal prey given in Table 8.1. No intensive sampling was carried out in dune habitats. Worms (Oligochaets) had the highest levels of biomass in most habitats. Dung and manure contained high densities of Aphodius larvae, Aphodius adults and Muscid larvae. Pasture habitats supplied a high biomass of Tipulid larvae, with moss pasture and moss associated with rock outcrops supporting a high biomass of *Tipula marmorata* - group larvae. A greater diversity of invertebrates was present in more mature improved pastures, permanent pastures and moss-pastures, though the total biomass in these habitats tended to be lower. Some additional results from *ad hoc* sampling at feeding sites are described in the Discussion.

8.4 DISCUSSION

8.4.1 Diet

This study confirmed the findings of previous workers that the Chough's diet in Britain is comprised mostly of invertebrates, with many of the same taxa as previously recorded being identified (Bullock 1980, Warnes 1982, Roberts 1982, Meyer 1991, McCracken *et al.* 1992).

This study is the first Chough study in Britain to have attempted to quantify the number of prey fragments within individual Chough faeces and to convert this into weight of prey ingested. Although faecal remains were not experimentally calibrated against prey intake, this approach still provides a better overall impression of the importance of individual prey types in terms of energy intake. Figure 8.1 shows the value of using the biomass approach rather than simple prey frequency, there are 50-fold differences in the weights of some of the Chough's prey items.

Most prey species were relatively immobile soil-dwelling invertebrates of pastures, rock outcrops and dykes, or were associated with herbivore dung or carcases. The seasonal pattern of diet reflected that of habitat and patch use (see Chapter 7) in that it was least diverse in spring and summer, more diverse in winter, and most diverse in autumn. The latter two periods were also those in which stubble-feeding and beach feeding were recorded, and during which worms were most frequently recorded in the diet. This may suggest that food availability is at its minimum at this time of year forcing the birds to feed in a wider range of habitats and on a diverse range of prey items.

Though it was not possible to quantify food availability directly, it is clear that autumn and winter are times when only small, immature stages of summer-breeding invertebrates are available to feeding Choughs. A good example of this is the larval form of *Tipula paludosa*, one of the Chough's staple prey items on Islay. Larvae hatch in September from eggs laid in August, and during the autumn weigh only *c.* 0.03g, whereas by the spring they have increased in size more than 10-fold to *c.* 0.45g (see Chapter 5). A similar growth pattern occurs with many Lepidopteran and Carabid larvae (Heath 1983, Thiele 1977).

However, many dung-inhabiting larvae have a late summer/early autumn peak in numbers (e.g. *Aphodius rufipes* and *Scathophaga stercoraria* (Skidmore 1987, Ward and Simmons 1990)), and these are probably very important to Choughs at this time, particularly to 1st winter birds (see Chapter 7). However, by late autumn/early winter these invertebrates leave the dung to over-winter in the soil. It is at this time that Choughs switch to pasture-feeding (see Chapter 7), and Carabid larvae and Tipulid larvae become the main prey items (Figure 8.3). It may be crucial that these the larval forms have grown sufficiently during the autumn/early winter to satisfy the energetic requirements of the Chough at this time. It was demonstrated in Chapter 5 that over-winter larval growth is facilitated by the mild winters which characterise the Chough's British range.

By the spring Tipulid larvae average *c.* 0.45g, and become the Chough's staple prey item. The diet in spring and summer is dominated by Tipulid larvae, Aphodius larvae, and Lepidopteran larvae. Tinbergen (1981) showed that breeding Starlings needed a balance of Tipulid larvae (high in energy) and Lepidopteran larvae (high in nutrients) to ensure good chick growth and condition. It seems likely that Choughs have similar requirements. The white, fatty larvae of Aphodius probably fulfil a similar role to Lepidopteran larvae at this time of year. During spring and summer Choughs fed primarily on a few abundant groups - mostly Tipulid larvae, Scarabid Larvae, and Lepidopteran larvae, despite there presumably being a wide variety of alternative prey available at that time.

Soft-bodied prey predominated in the diet, a finding which has not been previously noted, presumably due to the "biomass" approach to faecal analysis used in this study. Over 80% by weight of animal prey items taken in each season were soft-bodied. This estimate is in itself likely to be an under-estimate since a) soft-bodied prey are much less likely to survive digestion compared to hard-bodied prey (Green & Tyler 1989), and b) soft-bodied prey leave fewer identifiable fragments in faeces. I attempted to overcome the latter bias by using the same body structures (mostly mandibles) for identification of each taxa, but hard-bodied prey such as adult beetles are broken down into many chitinous fragments in faeces, and these can easily obscure the less abundant remains of soft-bodied prey.

It was mainly through observations of feeding birds that it became apparent that some regularly taken soft-bodied prey are almost completely undetectable in faecal samples. In November 1988 I followed a flock of 6 first-winter Choughs (the "November flock") which fed on (soft-bodied) Scathophagid larvae in cow dung throughout most of the day. Faeces collected from these birds revealed only an amorphous mass, within which it was clear that the friable mouthparts of the Scathophagid larvae had been almost completely broken down, and were thus difficult to identify and impossible to quantify. It is likely that the remains of other Cyclorrhaphan fly larvae (ie. most maggot-type larvae) are broken down in the same way. A similar scenario may explain the almost total absence of ant remains in Chough faeces (Meyer 1991, McCracken *et al.* 1992, and see Table 8.2) despite frequent observations of Choughs feeding at ant nests (Cowdy 1973, Meyer 1991, and see below). The most likely explanation for this is that the Choughs are feeding on the soft-bodied ant larvae (which possess no chitinised body parts) rather than on the adults (whose chitinised jaws are easily detectable in faeces when present). Similarly in May 1988 I watched Pair C feeding repeatedly on beetle prepupae which they extracted from burrows in earth banks in which they were metamorphosing. Dissection of these prepupae showed that they possessed no hard parts at all, and thus these too would have been undetectable in Chough faeces.

A preference for prey items with a low proportion of chitin has been shown experimentally for another primarily insectivorous bird, the Ovenbird (Parulidae) (Zachs & Falls 1978). It is possible that Choughs on Islay, at the north westernmost periphery of the world range have to maximise their digestive efficiency by feeding primarily on soft-bodied prey. This may be particularly important in the winter months when day-length is shortest.

The Chough's preference for soft-bodied prey means that conclusions about its diet based on faecal analysis should be restricted only to those species with chitinised body fragments that are not destroyed by digestion. Experiments with captive Choughs by Meyer (1991) showed that worm chaetae survive digestion and are present in faeces for several hours after ingestion. This suggests that most species with chitinised body parts should be detectable in Chough faecal samples.

The low frequency of worms in the Chough's diet in this study is remarkable considering their abundance in most feeding habitats (see Appendix 3) and the fact that they are soft-bodied. Moreover, the data on frequency of occurrence (Figure 8.2) are likely to be maximal estimates, since they are based on presence/absence in faeces alone. The avoidance of worms by Choughs has been noted in captive birds (Turner 1977) and by all previous authors (Bullock 1980, Roberts 1982, Warnes 1982 and McCracken *et al.* 1992) except Meyer (1991), who found evidence of worms in up to 31% of faeces collected in south-west Wales, and up to 74% in Cornwall. He suggested that some observers may have failed to identify worm chaetae in their analyses. However, in this study, and that of McCracken *et al.* (1992), special efforts were made to locate worm chaetae in faecal samples, so it is likely that their low frequency in Islay samples was real. This is backed up by my own extensive field observations on feeding Choughs (see Chapter 7) during which worms were only seen to be taken on less than 10 occasions.

Non-preference of worms is shared by the Jackdaw (see Chapter 4), and it may be that there are costs associated with the digestion of slime-producing invertebrates such as worms and slugs (slugs were not recorded in the diet at all in this study, but were frequent in Chough feeding habitats (Appendix 3)). Choughs and Jackdaws may also avoid eating worms in order to avoid infection by the parasite *Syngamus trachea*, for which worms are one of the main intermediate hosts (see chapter 4). It is notable that the faecal samples with the highest percentage of worms in Meyer's study came from two extra-limital (and probably first-winter) birds in Cornwall, which only survived for 2-3 months (see Meyer 1990). One of these birds was in poor condition and suffering from *S. trachea* infection before it died, though it is not known whether this was the cause of its death, or merely a symptom of its poor condition.

The frequency of occurrence of cereal grains was low in the current study. This contrasts with the findings of McCracken *et al.* (1992) who state that "cereal grains were the most frequently taken food items [on Islay] during the winter months", and also McCracken & Foster (1992b) who state that "cereals are extremely abundant in the diet [on Islay] from October to April". It seems likely that the high proportion of cereal grains in the samples used by McCracken *et al* (1992) and McCracken & Foster (1992b) may have resulted from their using non-fresh and nocturnally produced faeces and pellets only. I demonstrated above that pellets are more likely to contain fragments of both hard-bodied animal prey and vegetable matter. Choughs tend to feed on cereals late in the day (*pers. obs.*), as has been noted for Rooks (Feare *et al.* 1974) and Starlings (Feare 1984), thus they are more likely to be present in nocturnal faeces and pellets. In an analysis based entirely on pellets produced at a communal roost site, Soler & Soler (1993) also found a high proportion of cereals and wild grains in the diet. Again, the use of pellets may biased their results in favour of less easily digestible food items and/or those eaten late in the day.

8.4.2 Feeding behaviour and feeding sites

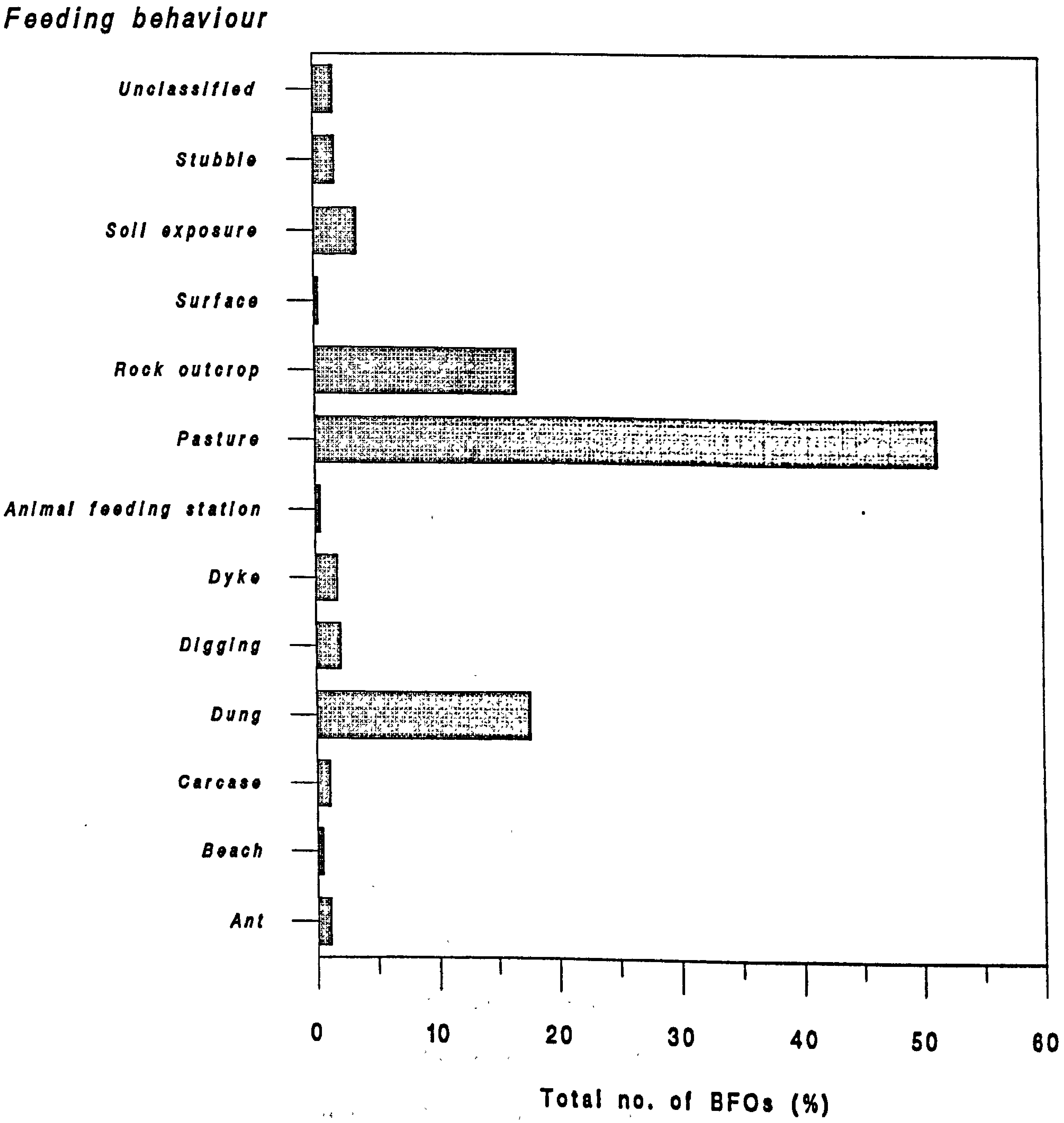
Soil cores were considered the most appropriate method for invertebrate sampling because Choughs feed primarily on sub-surface invertebrates (see section 8.2.4). However, sampling of some feeding sites was difficult due to the nature of the site (rock outcrops, field boundaries, carcasses, dung etc.). Moreover, it was clear from observations of feeding birds that even within feeding patches birds were selecting micro-habitats, based either on visual cues (burrow entrances?) or tactile cues (exploratory probes in the substrate). It was impossible for the sampling technique used here to replicate this level of site selection. Therefore it is likely that random sampling of such sites will under-estimate prey densities. Conversely, in patches of limited extent such as moss-covered rock outcrops, it was very difficult to take a large number of samples without seriously damaging these sites. For this reason the number of cores taken was kept to a minimum (10-15) and only a few such samples were taken. It should be noted that few samples were taken from dung or from dune habitats, as these were being sampled contemporaneously on Islay by David McCracken as part of another study on the importance of dung to feeding Choughs (McCracken 1990).

In Appendix 3 I have presented the results of invertebrate sampling in different habitats as maximum recorded densities of live prey (g/m^2). The use of maximum values may help to offset the problems of the sampling technique described above. However, for several reasons, these results should be interpreted with caution. Firstly, sample sizes were small in many habitats (though note that each feeding-site sample compared 10-15 soil cores, and each field sample 40+ soil cores). Secondly, the fact that a certain biomass of prey is present does not mean that this biomass of prey is available to feeding Choughs (see Tinbergen 1981). It is likely that physical characteristics of the feeding site are equally important. These include sward height, substrate bareness and type of substrate. It was shown in Chapter 7 that study pair C foraged in fields with the highest component of bare ground, despite adjacent fields having a higher biomass of Tipulid larvae.

The Chough's most commonly employed feeding technique was "pasture-feeding" (Figure 8.5). This basically involves the location and extrication of sub-surface prey items such as the larval forms of *Tipula paludosa* (maximum biomass in pastures 58.4 g/m^2, see Appendix3), the Ghost Swift Moth *Hepialus humuli* (Lepidoptera:Hepialidae), the Large Yellow Underwing Moth *Noctua pronuba* (Lepidoptera:Noctuidae), Bibionids (maximum biomass in pastures 41.3 g/m^2) and Elaterids (maximum biomass in pastures 4.5 g/m^2). Worms were by far the most abundant invertebrates in terms of biomass in all pasture habitats (maximum biomass 232.8 g/m^2). This contrasts with their low frequency in faecal samples, which strongly suggests that they are a non-preferred prey item. Recently reseeded pastures had a lower diversity of invertebrates than older pastures; the fact that younger pastures are highly preferred feeding habitats at certain times of year appears to be due to their structural characteristics rather than to prey biomass/diversity *per se* (see Chapter 7). Older pastures held more Bibionids, Lepidoptera and especially Elaterids.

Pasture-feeding also included the turning over of stones and dung, to expose surface-living prey such as Staphylinid beetles. Sand/moss pasture at Lossit Bay was used extensively by pasture-feeding Choughs in June and July 1988. Sampling revealed a high density of *Tipula marmorata* larvae (biomass 25.1g/m^2), probably associated with the high moss content

Figure 8.5 Proportions of different types of Chough feeding behaviour, Rhinns transects, Islay 1988 (n=1307 Bird Feeding Observations (BFOs)).



of the pasture.

Surface-feeding was uncommon in all habitats and it seems that Choughs are poorly adapted for feeding on mobile surface-living prey. However, surface-feeding is the likely source of Elaterid adults which were frequent in the diet in May. It was also recorded in moss-pasture in early May, when study pairs B and C were noted feeding on surface active Wolf Spiders (Araneae:Lycosidae) possibly for provisioning to their newly hatched chicks. Royama (1970) and Tinbergen (1981) found that spiders were provisioned to young chicks of Great Tits *Parus major* and Starlings *Sturnus vulgaris* respectively, and they considered that spiders contained nutrients essential to chick growth at this stage of development. It is also possible that the staple food items of older chicks - Tipulid and Lepidopteran larvae, may simply be too large for small chicks to ingest, as suggested for Starlings by Tinbergen (1981).

Surface-feeding was also recorded in late summer in permanent pasture and heath/ pasture mosaics, where direct observations showed that harvestmen were super-abundant (Opiliones). It was also recorded in dune habitats for pairs D and E from May to July when direct observations showed that Choughs were feeding on an abundance of surface-active Garden Chafer *Phyllopertha horticola* (Coleoptera:Scarabidae) beetles, and on the larvae of the Belted Beauty Moth *Lycia zonaria* (Lepidoptera:Geometridae), a Red Data Book moth species (Hadley 1984).

Dung, including manure heaps and spread manure, was an important feeding site from May to December. Dung supports high densities of invertebrates, mostly dung beetle larvae and adults (mostly *Aphodius*), and dung fly larvae (*Scathophaga stercoraria*). However it should be noted that the biomass estimates for dung patches in Appendix 3 represent densities within the dung itself (ie. g/m^2 of dung); this does not allow for variations in the density of dung per m^2 of habitat. Worms were abundant below dung, but were apparently not taken. In the drier summer months Tipulid larvae aggregated below cow pats, and older drier pats also harbour Elaterid larvae. Bibionid larvae, which though small (*c.* 0.01g) occur in very high density clumps, may also be associated with very old decomposed dung.

I found little evidence to support the suggestion of Warnes (1982) and McCracken (1990) that Choughs feed on semi-digested cereal grains within dung. Grain was absent from most cow-pats inspected whereas *Aphodius* and *Scathophaga* larvae were abundant. Moreover, cow-pats were not exploited when fresh, only when they contained mature larvae. If birds were feeding primarily on grain in cow dung one would expect them to exploit fresh dung as well as more mature dung.

Rock outcrops, soil exposures and earth banks/dykes were favoured feeding sites, particularly in the late summer and winter. Within these sites a variety of prey types is available. In winter, Carabid larvae and earwigs (Dermaptera) burrow into soil exposures within these habitats where they remain inactive throughout the day. At night (in both summer and winter) the Carabid larvae move out into the fields to forage (Thiele 1977), probably resulting in a nocturnal turnover of individuals which can be exploited by Choughs the following morning. Nocturnal activity of larvae may be facilitated by the mild winters in areas occupied by Choughs: Thiele (1974) noted that Carabids which over-winter as active larvae are mostly found in areas with mild winters. High densities of Carabid larvae (up to 1100/m^2) have been recorded in field boundaries (Thomas *et al.* 1992), and Thomas *et al.* (1992) proposed the creation of artificial linear habitat "islands" within fields as refuges for these predators to aid biological control of pests. The creation of such habitats would almost certainly be beneficial to feeding Choughs, especially in arable/dairy farming areas and in areas with large field sizes.

The variety of physical niches and micro-habitats associated with rock outcrops supports a wide range of invertebrates. The shallow vegetation and soil may help Choughs to exploit these prey items. For example, I have found hibernating *Aphodius* larvae in mid-winter just below the vegetation surface on rock outcrops, a time of year when they would normally be much deeper down in the soil horizon and unavailable to Choughs. The moss carpet which covers most rock/vegetation interfaces often supports high densities of *Tipula marmorata* larvae (maximum biomass 64g/m^2. Though smaller than *T. paludosa* larvae, they are probably easily located in this "shallow" habitat. Staphylinid larvae, Carabid larvae and Earwigs (Dermaptera) are also frequent in this micro-habitat,

Yellow Mound Ant nests are often situated on rock outcrops, and these are a favoured feeding site in the late summer. The increasing exploitation of ant mounds later in the summer by feeding Choughs lends support to the hypothesis proposed above that they are feeding on larvae rather than adults: the larvae develop considerably in size through the course of the summer, whereas adult size remains the same throughout (Brian 1977). Perhaps the larvae only represent a profitable prey item when they are mature.

Choughs were never observed feeding in deep-ploughed fields, though this behaviour was noted on Cape Clear Island in Eire by Sharrock (1984). He considered that the behaviour was overlooked in other areas, but I made special efforts to check recently ploughed fields (which are common on Islay) for feeding Choughs and saw none. However, Choughs were twice recorded feeding in shallow-harrowed fields in which sods of turf or small stones lying on the surface were turned over by Choughs to reveal Tipulid larvae which had congregated beneath them, sometimes at high concentrations (58.1g/m^2).

The frequency of stubble-feeding observed in this study (1.8% of all Rhinns feeding observations) is not consistent with the findings of Warnes (1982) and McCracken *et al.* (1992) on the predominance of grain in the Chough's diet in autumn and winter (see above). However, even though Warnes (1982) recorded high frequencies (up to 100% occurrence) of cereals in winter roost faeces, less than 20% of her own Chough feeding observations in any one season were in stubble fields. This discrepancy highlights the biases inherent in analysing faeces or pellets from roosts, which may over-represent food taken in the latter part of the day, as well as over-representing less easily digestible food items (see section 8.4.1).

I only recorded one instance of Choughs feeding at an animal feeding station on food put out for stock - an incident involving three birds feeding on oats (in the late afternoon). Such sites were widely exploited by other corvids (and see Feare *et al.* 1974). However, Choughs often fed on Bibionid larvae which appeared to be associated with long-decayed vegetable and dung matter at feeding stations, especially those in dune systems.

Feeding by digging occurred mostly in friable substrates, especially in sand associated with dune systems. Feeding site samples showed that this technique was used to expose adult weevils (Curculionidae) in grey dunes in April-May, *Aphodius* larvae burrowing in sand and/or beneath dung throughout the summer and autumn, and larvae of the Sand Dart Moth *Agrostis ripae* (Lepidoptera:Noctuidae) in May and June. Clarke & Clarke (1995) recorded Choughs using similar methods to reveal larvae of the Mining Bee *Colletes succinctus* in dune systems on Colonsay.

Only 1.1% of feeding observations were at carcases, but it is possible that this behaviour was under-recorded since carcases are often located in ditches and hollows where the Choughs would be hard to locate. Carcase-feeding included birds using carcase dumps (specific areas on each farm for disposing of carcases). Choughs fed on the Cyclorrhaphan fly larvae (maggots, referred to here and in Appendix 3 as Muscid larvae) and beetles and their larvae which associate with carcases, but not on the carcases themselves (for which the bill would be ineffectual). Choughs appear to specialise in feeding on the full-grown maggots which move away from the carcase to pupate in the surrounding pasture or in peat/earth banks in the vicinity of the carcase. Maggots occurred at a density of up to 48.8 g/m^2 in the immediate vicinity of carcases, representing a highly profitable feeding site. Presumably there is competition from Hooded Crows *Corvus corone* for maggots within the carcase, but those pupating away from the carcase are probably only exploitable by Choughs. There is a daily emigration of mature maggots from a carcase (Putman 1977), and the total biomass of maggots "produced" by one carcase must be very high. As such they represent a valuable component of Chough feeding territories, though one which is countered by the fact that carcases on agricultural land are required by law to be buried.

In the autumn of 1989 I carried out a small scale Chough "feeding" experiment with the help of Mike Peacock, the RSPB warden at the Gruinart reserve on Islay. A maggot-infested sheep carcase was buried in a shallow pit in a peat substrate and covered with a layer of peat 10 cm deep. A purpose built 20-30 cm bank was cut into the peat around the rim of the grave. As expected, the maggots left the carcase to pupate in the peat bank, and the resident pair of Choughs fed at this site regularly for at least 2 months subsequently (Mike Peacock *pers. comm.*).

Beach-feeding accounted for only 0.5% of Rhinns feeding observations. It was recorded only from the beach at Kilchoman. Direct observations and feeding site sampling showed that the birds were feeding on sandhoppers *Orchestia gammarella* (Amphipoda). Choughs located the sandhoppers by turning over sea-weed or by digging in sand banks where the dunes meet the beach and in which their burrows were easily visible. Beach-feeding on Islay is clearly much rarer than on Bardsey (Roberts 1983) or the Isle of Man (Cullen & Jennings 1986) where Kelp Fly *Coelopa frigida* larvae are the main food item. Kelp flies occur in mature beds of rotting seaweed, which are relatively scarce on the exposed western coasts of Islay. One such site present within the Rhinns transect area near Portnahaven was never seen to be used by Choughs, despite the fact that its presence was advertised by large numbers of Starlings feeding on Kelp Fly larvae. This highlights the regional variations which exist in Chough feeding behaviour. It is notable that Choughs on Colonsay appear to have recently developed the trait of feeding in kelp beds (D. Beaumont *pers. comm.*).

Food hoarding, though common in other corvids (Goodwin 1986), was never recorded, although it has been noted in captive birds (Turner 1959). The perishability of the Chough's soft-bodied prey probably makes food hoarding unprofitable.

8.4.3 General discussion

The predominance of soft-bodied prey in the Chough's diet suggests that it may be constrained in some way to feeding on the most easily digested food (see Fisher 1972). This could be the result of physiological or environmental constraints. A physiological constraint is implied by the fact that cereals comprise a much larger proportion of the diet of the closely related Jackdaw and Rook (Feare *et al.* 1974, Holyoak 1968), whose abundance suggests that cereal-eating is a successful strategy. However, the fact that Choughs in other parts of the world range <u>are</u> much more dependent on cereals (Goodwin 1986, Soler 1989) suggests that the species <u>is not</u> physiologically incapable of digesting vegetable food. This then suggests that the physiological difference between Chough populations has an environmental basis. Two hypotheses suggest themselves: a) that the short day-length in winter in Britain, the most northerly part of the species' world range, may limit the time available for collection of sufficient invertebrate food to balance the cereal portion of the diet, or b) that competitive exclusion may have "forced" the Chough to adopt a specialised invertebrate diet.

The first hypothesis is based on the findings of Feare & McGinty (1986) who studied Starlings feeding on barley at cattle feeding stations. They found that during winter barley alone represents an inadequate food, but provided that over half of their daily food intake consists of invertebrates, then Starlings can utilise barley as a high energy food source. The possibility of a similar constraint operating on food intake of the Chough can be examined by comparing the British race with a race in a contrasting, but almost equally northerly part of the range: *P. p. brachypus* is resident in Mongolia, where day length is probably only slightly longer in winter than in Britain. In Mongolia Choughs subsist on household scraps and vegetable matter through a winter of constant sub-zero temperatures (Kitson 1985). The energetic requirements for survival in this environment must be considerably higher than in Britain, notwithstanding the slightly longer feeding day. The survival of these birds in this extremely harsh environment suggests that a non-invertebrate diet can satisfy a high daily energy requirement, and there is no obvious reason why such a diet should not be equally successful for Choughs in Britain. This suggests that inter-specific competition may influence the Chough's feeding ecology in the British Isles. It is notable that in Mongolia both the Rook and Daurian Jackdaw *Corvus daurica* (the Jackdaw's counterpart there) leave the area in the winter (Kitson 1985 and *in litt.*).

The Chough's potential interspecific feeding competitors in Britain were discussed in Chapter 4. The Rook was considered to be the most likely competitor, due to the similarity of its sub-surface feeding techniques with those of the Chough. The diet of the two species shows some overlap, but the Rook is a much more successful granivore than the Chough. If British Choughs shared the diet and body size of their continental congeners, then the degree of overlap with the Rook would be much greater, which would presumably lead to greater inter-specific competition. Lack (1971) showed that similar sized congeneric species rarely coexist in the same habitat - they are usually separated by range, body size or feeding adaptations. Perhaps then the small body size of the British race of the Chough (compared to its conspecifics) is a response to competition from the Rook. Moreover, any such reduction in body size would tend to bring the Chough into more direct competition with the smaller-bodied Jackdaw, another successful granivore. It is perhaps as a result of the large difference in body size between the Rook and the Jackdaw that the two can co-exist so successfully. The Chough, on the other hand is sandwiched between these two species, with a bill structure not well adapted to gleaning. These factors may help to explain the high proportion of invertebrate prey in the diet of the Chough in Britain as compared to elsewhere in its world range.

There is some circumstantial evidence to support this hypothesis. In most of the mountains and steppes inhabited by Choughs in Eurasia Rooks are absent (see Figure 4.1 and Cramp & Perrins (1994)), and in Mongolia, the Chough is the only resident corvid (see above). On Islay, the Chough's strongholds (the Rhinns and the Oa) are areas with few Rooks but more Jackdaws (Jackdaws being more abundant than Choughs on the Rhinns) (*pers. obs.*). In the Canary Islands, the only corvids present are the Chough and the Raven *Corvus corax*; Choughs are restricted to the westernmost island of Palma. Here in the absence of other medium-sized corvids, it appears to have undergone niche expansion: it feeds in a wide range of pastoral and agricultural habitats (Cullen *et al.* 1952), feeding on figs and oranges as well as invertebrates, and has even been seen feeding in Canarian Pine *Pinus canariensis* woodlands on a temporary abundance of caterpillars (Piersma & Bloksma 1987). This behaviour is consistent with the ecological release hypothesis where, in the absence of competition, a species' feeding niche becomes much broader (Lack 1971). An analogous situation occurs with the Chiffchaff *Phylloscopus collybita* in the Canary Islands. Here, in the absence of its congeners it occupies a much wider range of habitats than it does in continental Europe, where it is part of a guild of several similarly sized species of leaf-gleaning warblers (Lack 1971).

Corvids are one of the few groups for which there is clear experimental evidence of competitive exclusion: Hogstedt (1980) showed that there is competition between Jackdaws and Magpies for food during the breeding season. One suspects intuitively that Choughs and Rooks may be at least as similar to each other as the Jackdaw and Magpie, and I suggest that competition for food with the Rook and perhaps the Jackdaw may have led to the Chough's specialised invertebrate diet in Britain. If so, this would be the ultimate cause of the Chough's restricted range, which, mediated through the climatic requirements of its invertebrate prey, is restricted to areas characterised by summer warmth and winter mildness.

Chapter 9

GENERAL DISCUSSION

9.1 The Chough in the British Isles

The Chough is a unique bird in a British context. Its British population represents almost the entire population of the nominate sub-species (+/- the Brittany population, depending on their classification), which occupies an ecological niche unlike that of the other continental sub-species, and which experiences very different environmental conditions. In Chapter 4 it was shown that dispersal from island Chough populations is restricted by their very insularity; this would also apply to the British Isles as a whole. The British population is probably effectively isolated from its con-specifics (assuming that gene flow between the Pyrenees and Britain is at most negligible), and these are conditions under which allopatric speciation can occur (Mayr 1963). The British Isles supports only one endemic bird species, the Scottish Crossbill (Voous 1978), but the British Chough, given time, may be a candidate for full specific status.

Inter-racial differences between Chough sub-species may help to account for some of the contradictory findings of this study. For example, the Chough's apparent dependence on extremely mild winters in the British Isles does not sit easily with the knowledge that Choughs in Mongolia are resident in areas where mean monthly temperatures range from -12°C to -21°C between November and March (Willett 1983). Likewise, in Mongolia and Iberia, it appears that Choughs feed more on cereal grains and household scraps (Kitson 1985, Soler 1989), more typical of a generalist corvid. Rather than invalidating the findings of Chough research in Britain, these differences suggest that direct comparisons between races which occur in greatly contrasting environments should not be made. However, a better understanding of the basis of these differences may help us to better understand the processes which brought them about, as, for example, in the potential role of inter-specific competition (see Chapters 4 & 8) in moulding the Chough's ecological niche in Britain.

The Chough in Britain occupies a unique ecological position at the north-western extremity of the species' world range. It is subject to a unique set of environmental conditions, and apparently has its own set of ecological requirements. The fact that the British race is the smallest of all Chough races (Vaurie 1954) is clear evidence of the uniqueness of this sub-species. Interestingly, the small body size of the British race fits the general positive correlation between body size and temperature (see James 1970), in that the climate experienced in the British Isles is probably much milder in winter than that experienced by other European races, except those on the Mediterranean islands, Coastal Portugal and the Canary Islands. This also shows that temperature gradients do not necessarily operate on a simple north-south axis. None of these unique characteristics of the British Chough population are mentioned by Batten *et al.* (1990) in *Red Data Birds in Britain*, but they surely should add a qualitative component to assessment of the importance of this population, over and above a simple estimate of what proportion of the European population occurs within these islands.

9.2 Constraints on the Chough's range in Britain

The areas where an animal is found and where it chooses to feed can be considered to have a hierarchical nature, since an order of selection processes can be identified (Wiens 1973). Geographical range, home range, habitat use and food selection by a species are all of different orders, with the selection at the later orders depending on selections in the earlier ones. In this study I have addressed the main levels of this selection process by assessing the influence of climate, nest-site availability, habitat type and patch type on the distribution of Choughs in Britain and on the Island of Islay.

The analyses in Chapter 5 suggest that Choughs in Britain require extremely mild winters and warm summers, brought about by climatic influences on the life cycles, growth and availability of the invertebrates which make up most of their diet. The exposed nature of Chough feeding sites means in turn that the invertebrates in these sites are unprotected from the vagaries of climatic effects, which may explain the close relationship between Chough distribution and climate. It is suggested that cold winters may affect the over-winter survival of Choughs, particularly of inexperienced first-year birds, whilst summer warmth may be linked to breeding success, which is known to be higher in the warmer parts of the range (Bullock *et al.* 1983). It should be possible to test these hypotheses more rigorously in years to come when more survival data become available from colour-ringing schemes.

Assessment of the Chough's range showed no difference in the climatic determinants of its past and present distribution. This strongly suggests that climatic change was not the cause of the wide-spread declines and extinctions reported at the turn of the century. It seems likely that persecution by man was the main cause of these declines, particularly during the Victorian collecting era. However the species' range achieved its minimum recorded extent in the 1970s, long after persecution had ceased, but following a prolonged period of climatic cooling (Burton 1995). This would be expected if the climatic correlations of the Chough's current range (described above) have a causal affect on the species' distribution. Ironically some of the areas in Scotland and England with the mildest winters and warmest summers (the Rhinns of Galloway in Scotland, and Cornwall in England) were those in which the Chough's decline was most dramatic. This suggests a possible indirect relationship with climate through its influence on land-use: areas with mild winters and warm summers may have facilitated greater agricultural intensification, with Choughs only surviving in fringe areas where climate is sub-optimal both for farming and for the birds themselves. An analogous situation applies to the Red Kite *Milvus milvus* in Britain, which became restricted to a small area in mid-Wales due to persecution. This population has been very slow to expand its range this century due to poor breeding success, and this is thought to be due in part to the cool, wet climate of the area (Davis & Newton 1981). Reintroduction of Red Kites to climatically more favourable areas in Britain has met with immediate success (Carter and Crockford 1995). Ironically, Choughs may benefit from "global warming" - milder winters would make inland areas more suitable than at present, whilst warmer summers would increase the suitability of both upland areas (e.g. mid-Wales) and areas on the northern perimeter of the range (e.g. the islands of Mull and Skye in Scotland).

Within climatically suitable areas, nest-site availability has a strong influence on where Choughs are found. Within Scotland, the historical absence of Choughs from areas climatically equivalent to Islay such as Coll and Tiree, can be explained in terms of the absence of nest-sites in these areas. The use of a nest-site availability index also identified currently occupied areas where nest-site availability appears to be limiting, such as Colonsay, where the provision of artificial nest-sites could lead to a significant increase in population size (see Appendix 4). Results presented in Appendix 4 show that the juxtaposition of suitable dune and pastoral feeding habitats to nest-sites is also important in determining whether such sites are occupied by nesting Choughs.

The constraints on the Chough's distribution in Britain imposed by climate and nest-site availability mean that any conservation plan for the species should take into account certain "geographical" effects, in particular, the lower dispersal of Choughs from island as compared to mainland sites. Choughs in Scotland, appear to represent a series of "metapopulations" (Levins 1969), i.e. a series of sub-populations connected by dispersal. It was suggested that the Chough population on the Mull of Kintyre in the 1970s was a "sink" population (*sensu* Pulliam 1988) dependent on the productivity of the nearby "source" population in Northern Ireland. As the latter population declined, the smaller Kintyre population became extinct. Likewise, the population on Colonsay which became extinct early in the 20th century but which has subsequently been recolonised, appears to be dependent on recruitment from Islay. The single pair in Wigtonshire almost certainly originated from the Isle of Man. These source areas (Islay, the Isle of Man) should be targeted for special Chough conservation measures in order to facilitate potential range expansion. However, due to the lower rate of dispersal from island as compared to mainland sites, it is important that breeding pairs at new sites on the mainland also be the subject of special conservation efforts in an attempt to establish viable populations in areas with greater potential for future dispersal.

9.3 Habitat use and management on Islay and in relation to other areas

The main habitats used by Choughs on Islay are a mixture of improved and unimproved pasture, dune systems and grazed heath. Important patches within these habitats include rock outcrops, field boundaries (especially earth banks/dykes), herbivore dung, ant mounds, spread manure and manure heaps and carcases. A diversity of these habitats and associated favourable land-uses within a small area appears to be crucial, particularly in autumn and winter. Monocultures of any habitats, even favoured ones, would not provide the year-round requirements of the species. Moreover, many of the important habitat components mentioned above are considered undesirable or "untidy" in a well run farming unit. It can only be hoped that the Chough's requirements will be taken into account in any schemes designed to promote agricultural extensification in areas where Choughs are found, such as within the Argyll Islands "Environmentally Sensitive Area" (ESA).

There was some variation in habitat use between study areas in Scotland and Wales, with unimproved habitats such as heath and permanent pasture being more widely used in Wales (Bullock 1980, Roberts 1983, Meyer 1991) than in Scotland. However, the structural characteristics of preferred feeding habitats were constant between habitats and study areas - with close-cropped swards and bare ground being essential. In most habitats this type of structure is generally produced by grazing animals, especially the smaller herbivores such as sheep and rabbits. Cessation of grazing, or intermittent grazing, such as that employed with dairy cattle, is thus detrimental to Chough feeding sites. This emphasises the controlling role of Man in the ecology of the Chough, particularly through his influence on grazing regimes within agricultural environments.

Unfortunately, in certain habitats the production of the right habitat structure for feeding Choughs almost constitutes habitat destruction. Two examples of such conflicts in favoured Chough habitats are 1) heavily grazed dune systems whose botanical interest is seriously damaged by over-grazing (Boorman 1989), and 2) heath/acid grassland mosaics and moss pasture habitats, both of which result from heavy mixed grazing and/or burning, processes which are usually considered anathema to maintaining heathland integrity (Cadbury 1993). Indeed, over-grazing of upland and coastal habitats brought about in part by agricultural subsidies has been a subject of some concern in recent years (see Usher and Thompson 1988). However, within pasture habitats many foraging bird species require a short sward (Fuller 1982, Green 1988), and the presence of herbivores in rough-grazed areas provides dung which supports a rich invertebrate fauna, and carcases which are important to carrion-feeding birds of prey such as the Raven (Marquiss *et al.* 1978) and Golden Eagle (Watson *et al.* 1992). There is a clear need for a balanced approach to habitat management within areas occupied by Choughs.

9.4 The diet on Islay

The diet of the Chough on Islay was shown to be comprised primarily of soft-bodied invertebrate prey (Chapter 8), mostly soil or dung-dwelling larval forms of beetles; fly and moth larvae. Differences in the composition of prey types in faeces and pellets were shown. The analysis of the Chough's diet is complicated by the fact that the birds feed on many soft-bodied prey items which may not show up in faecal or pellet analysis. Differences between methods and samples used make comparisons between studies difficult. For example, the findings of this study did not support those of other studies on Islay (Warnes 1982, McCracken *et al.* 1992) which suggested that cereals were one of the most important food items in autumn and winter. Before any further dietary studies are made on the Chough, it is essential that the effects of the time of day, type of prey and type of sample are investigated experimentally.

9.5 Causes of the recent decline of the Chough in Britain

It was suggested in Chapters 4 & 5 that the recent decline of the Chough in Britain may be part of a longer term range contraction which may have begun in Neolithic times, perhaps brought about by long term climatic change. However, climate cannot be implicated in several recent extinctions in areas which share similar if not milder/warmer climates than those currently occupied (see Chapter 5). In these areas persecution was certainly one contributory factor in this process, with Victorian trends in collecting and game-preservation undoubtedly reducing Chough numbers. It is difficult to determine whether there were concurrent detrimental changes in land-use (see Chapter 7 & Meyer 1991) which could also have contributed to the decline - many of the most crucial land-use practices, such as whether animals were wintered out of doors, or what type of habitats were used for grazing, go unrecorded in parish records, the main source of historical land-use data. Only the decline in horse numbers (and the associated growing of oats for fodder) mirrored the timing of the Chough's decline. Horses grazed on rough ground and wintered outside would have filled a similar grazing role to that of beef cattle on Islay today. Their disappearance would certainly have reduced the number of feeding opportunities for Choughs.

It seems likely that persecution and man-induced changes to the environment brought about the Chough's extinction in several areas. With our increasing knowledge of the species' ecological requirements, the time may be ripe for attempts to be made to create and manage appropriate habitats within climatically suitable areas with a view to re-establishing Choughs in parts of their former range. As the Chough's low dispersal would make natural recolonisation of areas such as Cornwall unlikely, a re-introduction programme as envisaged by Meyer (1991) could be undertaken. Such a programme could be modelled on that used successfully over the last 5 years for the Red Kite *Milvus milvus* in England and Wales (Carter and Crockford 1995). The fact that Cornwall may be climatically "better" for Choughs than any other part of Britain suggests that, given the availability of the right habitats, a reintroduced population could be highly productive, and act as a source of birds for colonisation of adjacent areas. In a Scottish context the same applies to the coast of Wigtonshire.

In considering the conservation status of the Chough in Britain, Stroud *et al.* (1989) wrote "Choughs were formerly more abundant and widely distributed, extending to north, east and inland Scotland...", and Batten *et al.* (1990) reiterated this assessment of past distribution. In Chapter 3 I demonstrated that the breeding range of the Chough in Scotland since 1750 was in fact not as extensive as it has come to be accepted in the literature. This is an important finding since it delimits a much smaller area within which future conservation measures in Scotland can be expected to be successful. Moreover, any successes in extending the species range can be measured against a more realistic (and conservative) estimate of the past range.

9.6 Opportunities for conservation management

The Chough is now a rare species in Britain and Europe, and its fortunes are influenced by a range of factors. Some of these, such as climate and natural nest-site availability are abiotic factors, over which man has little influence (not-withstanding the recent concerns over global warming). Others, such as the influence of land use on habitat structure and food availability, are directly determined by Man, and thus provide opportunities for "conservation management". At one extreme this could involve the reintroduction of the Chough to parts of its former range (see above) as proposed by Meyer (1991). At the other extreme it could simply involve the encouragement of beneficial land-uses or the creation of artificial nest-sites within the core of the Chough's range. The designation of Sites of Special Scientific Interest (SSSIs), Special Protection Areas (SPAs), Special Areas for Conservation (SACs) and Environmentally Sensitive Areas (ESAs) should provide a framework within which positive prescriptive management can be supported. Full advantage should be taken of these opportunities.

The Argyll Islands ESA is a particularly positive development, which may help to promote Chough-friendly land-uses in these islands. It remains to be seen whether the ESA scheme will become a long-lasting and economically viable part of the farming environment, or whether it will represent a temporary resistance to the rising tide of agricultural intensification. There is always the potential for gross changes in stock-rearing land-uses to be brought about almost overnight by changes in agricultural subsidies (see Egdell *et al.* 1993). The changing fortunes of the Lammergeier *Gypaetus barbatus* in Corsica have been linked to changes in animal husbandry brought about by changes in agricultural subsidies (Thibault *et al.* 1993). The Inner Hebrides currently benefit from their "Less Favoured Area" status within the European Community and from the support of the Hill Livestock Compensatory Allowance subsidy. Both help to maintain the number of grazing animals, and therefore farmers and crofters on these islands (Egdell *et al.* 1993). It is to be hoped that this status will be retained in the future.

On an island such as Islay, with a rich and diverse fauna, conservationists involved in environmental management are forced to juggle with the conflicting requirements of a range of protected species. The habitat structures preferred by Choughs are mostly inimical to those of other rare birds on the island, including the Corncrake *Crex crex* (see Stowe *et al.* 1993), Hen Harrier (Watson 1970), Short-eared Owl (Avery and Leslie 1990), Barn Owl (Taylor *et al.* 1988) and Greenland White-fronted Goose (Mayes 1991). In general these species all prefer ungrazed habitats, and young forestry is of particular benefit to some.

This makes land management decisions difficult - should an improved pasture be heavily sheep-grazed in the summer for Choughs, or left for hay or silage growth for Corncrakes? Clearly there is a need to balance the conflicting requirements of all these species, and to encourage species in those areas which, by virtue of natural habitat availability, topography, drainage etc. are most appropriate for them. Islay represents the core of the Chough's range in Scotland, but the productivity of this population is not high compared to other parts of the British range (Bullock *et al.* 1983, Bignal *et al.* 1987b). Unfavourable land-use changes could easily tip the balance against this population. Indeed, the population on the Mull of Oa which comprised 19 confirmed breeding pairs in 1986 (Monaghan *et al.* 1989) has declined to less than 10 pairs in 1994 (Douglas Gilbert (Scottish Natural Heritage) pers. comm.), thought to be the result of more cattle being wintered indoors. Priority should be given to conserving preferred Chough habitats, such as dune systems and grazed pastures, and to favourable land use practices such as out-wintering cattle, mixed permanent grazing regimes and high grazing pressure. Special attention should also be focussed on maintenance of highly preferred feeding patches such as rock outcrops and dykes.

What specific habitat and land-use measures should be undertaken within the Chough's current range to maintain or increase its population, or within its former range to encourage recolonisation? In Table 9.1, a synthesis of favourable/detrimental management practices based on the findings of this study are listed. The recommendations include some previously made by Meyer (1991); he also proposed strip-cultivation of unharvested cereals to provide supplemental food in late summer and autumn. Most of the recommendations are self-explanatory. The creation of linear "island" habitats within agro-ecosystems is an intriguing possibility. Island habitats have been created within arable farm units to act as over-wintering sites for predatory arthropods in an attempt to provide biocontrol of pests in cereals (Thomas *et al.* 1992). These islands consisted of earth-ridges 1.5m wide, 0.4 m high and up to 580 m long sown with grass species. The ridges bisected large agricultural fields. Their structure resembles that of earth banks, favoured Chough feeding sites. The ridges sites, and they supported high populations of Carabid larvae (up to 1100/m^2) (an important winter prey item of Choughs) and other invertebrate predators. The potential for such structures to provide winter feeding for Choughs and summer crop protection for farmers is surely worth exploring further. Even the simple production of tractor ruts in a field can provide day refuges for Carabid larvae, and there is scope for experimentation with a range of such "habitats-features". In Chapter 8 I described a small-scale experiment based on the shallow-burying of a sheep carcase. Such work could be refined, and the establishment of permanent carcase dumps with shallow-buried carcases within suitable substrates (well-drained peat or sand) could be encouraged.

Table 9.1 *A synthesis of habitat/land-use practices considered to be favourable/detrimental to Chough feeding requirements.*

Favourable land-uses	Impact not clear	Non-favourable land-uses
Short/bare vegetation		Rank vegetation
Diverse pastoral habitats		Habitat monocultures
Low % of arable crops?		High % of arable crops
Low % of cereal crops		High % of cereal crops
Permanent grazing		No/intermittent grazing
High grazing pressure (= short sward /soil exposures etc)		Low grazing pressure (rank vegetation)
	Silage growth ?	
Mixed large and small grazing animals (rabbits, goats/sheep, cattle/horses)		Single-species grazing
Out-wintering of stock (especially cattle)		In-wintering of stock
Presence of carcases /permanent carcase dumps		Deep-burying carcases
Earth banks/dyke field boundaries		Non-structural field boundaries (fences)
Creation of linear "habitat islands"		Removal of field boundaries (except hedgerows)
Manure-spreading		Slurry spreading
Manure heaps		Slurry production
		Ivermectin use?

9.7 Future threats

It is impossible to fore-see where future threats to Choughs may come from. Even so, detrimental changes in land-use can be inferred from the above descriptions of preferred habitats and land-uses. The designation of the Rhinns SSSI precluded the possibility of further afforestation within this area. As long as sheep and beef farming remain profitable on Islay, it is unlikely that the Chough's favoured feeding habitats will be given over to forestry. However, should the economic climate change by, for example withdrawal of Less Favoured Area status, rough grazing ground may once again come under threat.

The high diversity of habitats and land-use required by Choughs means that the development of monocultures is a particular threat. Much of inland Wales now represents a sheep-rearing monoculture. Chough breeding success here is good, but preliminary results suggest that recruitment is poor, perhaps as a result of low over-winter survival of first-year birds (Mckay 1990, Cross *et al.* 1993) and there has been a decline in the number of inland breeding pairs in Wales in the last decade (Green & Williams 1993). The absence of beef cattle or other large herbivores in these areas may be implicated here. Mixed grazing could be encouraged in this area under the Cambrian mountains ESA scheme.

Increased levels of tourism *per se* may not pose a particular threat to Choughs, but certain recreational activities such as rock-climbing on nesting cliffs, or mine-exploring in occupied mines need to be carefully monitored. The Welsh Development Agency recently embarked on a programme of mine-capping, essentially for safety purposes. This represents another case of tidying up the environment, and is being monitored closely by RSPB Wales (S. Tyler *pers. comm.*).

Other threats may come from less easily identified sources, of which inter-specific competition from Rooks, Barn Owls and Kestrels, as well as predation by Goshawks, has already been discussed. If these species are a source of competition/predation, then they only pose a threat where the range or size of their populations expands/increases. Such changes could be brought about by afforestation or planting of copses within or adjacent to areas occupied by Choughs, as on the Rhinns of Islay.

There is a clear need to monitor agricultural policy, and environmental and land-use change as it affects the Chough's range, not only to identify and deal with potential threats, but also to make maximum use of opportunities for conservation which may arise through schemes such as ESA designations. The drawing up of a "Species Action Plan" for the Chough by the RSPB (RSPB 1994) is to be applauded in this respect.

9.8 Future research

Many questions concerning Chough ecology remain unanswered. What proportions of each habitat type represent an ideal Chough feeding territory? What is the basis of the differences in habitat use and diet between study areas in Scotland and Wales? Do silage crops represent a net benefit or loss to Choughs, and how does their profitability differ in areas with and without grazing geese? How efficient are Choughs at digesting cereal grains? Are oats preferred to barley? On Islay, the role of dune systems in the feeding ecology of Choughs was not fully addressed in this study, yet it is clearly very important.The role of dune systems in the ecology of the Chough is worthy of a study in itself. There is scope for research on the phenology of dung fauna, and on the role of different types of animal dung in Chough feeding ecology. Further experimental work on habitat and patch creation methods would be invaluable, as described above for "island" habitats and carcase-burying.

There is a need for experimental feeding studies with captive Choughs to be carried out in order to calibrate the results of faecal analyses made to date. The successful use of roost balances in this study showed that the body mass of wild Choughs can be measured throughout the year. This could be a very powerful tool in assessing the main periods of food shortage, and could provide a unique interpretation of seasonal habitat use, particularly if the latter could be studied using radio-tagged birds.

There is perhaps a tendency amongst British and Irish ornithologists to think of the Chough in the British Isles as something of a curiosity, a far-flung representative of mountain ranges and steppes not entirely at home on these shores. But the Chough has its own special niche in the British Isles, evolved at least over several thousand years, and moulded by a set of circumstances which we are still in the process of unravelling. It is a bird which depends on our mild and wet climate, pastoral land-uses and rugged coastlines, and embodies the spirit of the Celtic fringe.

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Appendix 1.

HISTORICAL RECORDS OF THE CHOUGH IN SCOTLAND

Abbreviations of references used in text:

B&R = Baxter & Rintoul
H-B = Harvie-Brown
H-B&B = Harvie-Brown and Buckley
H-B&M = Harvie-Brown and Macpherson
RSM = Royal Scottish Museum
SBR = Scottish Bird Report
OSA = Old Statistical Account
NSA = New Statistical Account

Square brackets enclose 1) my comments within direct quotations or
2) the national grid reference to the nearest 1km of a locality, as used in the production of the distribution maps in Chapter 3.

Characters in left hand column indicate:
A - accidental occurrence
1 - possible breeding
2 - probable breeding
3 - definite breeding
? - questionable record
P - "Pre-historic" record
. - no available information

AB - ABERDEEN [c.NJ 7030]

. 1750 - No information available.

0 c.1825 - Not mentioned from Deeside ([c.NO 5298] and Braemar [c.NO 3796] (MacGillivray 1855).
0 c.1875 - No records from Deeside (Sim 1903).
0 1882 - Mr.Sim of Aberdeen informed Buchanan (1882) "that the Chough does not occur on the Aberdeenshire coast [c.NK 0733]."

0 1990 - No recent records form Grampian region [c.NJ 7030] (Buckland *et al.* 1990).

AN - ANGUS [c.NO 4050]

0 1791-1799 Not mentioned in the *OSA*.

. 1800 - No information available.
? c.1870 - Don in his "List of the Birds of Forfarshire" (now Angus) spoke of it as "resident in the mountains of Clova" [c.NO 3070] (H-B 1906). But H-B continues - "be that as it may, it seems almost indisputable that all our accounts of Choughs breeding at inland places are sadly awanting in authenticity".
0 1874 - Mr. Henderson of Dundee assured H-B (1906) "*viva voce* that Choughs were not uncommon near Arbroath [NO 843], and he added that "the birds

were known to the boys there by that name". However, he also offered to obtain eggs for [H-B] (February 27, 1874) but "had not done so by 1886, nor since...[1905]".

0 1900's - No records (B&R 1953, *SBR*).

AA - ARRAN [c.NR 9030] & **BU - BUTE** [c.NS 0666]

0 1769 - In a detailed list of birds seen on Arran in the summer of this year Pennant (1771) mentions "stares, pewits, daws and hoodies" but makes no mention of Choughs.

. 1800 - No information available.
1 1863 - Gray (1871) states that the Chough has not bred in Arran for the last seven years - since "one of the Duke of Hamilton's keepers shot the only pair on that island [at Kilpatrick NR 9027 (Gibson 1956)] in 1863, and I have been assured that no Choughs have been seen there since".

0 1927 - not mentioned from Bute by McWilliam (1927).
0 pre-1955 - Gibson (1955) could trace no later record than Gray's [see 1861 above].
? c.1970 - Gibson (1975) states "during the past 10 years I have received several sight records of Choughs seen in various parts of Arran. Although the observers have not been ornithologists in the accepted sense, there is little doubt that these records are perfectly authentic. I myself have not yet seen a Chough on Arran, but I hope that it may soon return as a breeding species. It is certainly on the increase in Kintyre".
0 1988 - No recent records (*SBR*).

AR - ARGYLL (mainland, excluding Kintyre peninsula) [c.NN 1040]

3 1791 - Found nesting on the rocks on Lismore [NM 8340] (*OSA*).

2 c.1800 - Gray (1871) states that "flocks of Choughs existed in the district of Appin [NM 9548] at the beginning of the present century".
0 1871 - Gray (1871) states that "the Chough is no longer found on the island of Lismore or in the district of Appin".
0 1895 - Not mentioned in *Birds from Moidart and Elsewhere* [c.NM 7573] (Blackburn 1895).

A 1944 - John Fraser told B&R (1953) that "a pair were seen on the Glen Crutten estate [NM 8730] near Oban in the winter of 1944".
2 1959 - John Whyte (1958-61) states that "on a day between 30th May and 14th June 1959 my wife and I saw a bird which we are convinced was a Chough *Coracia pyrrhocorax* on a cliff face about a mile north of Gannavan Sands [NM 8733], near Oban. Its unusual boisterous note first attracted me and, as it was disturbing the foliage of a creeper covering the cliff, I was able to focus my glasses on the spot before the bird showed itself. In size it resembled a Jackdaw, certainly no smaller, and its plumage was shiny bluish black. Its head was slightly elongated with a very bold eye and its most striking feature was its long, slightly down-curved bill, which was bright orange-red. I was unable to see the bird's legs because of its position". [Behaviour and bill colour suggest a recently fledged juvenile?].
A 1970 - *SBR*: One in summer on a sea-cliff, N. Argyll (J.H.Wood).

0 1973-88 - *SBR*: no records.

AK - ARGYLL (Kintyre peninsula) [c.NR 2715].

. 1750 - No information available.

1 1843 - B&R (1953) quoting the *NSA* say the Chough "is recorded from Killean [NR 6944, opposite Gigha] and Kilchenzie [NR 6725, Machrihanish]."
3 1870-90 - Colville (1980) states that the Chough formerly nested on the island of Davaar [NR 7620] close to Campbeltown: "My father shot several there between 1872 and 1877, and there are frequent references to nesting Choughs in his diaries. The late Mr. John Bailie, formerly head keeper in Kintyre, told me that Choughs nested on Davaar until the 1890's."
3 1873 - B&R (1953) state that "in 1873 a young Chough from Kintyre [c.NR 7040] was shown to the Glasgow Natural History Society."
3 c.1890 - Mr. Bailie, the head keeper on Kintyre told Colville (1980) that he remembered Choughs nesting "very plentifully" at Southend, breeding in the cliffs at Keil [NR 6708] and Dunaverty...until just before the turn of the century.
3 c.1895 - Colville (1980) asserts that "several pairs of Choughs...used to nest on the steep cliffs at the Learside [c.NR 7714] between Campbeltown and Southend" until at least the turn of the century.

0 1900's - not known from the island of Davaar in this century (Bailie in Colville 1980).
3 c.1919 - Colville (1980) was "given good information that a few pairs [of Choughs] had continued to nest [at Learside] until just after the first world war...[but] that any remaining birds would appear to have been shot out when the gamekeepers returned after the war...about 1920."
3 1919-20 - D. Macintyre recorded that in one of these years a pair reared young [at the Mull of Kintyre] and that they used to breed freely in the caves on the western sea-board of Kintyre [c.NR 5915] (B&R 1953).
A 1934 - Colville's (1980) last record of a Chough at Learside was of one shot by the gamekeeper at Achinhoan [NR 7717] in September 1934.
1 c.1936 - "Fairly often seen or shot still on the western sea-board of Kintyre" [c.NR 7040] (McWilliam 1936).
? 1950 - Colville asserts (1980) that "Choughs have been nesting again at the Mull of Kintyre since the early 1950s" but gives no direct evidence. [This reference is given "?" status since it conflicts with other contemporaneous reports (see below) and was made as a rather vague statement in 1980].
1 1951 - Greenleas (1953) states that the Chough "used to nest at the Mull of Kintyre. In 1951 a pair frequented the cliffs beside the lighthouse [NR 5908]. They appeared to be about to nest but suddenly they disappeared; either shot or taken by a Peregrine."
0 1954-56 - not mentioned from Southend [NR 6978] by Greenleas (1957).
1 1964 - 3 at the Mull lighthouse (B. Zonfrillo *in lit.*).
3 1967 - A family of 5 seen on 22nd July near the lighthouse (F.Traynor *pers. comm.*).
2 c.1970 - probably bred (see Sharrock 1976) at the Mull.
2 1973 - SBR: 4 pairs mainland, 18th July (W. Wyper).
2 1974 - SBR: 21 mainland Argyll is better than usual (W. Wyper, B. Zonfrillo).
2 1975 - SBR: 10 mainland site, April.
3 1976 - one pair made a definite breeding attempt at the Mull (B. Zonfrillo *in lit.*).
2 1978 - SBR: 16 mainland site, 3rd Feb.

A 1979 - SBR: 1 at Southend, 24th June "is away from usual mainland site."

A 1980 - 2-4 on Sanda [NR 7304] from 26-30 September were the first records for this locality (Maguire 1980).

3 1980 - Colville (1980) states that "there is now a small but thriving colony [at the Mull of Kintyre]".

3 1981 - SBR: 20, Mull of Kintyre, 4th July (per R. Coomber) and at least one nest used.

2 1982 - At the Mull of Kintyre Warnes (1983) records the presence of a non-breeding flock of 7 birds, with one pair present at a suitable nest-site in May, and a single bird at another traditional nest-site in February and May, but no proof of breeding at either. The Argyll Bird Report notes flocks of 7 on 26 Feb, 4 on 12 July and 3 on 7 Sept.

1 1983 - pair present but did not breed (B. Zonfrillo *pers. comm.*).

0 1984-86 - no records (SBR, B. Zonfrillo *pers. comm.*).

0 1986 - no birds found on survey of former sites, Kintyre peninsula April-May (Monaghan *et al.* 1989).

0 1989 - SBR: no records since 1983.

AY - AYR [c.NS 5020]

0 1769 - Listing the land-birds seen on a visit to Ailsa Craig [NS 0200] Pennant (1771) mentions only "hoodies, ravens, rock-larks and pigeons".

1 1824 - Mr. Anderson informed Gray (1871) that the Chough "frequented the cliffs at Culzean Castle [NS 2310]" and that a "specimen shot there is still preserved".

2 c.1866 - Gib Graham, writing in 1926, told Paton & Pyke (1929) that the Chough "was fairly common sixty years ago. No doubt the Jackdaw was the cause of its disappearance... In the old days it was very common on Knockdolian Hill" [NX 1185].

1 1871 - according to Gray (1871) still seen on the south coast in reduced numbers, with occasional stragglers as far north as Ballantrae" [NX 0882].

1 1882 - Buchanan (1882) reports [with no explicit evidence] that the Chough is "also met with at Ballantrae but is apparently almost or quite extinct on the confines of that county and Wigtown" [perhaps merely reproducing Gray's statement (1871 above)].

1 1895 - George Rose (1904-07) mentions that he saw a pair of Choughs on the cliffs of Ayrshire about the year 1895, and adds: "A pair or two may still be seen, though not so common as formerly".

2 c.1895 - Lawson (1895) in "latest notes from Ailsa" reports the presence of "a number of Choughs or Red-legged Crows".

3 c.1895 - Berry (1908) writes of the Chough "I am sorry to say this pretty and interesting bird is not so plentiful here as I have seen it, still a pair or so may be seen occasionally. I have seen it breeding not far from Lendalfoot not so very long ago. I am afraid this splendid bird is deceasing quickly".

2 c.1896 - Gib Graham, writing in 1926, told Paton & Pyke (1929) that "the last pair [of Choughs] nested about thirty years ago" [presumably in the vicinity of Knockdolian Hill/Ballantrae (see c.1886 above)].

A 1920 - George Cassidy (of Culzean [c.NS 2410] told Paton & Pyke (1929) that he had seen only one Chough, "a mile from the coast, feeding at a sheep trough".

1 1922 - The Rev. J. MacWilliam saw a pair of Choughs [in Ayrshire, exact locality not given] (Paton & Pyke 1929).

3 1929 - Paton & Pyke (1929) say that one, and occasionally two pairs nest in a locality in Ayrshire which they leave nameless [c.NX 1998].

3 1936 - "A few pairs still nest on the cliffs in south Ayrshire, where I have seen them" (McWilliam 1936).
A 1980 - One shot 4th November at Bracken Bay, Ayr [NS 3319] (*SBR*).
0 1988 - *SBR*: no records since 1980.

BA - BANFF [c.NJ 6066]

. 1750 - No information available.
. 1800 - No information available.
? c.1855 - Gray (1871) states "it may be questioned if a single Chough has been seen at ...Troup Head [NJ 8266]...for the last ten or fifteen years" without giving any evidence that Choughs <u>ever</u> <u>had</u> been seen there.
? 1882 - Buchanan (1882) quotes from Gray (1871), offering no new information concerning the Chough's status in Banff.

0 1900's - No records (B&R 1953, *SBR*, Buckland *et al.* 1990).

BE - BERWICK [c.NT 7050]

3 1578 - Buchanan (1882) reports that 'Bishop Leslie in his "De Origine Scotorum", states that in his time (the Chough) bred on the Berwickshire coast between St. Abb's Head [NT 9169] and Fast Castle [NT 8671].'

. 1750 - No information available.

3 c.1825 - Robert Cowe informed Muirhead (1889) that as a schoolboy "he often saw the Red-nebbed Crow about the rocks of the sea-coast immediately to the west of Petticowick [NT 9069], and that it built in a steep precipice there; also that his school-fellows sometimes took the young ones to be kept and tamed like Jackdaws".
3 c.1825 - According to Muirhead (1889), Wilson wrote that "the Red-legged Crow or Kay built formerly at Biter Cove and Thrummycar Heugh [** ****], but is now extinct in this neighbourhood".
2 1832 - Dr. Johnston in an address to the Berwickshire Naturalists's Club in 1832 says, with regard to the visit of the Club to St. Abb's Head in the previous July: "I must not leave this majestic coast without mention of another of its feathered tenants, the Cornish Chough, which indeed was not seen by us on this occasion, but is certainly ascertained to breed in the rocks between St. Abb's Head and Fast Castle" (Muirhead 1889).
1 c.1838 - Hancock (1874) states "with regard to the Chough, a specimen in my collection was ...shot at Redheugh [NT 8270], near the place where it was breeding.
2 1841 - Selby writes that "the Chough finds a congenial retreat in the precipices of St. Abb's Head and adjoining coast", and that "here it is not uncommon, but being a bird of wary habit, it is very difficult to approach within gunshot, and specimens are not easily obtained" (*Hist. Ber. Nat. Club. Vol 1., p.253*).
3 1846 - Hardy, *in lit.* to Muirhead (1889) noted that "a pair were then seen at Fast Castle, and that the young used formerly to be climbed for, and taken out of the nests, to be tamed".
2 1850 - Hepburn (*Hist. Ber. Nat. Club. Vol 3., p.72*) visited St. Abb's

Head on an ornithological excursion in June 1850, and stated that "the interesting Chough, or Red-legged Crow is now extinct, except a solitary pair, which I am informed seldom strayed far from Fast Castle, a few miles to the eastward of the head".

0 c.1855 - Muirhead (1889) considered that the Chough had become extinct "about St. Abb's Head and Fast Castle between 1846 and 1855, and to have remained so; for had this not been the case, the bird would surely have been seen after the last-mentioned date by fishermen and others.. Notwithstanding numerous inquiries, I have not been able to find any person who has seen it on the Berwickshire coast within [the last thirty years]".

? 1866 - Turnbull in *Birds of East Lothian* considered that a single pair still frequented [St. Abb's] (Muirhead 1889).

? 1895 - the Berwickshire Naturalist's Club met at St. Abb's on 26th June 1895, and were informed by fishermen that a pair of Choughs were nesting at Petticowick [referred to by B&R 1953 as "an unsubstantiated report"]. B&R also add that "there are several later records of Choughs being seen in the neighbourhood of the St. Abb's cliffs" [in the absence of any further details I can only assume that they refer to records from inland sites in Peebles (see Peebleshire), the nearest locality to St. Abb's with records for this period.

A 1903 - The most recent Berwickshire record is of a bird seen at Fast Castle in July 1903 (Murray 1986, source not known).

0 1904-88 - No records (Murray 1986, *SBR*).

CA - CAITHNESS [c.ND 1050]

. 1750 - No information available.

0 pre-1887 - no records from Caithness (H-B&B 1887).

0 pre-1953 - no records (B&R 1953).

A 1965 - The first record for Caithness was reported to D.M. Stark by Mrs. Simpson (*Scot. Birds* 3: 374) as a "black crow with curved red bill and red legs" - undoubtedly a Chough - seen in Clett on the island of Stroma [ND 3577] in May. [Perhaps the same bird as the one seen less than 15km away in South Ronaldsay the preceding January (see Orkney)].

0 1988 - no recent records (*SBR*).

DF - DUMFRIES [c.NS 3590]

. 1750 - No information available.

1 1848 - Service (1885) states that a pair of Choughs "took up their abode at an old ruined building at Bogrie" [NX 8184] , this being the only inland record that he could confirm. "Though the birds were evidently preparing for nesting, they disappeared after frequenting the place for several months. There was a strong suspicion that the gun terminated their career." Bogrie lies 20 miles inland near Moniaive.

0 1882 - No recent records according to Buchanan (1882).

0 1900's - No records (B & R 1953, *SBR*).

DB - DUNBARTON [C.ns 3590]

. 1750 - No information available.

A c.1850 - Lumsden (1876) stated that "the Chough has been obtained near Bowling" [NS 4574], but Buchanan (1882) was unable to fix a date to this occurrence.

? c.1850 - Lumsden & Brown (1895), in contrast to the above reference of Lumsden's (1876), state "this species at one time bred near Bowling - I think on the rocks at Auchentorlie".

? ???? - B&R (1953) state that "the species is said at one time to have bred near Bowling, Dunbarton" [NS 4473] presumably based on Lumsden & Brown's statement (1895).

A c.1928 - Bartholomew (1953) states "when I was counting Rook's nests at Cumbernauld [c.NS 7574] on 19th April, 1946 the gamekeeper there, Beaton, told me that about 18 years previously (ie. about 1928) he shot a bird there in June and, after reference to a book with plates of birds, he identified it as a Chough. I don't think he could mistake a Chough for any other bird".

0 1988 - No recent records (B&R 1953, SBR).

FF - FIFE, CLACKMANNAN & KINROSS [c.NO 3010]

. 1750 - No information available.

A c.1840 - B&R (1953) quoting the NSA (1844) say that the Chough "is also recorded as being occasional seen near Dunfermline" [NT 0987].

? 1882 - Buchanan (1882) was told that in bygone years the Chough frequented the Ochill Hills [NN 9000] but says "I have no evidence as to the accuracy of this report". H-B (1906) was equally skeptical about [presumably] the same record from the Alva precipices in the Ochills [NS 8798].

0 1900's - no records in this century from the Isle of May [NT 6599] (Eggeling 1974; SBR).

0 1988 - no records this century from Fife (Smout 1986; SBR).

INNER HEBRIDES

IG - GIGHA & CARRA [c.NR 6550]

2 1793 - Buchanan (1882) reports that "the Chough evidently occurred in Gigha [NR 6550] and Carra, Argyllshire, as Mr. Fraser, in writing an account of the zoology of this parish for the OSA states as follows: "Jackdaws are very numerous. Of the last there are two kinds - one with a dark blue head, all the rest black; another with red feet, having the body and head black".

2 1888 - H-B failed to find any Choughs on Carra during a visit there, but Captain Scarlett, factor on Gigha and Carra, whilst speaking of their existence, says "they do not appear to increase or diminish (*in litt.* 1888)...

0 1891 ...and later of its having been "driven away by the Jackdaws" (H-B & B 1892).

3 1902 - A clutch of five eggs in the Baldwin-Young collection at Oxford University Museum were taken on Gigha on 5 May, 1902. The collection

notes state that the "nest was on a ledge in the top of a cave, just within reach of a long ladder which we carried from a neighbouring farm. The keeper, McLachlan, says that this is the only pair on the island. Every egg was addled".

3 1930 - "Nests on Gigha" Alexander Blair *in litt.* 28th December 1930 (McWilliam 1936).

0 1949 - On a visit to Gigha from 11-23 June, Rintoul & Baxter (1950) did not see any Choughs, "nor did [they] hear of any recent records".

0 1982 - Not recorded during 1982 survey (Warnes 1983).

0 1988 - No recent records (SBR).

II - ISLAY [c.NR 3060]

. 1750 - No information available.

2 1843 - B&R (1953) refer to the NSA which records the Chough as occupying the rocks along the shore at Kilchoman in south-west Islay [NR 2163].

1 1864 - A skin in British Museum the was collected on Islay in this year.

3 1866 - A clutch of three eggs from the Jourdain collection in the BM (Tring) was taken on "Islay" on 2nd May, and another single egg from the Seebohm collection was from Islay c.late 1800's.

1 1866 - A skin in the BM (Tring), as collected on 2nd March on Islay.

2 1867-88 - Mr. Small a taxidermist in Edinburgh received six specimens from Islay during this period (H-B&B 1892).

2 1869-96 - Seven specimens collected on Islay during this period are currently in the skin collection of the RSM (Edinburgh).

1871 - Gray (1871) states that "the Chough is nowhere so common in Scotland as in the island of Islay, which is still frequented by the same numbers as were known to exist there 20 years ago. I have obtained yearly evidence of this both by observation and the acquisition of specimens. At

2 Bridgend [NR 3362] and Port Ellen [NR 3746] it is seen in small parties coming close to the village, and frequently approaching the refuse heaps near the dwelling-houses. A very handsome pair now before me were caught in a sieve trap. It is doubtful if any of their corvine allies could

3 have been captured so easily. At the Mull of Oe [Oa, NR 2742], in the same island, wandering flocks of Choughs are often seen, and I have many eggs in my collection from that headland". There follows a set of notes forwarded by a Mr. Elwes. These include a general (quite detailed) account of the species' habitats on the island, including the statement that the Chough "is also often seen about roads and houses especially in frosty weather" and that he thinks "it is rather decreasing at present, though unmolested by the inhabitants".

2 1875 - Two Choughs in the BM (Tring) skin collection were taken on Islay in this year.

2 1876 - Scott-Skirving writing on the natural history of Islay (1876) states that "the Chough is still found in some numbers, though subjected to much persecution on account of an increasing demand for the skins by dealers in natural history specimens".

2 1876 - The British Association for the Advancement of Science (1876) say of the Chough "even in Islay where quite abundant 'til five years ago, there is a sensible diminution of numbers, caused, it is sad to say, by the inroads of dealers in natural history objects".

2 1878 - Scott- Skirving (1878) adds to his previous reference in 1876 "it is pleasant to note that the lively, dapper and glossy Chough is as frequent among the sea-cliffs as in recent years, and its merry, and not unmusical cry, is often heard at a considerable distance from the

shore". [He also notes that the Rook is a common and permanent resident, and that gamekeepers have exterminated every hawk breeding in the island except the Peregrine, the Sparrowhawk and the mouse-devouring Kestrel].

2 1880's - James Lumsden of Arden who visited Islay almost every autumn in the shooting season considered the Chough to be "far from uncommon there" (H-B&B 1892).

3 1888 - Chough eggs were obtained by the son of the factor Mr. John Dixon (H-B&B 1892), though the local factor at Ballygrant designates the Chough as "scarce in Islay, formerly plentiful", and a gamekeeper long resident on Islay, "from whom we ourselves received eggs many years ago" says, "still found all around the coasts of Islay", but "getting much fewer, and their places are being taken up by Jackdaws".

2 1892 - Still occurs "where it is well cared for and preserved" (H-B&B 1892).

3 1907 - Ross (1913) knew only of two nesting places of the Chough on Islay: "the Mull of Oa and Ardmore [NR 4751, no longer present here]. At the latter the birds are not many, but there are still a goodly number nesting at the former. On the 22nd 1907 he saw c.34 birds in the vicinity of Ballychatrigan and Strimnish [on the Oa]. He also notes a nest in a crevice of a natural arch in a huge solitary stack [a nest-site (Oa 19) still in use at present]...In the winter months they are to be seen in Port Ellen".

2 1914-18 - Mr. Mackillop, factor of Islay House, told B&R (1953) "that during the 1914-18 war, Peregrines increased very much and Choughs were becoming scarce; now, however, Peregrines are less numerous and the Choughs have increased again". [Nothing changes!]

1 1914 & 1928 - Two specimens collected on Islay now in the RSM (Edinburgh).

3 1930 - "Nests in Islay" Alexander Blair *in litt.* 28th December 1930 (McWilliam 1936).

3 1936 - W.B. Alexander reported to B&R (1953) that "in 1936 they were numerous on the Mull of Oa, and he found a pair on Eilean Mhor, off the north-west of Islay" [NR 2270].

1 1939 - A skin in the BM (Tring) was collected on 11th November at Port Ellen.

3 1943 - Sandeman (1955) "saw six adults and six young on 19th June" at a locality on the Mull of Oa [c.NR 3342].

1 pre-1953 - B&R (1953) report that they "saw Choughs on the cliffs of Islay and watched with great pleasure, their wonderful flight and heard their characteristic calls".

3 1954 - Meiklejohn & Stanford (1954) report seeing "eight pairs of this species in only one locality", but also that "Mr. R. Huggins told us that one possible reason for its decrease is that a number get caught in rabbit traps in the winter". In addition, in their conclusions, they state that "it is possible that an increase in the Jackdaw may be correlated with a decrease in the Chough" but they give no substantiation of this statement.

2 1955 - Sandeman (1957) reported "Choughs seem to have declined in one district [see 1943 above] where I saw only 4".

3 1960-62 - Rolfe (1966) records the presence of up to 30 breeding pairs in Argyllshire [presumably all on Islay].

3 1963 - Rolfe (1966) estimated the Scottish population [primarily on Islay] to consist of 70 individuals and 11 breeding pairs. This represented a marked reduction from the previous two years when it was known that 30 pairs attempted to breed. Perhaps this reduction was a consequence of the severe winter of 1962-63. Booth (1981) notes that

Rolfe saw a flock of 47 birds on Islay in July 1963.

3 1970 - *SBR*: "Largest flock Islay, 25" (C.G. Booth).

3 1972 - *SBR*: Continued improvement in numbers on Islay, including a flock of 60 birds (Booth 1981).

3 1974 - *SBR*: 91 [in] different parts of Islay 16th March (R.H. Hogg). Booth (1981) records a single flock of 42 on 26th May.

3 1975 - *SBR*: 20+ Machir Bay 24th October.

3 1978 - *SBR*: 134 Islay, 14-15 February.

3 1979 - *SBR*: 40+ on the Oa, 11th July was highest count received. Booth (1981) records a flock of c.70 in October.

3 1980 - *SBR*: Breeding - no change Islay.

3 1981 - *SBR*: Census April-May gave 174-180 birds, two-thirds paired and attempting breed, poor success.

3 1982 - Warnes (1983) estimated the Islay population at 53-61 breeding pairs, with 32-50 non-breeding individuals (total 141-175 birds).

3 1983 - *SBR*: 39 Loch Gruinart, 28th September.

3 1985 - *SBR*: 104 known nests Islay, 67 occupied, young fledged from 25 out of 31 recorded nests (mean breeding success 2.76 young/successful nest).

3 1986 - Monaghan *et al*. (1989) found 78 confirmed or probable breeding pairs on Islay, with 105-130 non-breeders.

3 1987 - Probably slightly larger breeding population than 1986 (*pers. obs.*).

3 1988 - Breeding population continues to expand, utilising more buildings/man-made sites (*pers. obs.*).

IJ - JURA [c.NR 5880]

. 1750 - No information available.

. 1800 - No information available.

? 1871 - Gray (1871) considered it "doubtful if [the Chough] breeds in Jura".

2 1892 - still occurs where "it is well cared for and preserved" (H-B & B 1892).

3 1926 - The RSM holds a clutch of 5 eggs taken on Jura in May of this year.

2 pre-1953 - B & R (1953) state that the Chough "probably breeds on Jura".

3 1981-82 - Warnes (1983) estimated 6-8 breeding pairs, but there was only definite evidence of 2-3 pairs [c.NM 7000], with a flock of 17 seen on the Paps of Jura in September 1983, and four on Eilean Bhride [NR 5570].

3 1986 - Monaghan *et al*. (1989) found three breeding pairs but no non-breeders in a survey which covered most of the island [c.NR 5080].

IC - COLONSAY & ORONSAY [c.NR 3890]

2 1769 - seen by Pennant (1771) on Oronsay [NR 3588] "July 7: Ascended the very hill [Beinn Oronsay] that the saint [Columba] did: lofty and craggy, inhabited by Red-billed Choughs and Stares".

3 1795 - Buchanan (1882) reports that in vol xiv. of the OSA published in 1795, Mr. MacFarlane, in dealing with the history of the sea-fowl of the parishes of Kilbrandon and Kilchattan [NR 3795] states that "all the wild and tame fowl commonly seen on the other parts of Scotland are frequently seen upon this coast; and some that are now rare, particularly the jackdaw, with red bill and feet, hatches in this country."

1 1836 - Lord Teignemouth (1836) saw Choughs on the north-western cliffs of Colonsay [NR 3797]: "the scenery of the north and north-west coast of

the island is very grand...an Eagle and some Cornish Choughs were hovering about the rocks."

2 1871 - In notes to Gray, a Mr. Elwes states that the Chough on Islay "is said to have come first from Colonsay, where they are very numerous."

3 1880-87 - Frances Murray (1887) who visited Oronsay in these years says "we used to work in the garden and watch the Starlings and Red-billed Choughs nesting in the lofty and craggy, ivy-covered rocks." [The wording of this reference bears a curious likeness to that of Pennant 100 years before (see 1769 above)].

0 1882 - Buchanan (1882) gives no evidence of its presence on Colonsay.

2 c.1900 - Gathorn-Hardy (1914) said at the turn of the century "they were an everyday sight in the northern part of the island [NR 3998]." He also mentions that they had been eaten in the past and were "very palatable in Chough pie."

3 1910 - McNeill (1910) comments that "it used to nest in various places but has not been in evidence for a number of years."

A 1933 - a vagrant was seen in August of this year (Loder 1935), "otherwise no recent record."

3 1967 - a pair seen at the northern end of the island [c.NM 4200] raised hopes of breeding, and since then there has been a steady increase, with c.5 pairs in 1985 (Jardine *et al.* 1986).

3 1973 - D.R.Alexander reported a pair rearing 3 young (Jardine *et al.* 1986).

3 1975 - SBR: 1 pair with "reared young."

2 1980 - Warnes (1983) reports that the Brathay exploration group found 1 pair.

3 1982 - one pair reared 3 young (Warnes 1983).

3 1985 - SBR: up to five pairs on Colonsay, where total population 15-20 birds.

3 1986 - Monaghan *et al.* (1989) report finding 1 probable and 6 confirmed breeding pairs, plus 10 non-breeders in a survey of the whole island.

IM - MULL & IONA [c.NM 4030]

. 1750 - No information available.

1 1838 - Buchanan (1882) states that "there is in Mr. Smellie Watson's 'Egg Book' reference made to a Chough shot in Mull [c.NM 4030] in February 1838".

3 1852 - Graham (1852) states that "three pairs are constantly resident" on Iona [NM 2724], "one pair being permitted to breed in St. Columba's tower by the colony of Jackdaws while the other two breed in a sea-cave". Graham told Gray (1871) that "two nests [were] placed in sea-caves, very difficult of access, and the third is on the tower of the cathedral, among those of Jackdaws, with whom the red-legs seem to be on the best of terms, feeding with them abroad, and frequently accompanying them home to their roosting place".

? 1871 - Gray (1871) considered it "doubtful if [the Chough] breeds on Mull".

2 1871 - recorded on the Ross of Mull [NM 3020] by Mr. Sclater *in litt.* to H-B&B (1892): "I saw a slender-looking crow approaching, so I went to cover. The bird, which was a Chough (not uncommon here), pitched in a sandy place close by, and was shortly joined by another. Nothing in bird-life ever reminded me so strongly of a couple of emancipated schoolboys. They played one another all manner of tricks, pinched one another, tried to stand (almost) on their heads, put themselves into all sorts of absurd positions, and gave me half an hour's real amusement. I never saw any birds so full of fun. They did not do any of

their tricks with the preternatural gravity of a Raven, but abandoned themselves to unrestrained *high jinks*". [The behaviour described here sounds like that of first-year birds, suggesting that breeding took place in the vicinity].

0 1888 - "None now in Mull" (the Maclaine of Lochbuie *in litt.* to H-B&B 1892).

2 1890 - H-B&B (1892) write "as late as ...December 1890, we have undoubted evidence of the occurrence of the Chough both in Iona and Mull, notwithstanding other negative statements [Buchanan 1882?], although perhaps only one pair in Iona, and in a few places only in Mull".

0 1920 - "The Red-billed Chough has now gone" [from Iona] (Gordon 1920).

A 1924 - B&R (1953) "have no evidence that the Chough now nests on either of these islands".

A c.1971 - a bird was seen on the Torosay estate (from the Torosay estate Game Book, Mike Madders *in litt.*).

0 1982 - Not recorded from Mull, nor the Treshnish islands, despite coverage of likely areas (Warnes 1983).

1 1987 - *SBR*: pair present Mull 23 June - 1 Nov. These birds remained to the year end and were thought to be the same as a pair seen earlier in the year on Iona (Mike Madders *in litt.*).

2 1988 - Same pair as above present on Mull all year, but no breeding attempt was made, and a flock of 5 was present in December (*SBR*, Mike Madders *in litt.*).

3 1989 - One pair nested and were seen feeding chicks for c.3 weeks, but none fledged (Mike Madders *in litt.*).

IL - COLL [NM 2057] & TIREE [NM 0045]

. 1750 - No information available.

? 1871 - Coll and Tiree deserted "in last thirty years" according to Gray (1871), but he gives no evidence that it ever did occur there.

0 1892 - "Of the former occurrence of the Chough in Tiree we have no data at present" (H-B&B 1892).

A 1913 - Morton Boyd (1958) states that "there has been no record of breeding since before 1871", though "seen rarely at Ceann a' Mhara (Tiree) [NL 9441] about 1913 ..none recorded since".

1 1985-86 - One seen Ceann 'a Mhara winter 1985-86, with a report of two seen Tiree in June 1986 (Stroud 1989).

0 1989 - No recent records (*SBR*).

IR - THE GARVELLACHS [NM 6410]

. 1750 - No information available.

0 1800's - No early records (H-B&B 1892).

0 1949 - None recorded by Dunn (1954).

A 1977 - One seen in September (*SBR*).

0 1985 - None seen during a thorough island survey (Mike Madders *in litt.*).

1 c.1987 - Pair seen in summer (W.A.M.Muir *pers.comm.*).

IU - RHUM [NM 3797], IN - CANNA [NG 2505], IE - EIGG [NM 4685] & IK - MUCK [NM 4080].

0 1772 - Not mentioned in the following list of birds seen on Rhum by Pennant (1775): "ring-tail eagles, raven, hoodie crow, white wagtail, wheatear, titlarks, ring ousel, grouse, ptarmigan, curlews, green plovers, sascedders or arctic gulls [Arctic Skua], and greater terns

[Black-headed Gulls?]".

? 1871 - Canna supposedly "deserted in last thirty years" (Gray 1871), but Gray gives no evidence that it ever did occur there.

? 1871 - Rhum "deserted in last thirty years" (Gray 1871) but Gray gives no evidence that it ever did breed there.

A 1876 - A single bird noted on Eigg (in Evans & Flower 1967 [perhaps same record as 1879 below?].

A 1879 - In September 1879 the Rev. H.A.Macpherson observed a single Chough on the shores of Eigg (H-B&B 1892).

0 1879-84 - Not recorded on Eigg by Evans (1885).

? 1886 - H-B&B (1892) were told by a crofter that "four pairs frequented the northern cliffs [NM 4892] of Eigg and bred there. On one occasion [he] fired at one and kept the bird as a pet for some time. But ...old and young were all killed off by Peregrine Falcons, and since then they have not reappeared". H-B&B continue: "The same was repeated to us with unimportant variation again in 1891, only he put the date rather further back, -'about 10 years ago'1881]. But we do not attach much importance to this, as affecting the record".

[As these appear to be "word of mouth" references from crofters which conflict markedly with Evans' (1885) account of his six years' observations (in which he details the status of Hooded Crow, Raven and Rook) at a concurrent time, the authenticity of the records is considered doubtful].

0 1700, 1800, 1900-88 - no records from Muck (Evans & Flower 1967; *SBR*).

0 1988 - no 20th century record from any of these islands (Evans & Flower
1967, Love & Wormell 1987, *SBR*) apart from 3 seen on Eigg on 24th
1 July 1987 (*SBR*).

IY - SKYE [c.NG 4535] & **RAASAY** [c.NG 5747]

. 1750 - No information available.

1 1870 - A specimen currently in the Oxford Science Museum was shot on a cliff at Waternish [NG 2565] (price of skin 2 shillings and six pence) in October of this year.

3 1871 - Gray (1871) states that "the Chough is still found on the west coast of Skye [cc.NG 2040], where it breeds in limited numbers. Dr. Dewar has three eggs in his collection from that locality, which may be considered its most northern limit".

2 1879 - On June 21st H-B met with Choughs on the east coast [c.NG 5040] and on June 23rd on an "inland range of cliffs" [c.NG 5020] (H-B&M 1904).

1 1882 - Buchanan (1882) records that Mr. Osgood MacKenzie has observed
(the Chough) on the Storr Rocks [NG 5152] (Skye) and had also heard
that "years ago there were numbers in the island of Raasay, but he
0 does not fancy that there are any left there now".

3 1883 - Bred on one cliff at Durinish [c.NG 1649] (B&R 1953, their source not given).

3 c.1885 - According to a shepherd "breeds at Ardmore and Score [c.NG 2550], but not seen there this summer; thinks Peregrines have killed them off" (H-B&M 1904).

3 1886 - H-B reports: 1904? Bracadale, July 3rd Archie Morrison, an old crofter of Struan, informed me that he had known a few pairs of Choughs nesting in the neighbourhood of Loch Bracadale [c 3538], eg. at Harlish [Harlosh]. He called the bird by its Gaelic name, "Caag",

and said he had seen a pair rear their young in a ruined chimney".

3 1889 - Mr. MacDonald, *in litt.* to H-B&M (1904), April 1st 1890, says: "I do not know if I told you before about the Chough. If not I will take the opportunity of doing so now. I understand that they are getting pretty rare all over the British Isles now, but last year there were something like 20 (twenty) pairs of them on this estate, and I believe they all nested too. I think there are about the same number this season too".

3 1891 - Captain MacDonald wrote on May 25th: "A pair of the Choughs have a nest this year in one of the chimneys of --- House; they have evidently abandoned the hole in the rock where they used to breed, and which I think I showed you - from it I think their young used to drop into the sea and were lost; hence the change" (H-B&M 1904).

1 1898 - Collier, who lived on Raasay from 1894-1902 writes on the status of the Chough (1904) "Very scarce. Five on rocks to west of island, 3rd Jan., 1898, with three there on 5th. Afterwards I was informed
3 that a very small colony breeds yearly in some precipitous cliffs a few miles away in the Isle of Skye [c.NG 5040]. No doubt the birds seen were from this locality".

3 1904 - According to Captain Cameron "a pair [nests] annually in one or two (two or three? H-B) localities in the west of Skye [c. NG 3040] (H-B&M 1904).

3 c.1914? - B&R (1953) were told that Choughs "used to nest near Floddigarry [NG 4671], but none had been seen since the war (their reference not given).

0 1988 - No recent records (*SBR*, Andrew Currie *pers. comm.*

OUTER HEBRIDES

OB - Barra [NF 6800]

. 1750 - No information available.

1 1830 - MacGillivray in his account of the Long Island, published in the Edinburgh Journal of Natural Geographical Science, vol. ii, p.323, states "that it then frequented the southern extremity of the range, but was not met with elsewhere".

0 1888 - H-B&B (1888) considered the Chough to be extinct in the Outer Hebrides.

A 1895 - H-B (1902-03) states "Dr. M'Rury finds that this species 'undoubtedly' occurred in Barra, as recorded by Professor MacGillivray, and considers that it ought to be permanently included in the fauna of the Outer Hebrides, although there have been no recent instances of its occurrence in any of the southern islands of the group". H-B was of the same opinion.

A 1963 - Craw (1963) notes "A Chough on a Barra hillside on 10th August, feeding with two Hooded Crows was probably a migrant as a local crofter who had noticed it for the previous few days had never seen one before, though the local cliffs appear suitable for breeding".

ON - North Uist [c.NF 7525], South Uist & Benbecula [c.NF 8050]

1 c.400 - F.Beveridge found 2-3 Chough bills when excavating near Middle Quarter in North Uist [NF 8060] (B&R 1953], and "he heard of examples from Ronay but couldn't trace them".

. 1750 - No information available.

0 1830 - not known from the Uists (MacGillivray 1830).
0 1888 - Not mentioned by H-B&B (1888).
A 1902 - Guthrie (1903) "saw [a Chough on South Uist, NF 7525] in the summer of 1902".

0 1900-49 - not mentioned by B&R (1953).
* c.1970 - The record of confirmed breeding in the *Breeding Atlas* (Sharrock 1976) is not from the Outer Hebrides (Cunningham 1983).
0 1950-88 - no recent records (Cunningham 1983, *SBR*).

OH - Harris [NB 1000] & OL - Lewis [c.NB 2020]

P ???? Baden-Powell & Elton (1936-37) found possible Chough remains at an iron-age midden on a raised beach in Lewis, estimated 1500 years ago.

. 1750 - No information available.

0 1830 - not known here [Harris & Lewis] (MacGillivray 1830).
0 1888 - "extinct" in these islands (H-B&B 1888).
A 1895 - H-B (1902-03) records that a Chough "was shot near Stornoway, Lewis [NB 4233] on 13th September, by Mr. Duncan Mackenzie and recorded (*Ann.Scot.Nat.Hist.* 1896 p.122). There is some good reason to agree with Mr. MacKenzie that this bird may have been in company with the great flight of Rooks. Mr. D. MacKenzie, when I saw him in Stornoway in April 1902, told me he had seen what he took to be a Chough, at the same place, twelve months previously - probably the self-same bird he shot".
? 1893 - Cunningham (1983) records unconfirmed reports of Choughs from Pabbay (in the Sound of Harris), in the mountains of Harris and in East Loch Tarbert.

0 1988 - No recent records (*SBR*).

OK - St. Kilda [NF 0999]

0 1800-1988 - no records (Williamson & Morton Boyd 1960).

IV - INVERNESS [c.NH 3000]

. 1750 - No information available.
. 1800-49 - No available information.
A c.1870 - Booth in his *Rough Notes* (1881) states that a few years before "One was shot in Glen Cannich, Inverness-shire [NH 2734], and they are said formerly to have frequented the glen". H-B (1906) questions the authenticity of this record, so it is given category A rather than 1.
A 1890-1920 - Matheson (1931), the keeper of Glengarry estate wrote that occasional stragglers appeared in Glengarry [NH 1501]: "I have in all trapped nine, one in each of the years 1891, 1893, 1895 and 1900, three in 1907, one in 1916 and one in 1920. I have heard that they
? used to breed at Loch Hourn [NG 8605]; in June 1910 there were five, apparently young birds and an old pair, playing about together, but I did not find the nest".

A 1967 - An anonymous note in Scottish Birds (1967) states "Another unusual occurrence was a Chough seen briefly at the roadside near Daviot [south of Inverness, NH 7239], on 23rd April (C. Suffern)".

0 1988 - No recent records (Dennis 1984, *SBR*).

KC - KINCARDINE [c.NO 7080]

. 1750 - No information available.
0 c.1800-55 - Not mentioned from Deeside [c.NO 5298] (MacGillivray 1855).
0 c.1855-99 - No records in *A vertebrate fauna of Dee* (Sim 1903).
0 c.1900-88 - No records from Grampian region [c.NJ 7020] (Buckland *et al*.1990, *SBR*).

KK - KIRCUDBRIGHT [c.NX 7050]

1 1794 - in the *OSA* of 1794 B&R (1953) found the information that "Red-legged Crows are recorded from Kircudbright" [c.NX 7050].

2 1835 - a Mr. Dickson of Upper Glenstocking [Glenstocken? NX 8653], "a farm [near Colvend NX 8755] which is fronted by a great range of cliffs" [Gillis Craig? NX 8753] told Service (1885) "that about 1835 and for many years afterwards, the Choughs were not very much inferior in point of numbers to what the Jackdaws were at that time, and he says that Jackdaws are perhaps a third more numerous at the present time." Service continues "other gentlemen as well qualified to speak on the subject have also assured me of the abundance of Choughs in Colvend between forty and fifty years ago (ie. c.1830-40). Mr. Dickson stated that he never remembered noticing more than six or seven in company - they mostly kept in pairs, and were considered very mischievous".
2 1850 - Mr. John McKie...lately honorary curator of the Kircudbright Museum told Service (1885) that "Choughs were common on all suitable parts of the coast near Kircudbright [c.NX 6345] prior to about 1850, but between that date and 1870 they had all been exterminated".
3 1865 - "On the high rocks near to Douglas Hall [NX 8854]" (reports Service, 1885) "the last pair built a nest and laid their eggs in May, 1865. This nest was, I believe, the last one made in the county, for the pair of birds that owned it were shot before they built another...
...From the information that I have gathered, it appears that the
2 Choughs were much less frequent at the Heughs of Rerrick [NX 7645],
2,2 Muncraig [NX 6046] and Ravenshall [NX 5252] than on the Colvend [NX 8654]
3 part of the shore-line".
3 1869-70 - Choughs were said to have bred at the caves of Barlocco [NX 7846] and to have lingered there "until the winter of 1869-70" (Service 1885).

? 1871 - according to Gray (1871) "still apparently met with on the borders of Kircudbright, though in spots where a flock might have been met with twenty years ago, a solitary pair at most remain". [A vague reference, also encompassing Ayrshire and Wigtonshire].
? 1882 - Buchanan (1882) basically repeats what Gray said in 1871.
1 1883 - the last record of a Chough in Kircudbright (Service 1885) was of "a solitary bird that frequented the Rerrick Heughs [presumably Orroland Heughs NX ???? and Barlocco Heughs NX 7846] from February to April of 1883".
0 1885 - Service (1885) reports that the Chough "has completely disappeared from this county. Till nearly twenty years ago it was tolerably common on all the precipitous shore cliffs suited to its habits, but it then began to diminish rapidly in numbers, and shortly disappeared altogether".

0 c.1925 - no records in B & R (1953).

1 1940 - Mr. Whitford (of Barrhill) told me that in July of this year he saw Choughs near Ravenshall Cottage/Dick Hatteraick's Cave [NX 5353].

A 1958 - An article in the Glasgow Herald of 13th February 1959 (reported in *Scottish Birds* 1: 132) stated: Henry L. Martin observes that "a Chough *Coracia pyrrhocorax* was seen near Auchencairn [NX 7951] in the first fortnight of July 1958; it was flying with a flock of Jackdaws below the cliffs and was conspicuous because of its bright red bill and unusual flight".

0 1988 - no recent records (SBR).

LA - LANARK [c.NS 9030]

0 1769 - Pennant (1771) visited the Corra Linn Falls but does not mention the presence of the Chough.

1 1795 - B&R (1953) quote the *OSA* as recording the presence of the Chough "on the rocks near Corra Linn in Lanarkshire". This is presumably the same record as referred to by Gray (p.162, 1871): "about the same time as Pennant wrote ...it appears to have frequented the rocks at the Corra Linn Falls on the Clyde [NS 8841]". However, Pennant (1771 & 1775) makes no mention of the presence of Choughs (see above record).

A 1834 - Gray (1871) mentions a bird having been shot and preserved in the winter of 834 at Crawfordjohn [NS 8823] (Rev. William Goldie in the *NSA*, 1836), and suggests that "this is the last inland record of a species now confined entirely to the sea-coasts".

0 1882 - No records in Buchanan (1882).

1 1915 & 1920 - Stewart (1928) states that "in 1915 and again in 1920, we were informed that Choughs, each time a pair, had been seen in two widely separated and remote parts of Lanarkshire, on both occasions emerging from old pit-shafts" [c.NS 9030].

0 1921-88 - No recent records (B&R 1953, *SBR*).

LO - LOTHIANS (East, Mid & West) [c.NT 2060]

0 1882 - No records according to Buchanan (1882).

0 1900-88 - No records (Nash 1935, B&R 1953, Andrews 1986, Munro 1988, *SBR*).

MO - MORAY [c.NJ 4060]

0 1881 - Buchanan (1882) writes that the Rev. Dr. Gordon of Birnie [c.NJ 2254] in a letter to him "last summer reported that neither he nor any of his ornithological friends have ever heard of it being seen in that neighbourhood".

0 1882 - Not mentioned by St. John (1882).

0 1895 - Not mentioned by H-B&B (1895).

0 1900-88 No records (B&R 1953, *SBR*).

NA - NAIRN [c.NH 8050]

0 c.1870-99 - no records from Ardclach Parish [c.NH 5945] (Thomson 1900).

0 1900-88 - no records (B&R 1953, *SBR*).

OR - ORKNEY [c.HY 4020]

P Booth *et al*. (1984) mention that Chough remains have been found at an archaeological site at Bu, Stromness [c.HY 2509].

0 c.1750-1805 - Not mentioned from Orkney by Barry (1805).

0 1800's - no published records (H-B & B 1891).

A 1935 - "Mr. Duncan J. Robertson informs us (Anon. 1935-36) that T.Logie observed on Westray, Orkney [HY 4545], in the week ending October 19th, a bird sitting on a sheep's back, 'a good deal bigger than a Starling, with bright red legs and bill'. Presumably a Chough".
A 1942 - 1 on westray, 14th May (Booth *et al*. 1984).
A 1951 - 1 at Herston, South Ronaldsay [ND 4191] from 10-24 December, 1951 (Booth *et al*. 1984) [cf. record of a Chough in Shetland the following March].
A 1965 - 1 on 6th January seen on the cliffs at Windwick, South Ronaldsay [ND 4688] by H. McKenzie (*Scot. Birds* 3: 377).
0 1988 - no recent records (*SBR*).

PB - PEEBLES [c.NT 2540]

. 1750 - No information available.

0 1864 - Not mentioned by Chambers (1864).
A 1872 - Evans (1910) writes that he has a specimen of *Pyrrhocorax graculus*, said to have been shot at Leadlaw Hill, near Stoneypath, West Linton [NT 1453] about 1872 (Anon. 1910-11). [This specimen is now in the RSM (Edinburgh)].
A 1876 - Hancock (????) was told by Lord Glenconner that a Chough "had been picked up by a shepherd on Greiston Hill, adjoining the Glen [Innerleithen NT 3033] and brought to him in the flesh in October 1876.
0 1882 - No records in Buchanan (1882).

A 1919 - Simpson (1920) records that "on 2nd September a Chough was killed in the parish of Drummelzier [NT 1334] in this county. Two Choughs were seen at the time the one was got, and the second bird has been seen nearly every day since, in the same locality".
0 1921-88 - No records (B&R 1953, *SBR*).

PR - PERTH [c.NN 8040]

? 1771 - According to Gray (1871), in the second edition of Pennant's *Tour in Scotland* (1772) the Chough is referred to as being found "in the farthest parts of Glenlyon [NN 4542] and Auchmore [Achmore NN 5833]". [I have been unable to refer to this edition, but see below].

[However, in the first edition of this book (1771) Pennant makes no mention of the Chough in his personal notes (see pp. 89-93 for Glen Lyon; Achmore is not mentioned at all); it seems probable, therefore, that this is second-hand information. The records are considered doubtful here since the fourth (revised) edition of Pennant's *Tour in Scotland* (1775) makes no mention of Choughs at Glen Lyon or Achmore. Buchanan (1882) states that in the "*Statistical Account* (*OSA*) of these districts, published about thirty years later, no mention is made of the bird. Harvie-Brown (1906) questions the authenticity of these records, stating that "there is very little certain evidence that many of the notes on the Chough nesting in Scotland in inland localities are reliable".

0 c.1790 - Buchanan (1882) notes that, despite Pennant's records (see above) from Glen Lyon and Achmore, in the *Statistical Account* (*OSA*) of these districts ...no mention is made of the bird".

0 1800's - No records (H-B 1906) - "appears to have been a doubtful resident at a former period" and "in 1777 Pennant spoke of the Chough as of much more universal occurrence "in the further parts of Glenlyon and Achmore" and it seems almost needless to repeat that Mr. Horn could hear nothing of it there or anywhere in the north-west in 1879".

0 1900-49 No records (B&R 1953).
A 1960 - A Chough, presumed to be an escape, was seen in a Blairgowrie [NO 1745] garden on 20th January (*Scot. Birds* 1: 238).
0 1988 - No recent records (*SBR*).

RF - **RENFREW** [c.NS 5060]

0 c.1800-82 - No records in Buchanan (1882).
0 1900-88 - No records (B&R 1953, *SBR*).

RO - **ROSS & CROMARTY** [c.NH 2060]

. 1750 - No information available.

0 c.1800-82 - Buchanan (1882) states that he could find no records from the county of Ross-shire [c.NH 1060 & c.NH 6080].
A 1883 - According to Dixon (1886) "O.H.Mackenzie saw one at Tournaig, West Ross [NG 8783, near Poolewe] in the summer of 1883, the only instance he knew".
0 1897 - Not seen in the Summer Isles [NB 9808] (Dobbie 1898).
A 1899 - On 8th September Lord Middleton saw "when out stalking in the forest [of Applecross, NG 7546] a pair of Choughs or Red-billed Choughs". Middleton continues "they settled quite close to me, so I had a good opportunity of watching them through my glass. I believe they are scarce now in these parts, as I have never seen one here before. They were flying towards the sea, across the forest in a north-west direction" (H-B&B 1904).
0 1900-88 - No records (B&R 1953, *SBR*).
RX - **ROXBURGH** [c.NT 7030]

. 1750 - No information available.
0 c.1800-82 - No records according to Buchanan (1882).
0 1900-88 - No records (B&R 1953, Murray 1986, *SBR*).

SE - **SELKIRK** [c.NT 2818]

. 1750 - No information available.
0 c.1800-82 - No records according to Buchanan (1882).
0 1900-88 - No records (B&R 1953, Murray 1986, *SBR*).

SH - **SHETLAND** [c.HU 4741] & SI - **FAIR ISLE** [HZ 2070]

. 1750 - No information available.

0 c.1800-74 - Not noted in Shetland by Saxby (1874).

A 1952 - In the third week of March two observers noted "a smallish 'craa' with bright red (or reddish orange) legs and beak" at Exnaboe, Dunrossness [NU 3911]. Both noted the curve in the beak (Venables & Venables 1955). [cf. record of a Chough in Orkney in December of the previous year].

0 1900-88 - No records from Fair Isle (Williamson 1965, *SBR*).

A 1984 - The only recent record concerns one seen on Whalsay [HU 5664] on two dates between 6-9 February (*Shetland Bird Report*).

ST - STIRLING [c.NS 7993]

1? 1795 - Buchanan (1882) quotes the Rev. James Lapslie, in treating of the ornithology of the parish of Campsie [c.NS 5783] [in the *OSA*] states that "the red-legged crow is but scarce with us; we seldom meet with but a pair or two in the whole range of the Campsie fells; when we do meet with them, it is amongst the Jackdaws, of which there are a considerable number which haunt our rocks" (Buchanan 1882). Harvie-Brown (1906) questions the authenticity of this record.

0 1839-82 - Buchanan (1882) continues - "the Chough must however have entirely disappeared from this locality early in the present century, as no mention of it is made in the *New Statistical Account* published in 1839".

0 1900-88 - No records (B&R 1953,*SBR*).

SU -SUTHERLAND [c.NC 5040]

1 1768 - According to H-B&M (1904), James Robertson, who toured in the north of Scotland in this year says that he saw a species of crow "in a glen above the Kirk of Assynt [Inchnadamph NC 2720] with a red bill and red feet, which chattered like a Jackdaw". Harvie-Brown later (1906) mentions the Traiiligill Burn above Assynt as the precise locality of this record - interestingly there are caves present in the hillside at this site.

? 1771 - Pennant (1771) states that the Chough is found "in different parts of Scotland as far north as Strathnaivern [presumably Strathnaver c.NC 7050]. However he gives no evidence to support this statement.

1 1848 - St. John in his *Tour of Sutherland* (vol i. p.86) writes of one locality as follows: "While looking for Rock Pigeons [near Durness NC 4067], I saw a few of the Red-legged Crow, or Cornish Chough passing from rock to rock, and busily employed about the broken stones searching for food". However, Buchanan (1882) notes that "Mr. Harvie-Brown ...utterly failed in obtaining any further evidence of the presence of this species, and is inclined to think that the specimens seen by Mr. St. John were merely accidental visitors".

? c.1870 - In Harvie-Brown's "Supplementary Notes on the Birds Found Breeding in Sutherland" *Proc. Nat. Hist. Soc. Glasgow* Vol.3, p.239) a note is given of a specimen in the Dunrobin Museum [NC 8501] but the specimen bears no date or locality.

0 c.1850-87 - H-B&B (1887) were unable to trace any records since "St. John's time".

0 1900-88 - No records (B&R 1953, Pennie 1962, Angus 1983, *SBR*).

WI - WIGTOWN [c.NX 2060]

1 1684 - Sympson in *The Description of Galloway* (1684) wrote "an other fowl, which I know not the name of; it is about the bigness of a pigeon; it is black and hath a red bill. I have seen it haunting about the Kirk of Mochrum [NX 3446]."

. 1750 - No information available.

1838 - B & R (1953) quote the *NSA* of 1838 which states that the Chough "is
frequent among the Jackdaws, building its nest in dry holes in rocks and
3 caves at Portpatrick [NX 0054]...while the following year, the rocks
2 were tenanted by the Cornish Chough at Kirkmaiden [NX 0836]."
3 c.1850 - said to have been "fairly numerous" at Burrow Head [NX 4654] about
the middle of the 19th century (Jack. G. Gordon, in B & R 1953).
1859-60 - Buchanan (1882) reports that "Mr. Bell, in the Royal Physical
Society's Proceedings for 1859-60 that the Chough is common in the
3 neighbourhood of Stranraer [c.NX 0660], building in cliffs and in
caves along with his mischievous companion, the Jackdaw; but it is
certain that in this locality, as in most of the rest, it has greatly
decreased in numbers of late years."
1 1868 - Small, the Edinburgh taxidermist received a Chough from Stranraer
in January (Evans unpubl.).
0 1870 - derived from the notes of Jack G.Gordon, B & R (1953) state that
Choughs at Burrow Head apparently "died out about 1870."
c.1870 - Mr. A. Irvine Robertson, a correspondent of Gray's (1871),
states that: "he and his brother had seen as many as six together" in
the vicinity...
2 of Portpatrick [NX 0054], and others "occasionally as far south as
1 Drumore [NX 1436] and at the north extremity of Broadsea Bay [NW
1 9858]...They were most plentiful, however, within five miles of Portpatrick,
on either side of the village. We found five broods on the cliffs
3 to the south, and two to the north, and very probably there were more."
[See Gray (1871) for further details].
2 1871 - "still sparingly met with, for example at the Mull of Galloway [NX
1530] and Burrow Head, though in some places where a flock might have
been met with twenty years ago, a solitary pair at most remain" (Gray
1871).
1 1880 - Small, the Edinburgh taxidermist, received a bird from "Galloway" on
19th February of this year (Evans unpubl.).
2 1881 - Small, the Edinburgh taxidermist, received two birds from Wigtonshire
on 24th February (Evans unpubl.).
1 1882 - Buchanan (1882) reports that the Chough "probably occurs sparingly
at the Burrow Head...as I am informed by the Rev. G. Wilson."
2 1886 - two specimens currently in the RSM (Edinburgh) were shot at the
Mull of Galloway in November of this year.
1 1887 - B & R (1953) tell us that Service, who quotes Sympson (see 1684
above), says "the bird which Sympson describes is, of course, a Chough,
which may still (though rapidly decreasing) be seen about the locality
named [Mochrum]." [No reference given].

? 1904 - Service (1904-05) reporting on the decline and near extinction of
the Chough in Galloway states that the only exception may lie "now and
again towards the Portpatrick direction".
3 1907-19 B & R (1953) quote the notes of Jack G. Gordon "the headquarters
of this interesting bird in our county seems to have been the precipitous
line of cliffs on the west coast extending from the Mull of
Galloway lighthouse to near the mouth of Loch Ryan [c.NW 9872]". They
continue "he gives particulars of several nests found in various parts

of these cliffs between 1907 and 1919" [c.NX 0550].

3 1913 - A nest with young was found at Sinniness Head [NX 2153] near the mouth of the River Luce (Gordon *in litt.* to B & R 1953).

1 1935 - Sir Herbert Maxwell told B & R (1953) that "there were still Choughs on the Logan Cliffs" [NX 0940], though B & R failed to see any when they visited the cliffs [year not stated, 10-20 years later?].

1 1970 - According to Bignal *et al.* (1988) J.G. Scott saw two Choughs in a Galloway breeding haunt, but there was no evidence of breeding.

1 1987 - 2-3 seen between April and August at two sites (Watson 1988).

3 1988 - A pair returned to a site in Wigtonshire and attempted to breed (SBR).

3 1989 - Pair attempted to breed, but unsuccessful (Geoff Sheppard *pers. comm.*).

3 1990 - Pair bred successfully at same site as previous years, plus another bird found dead on the Glen Luce bypass near Newton Stewart, suggests there are other birds moving through the area (Geoff Sheppard *pers.comm.*).

Appendix 2

Pearson Correlation matrix of climatic variables used in Discriminant Function Analyses. The correlation coefficients have been abbreviated by x10. Variable descriptions are given in Chapter 5.

	O_{min}	O_{dev}	O_{max}	X_{min}	X_{dev}	X_{max}	T_{min}	T_{dev}	T_{max}	P_{min}	P_{dev}	P_{max}
O_{min}	-											
O_{dev}*	+9	-										
O_{max}*	+7	+9	-									
X_{min}	+5	+5	+4	-								
X_{dev}*	+5	+6	+5	+8	-							
X_{max}*	+4	+5	+4	+4	+8	-						
T_{min}	+1	+1	+1	+4	+1	-1	-					
T_{dev}*	+1	+1	+1	+4	+2	-0	+9	-				
T_{max}*	+1	+1	0	+3	+1	-0	+6	+8	-			
P_{min}	-0	+0	+0	+3	-0	-2	+6	+6	+3	-		
P_{dev}*	-0	-0	-0	+2	-0	-3	+6	+6	+4	+9	-	
P_{max}*	-0	-0	-0	+1	-1	-3	+5	+5	+3	+8	+9	-

* : variables with at least one coefficient >0.7

Appendix 3a. Maximum invertebrate biomass in field samples (number of soil cores per sample = 40+), Islay 1988-89.

Habitat[a]	Patch	No. of samples *n*	Species[b]	Age[c]	Max. biomass g/m[2]
Bog	Moss P	5	Araneae		.1
			Araneae:Lycosa		.2
			Bibionid	L	4.7
			Coleopt. unid.	A	.3
			Elaterid	L	8.7
			Elaterid	A	.8
			Gastropoda (slugs)		4.5
			Lepidoptera	L	2.5
			Lepidopt.:Noctuidae	L	4.5
			Muscidae etc.	L	.5
			Oligochaeta		117.5
			Staphylinid	L	.3
			Staphylinid	A	3.0
			Tipula marmorata	L	25.1
			Tipula paludosa	L	2.1
			Tipulid sp.	L	17.0
Old improved P	Old imp'd P	15	Aphodius	A	.5
			Araneae		.2
			Bibionid	L	9.2
			Carabid	L	.6
			Coleopt. unid.	A	.6
			Curculionid	A	.2
			Diplopoda		.2
			Elaterid	L	3.0
			Gastropoda (slugs)		33.9
			Muscidae etc.	L	.5
			Oligochaeta		232.8
			Staphylinid	A	.6
			Staphylinid	L	3.0
			Tipulid sp.	L	58.4
Permanent P	Permanent P	3	Bibionid	L	8.5
			Elaterid	L	1.5
			Lepidoptera	L	2.3
			Muscidae etc.	L	.5
			Oligochaeta		40.7
			Staphylinid	L	.6
			Tipula marmorata	L	1.9
Recently imp. P	Recent. imp. P	9	Aphodius	A	.9
			Araneae		.3
			Carabid	A	1.2
			Coleopt. unid.	A	.5
			Gastropoda (slugs)		2.3
			Muscidae etc.	L	.5
			Oligochaeta		81.4
			Staphylinid	L	1.0
			Tipulid sp.	L	24.1

contd./

Appendix 3a. (continued)

Habitat[a]	Patch	No. of samples *n*	Species[b]	Age[c]	Max. biomass g/m^2
Recently imp. P	Cow dung	1	*Tipula paludosa*	L	41.4
Recently imp. P	Silage cut	2	Oligochaeta		10.8
			Tipula paludosa	L	15.1
Reseed		4	Aphodius	A	.3
			Muscidae etc.	L	4.5
			Oligochaeta		65.5
			Staphylinid	A	.3
			Staphylinid	L	.6
			Tipula paludosa	L	30.1
			Tipulid sp.	L	15.1
Semi imp. PP		1	Araneae		.2
			Carabid	A	.6
			Curculionid	A	.2
			Elaterid	L	2.3
			Gastropoda (slugs)		2.3
			Oligochaeta		149.2
			Staphylinid	L	.6
			Tipulid sp.	L	5.7
Semi improved PP	Sand/moss P	1	Elaterid	L	.6
			Muscidae etc.	L	.7
			Oligochaeta		10.8
			Staphylinid	A	1.4
			Tipulid sp.	L	4.5

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[a] P = pasture, PP = permanent pasture, G = grassland

[b] includes all Cyclorraphan fly larvae: Calliphoridae, Scathophagidae etc.

[c] L = larva; A = adult

Appendix 3b. **Maximum invertebrate biomass in Chough feeding-site samples (number of soil cores per sample = 10-15), Islay 1988-89.**

Habitat[a]	Patch	No. of samples *n*	Species[b]	Age[c]	Max. biomass g/m^2
Arable rape	Moss/mud	1	Aphodius	A	.9
			Carabid	L	.6
			Curculionid	A	.3
			Tipulid sp.	L	49.0
Bog	Sheep carcase	1	Muscidae etc.	L	48.8
			Staphylinid	L	2.4
Coastal G	Thrift	1	Tipulid sp.	L	7.5
Dune P	Dune P	1	Bibionid	L	41.3
			Oligochaeta		4.5
Dune P	Cow dung	5	Aphodius	A	40.1
			Aphodius	L	58.8
			Tipula paludosa	L	26.4
Dune P	Under cow dung	2	*Tipula paludosa*	L	22.6
Dune P	Cattle feeder	1	Bibionid	L	6.0
Dune P	Manure	1	Aphodius	A	1.6
			Muscidae etc.	L	100.6
			Muscidae etc.	P	9.8
Dune P	Rock outcrop	1	Staphylinid	L	2.4
			Tipulid sp.	L	52.7
Dune P	Sand	1	Aphodius	L	.6
			Coleopt. unid.	A	1.0
			Tipulid sp.	L	1.5
Fore Dune	Bare sand	2	Lepidoptera	L	31.5
Grey Dune	Sheep carcase	1	Muscidae etc.	L	16.3
Old improved P	Below harrowed turves	1	Staphylinid	L	2.2
			Tipula paludosa	L	58.1
Quarry	Rock outcrop	2	Lepidoptera	L	9.0
			Tipula marmorata	L	22.6
			Tipulid sp.	L	67.8
Raised beach PP	Rock/PP outcrop	1	Araneae		.3
			Elaterid	L	1.5
			Formicidae	A	.2
			Oligochaeta		4.5
			Tipulid sp.	L	18.8

contd./

Appendix 3b. (continued)

Habitat[a]	Patch	No. of samples *n*	Species	Age[b]	Max. biomass g/m^2
Raised beach PP	Deer dung	2	Aphodius	A	93.1
			Bibionid	L	18.7
			Diplopoda		.2
			Elaterid	L	4.5
			Gastropoda (slugs)		4.5
			Oligochaeta		81.4
			Staphylinid	A	.6
			Staphylinid	L	.6
			Tipulid sp.	L	1.9
Rock outcrop	Rock/moss	4	Aphodius	L	4.5
			Araneae		.6
			Carabid	L	2.4
			Coleopt. unid.	A	2.4
			Dermaptera		3.6
			Lepidoptera	L	6.5
			Muscidae etc.	L	1.8
			Oligochaeta		36.2
			Tipula marmorata	L	64.0
			Tipulid sp.	L	52.7

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[a] P = pasture, PP = permanent pasture, G = grassland

[b] includes all Cyclorraphan fly larvae: Calliphoridae, Scathophagidae etc.

[c] L = larva; A = adult

Appendix 3b. (continued)

Habitat[a]	Patch	No. of samples *n*	Species	Age[b]	Max. biomass g/m^2
Raised beach PP	Deer dung	2	Aphodius	A	93.1
			Bibionid	L	18.7
			Diplopoda		.2
			Elaterid	L	4.5
			Gastropoda (slugs)		4.5
			Oligochaeta		81.4
			Staphylinid	A	.6
			Staphylinid	L	.6
			Tipulid sp.	L	1.9
Rock outcrop	Rock/moss	4	Aphodius	L	4.5
			Araneae		.6
			Carabid	L	2.4
			Coleopt. unid.	A	2.4
			Dermaptera		3.6
			Lepidoptera	L	6.5
			Muscidae etc.	L	1.8
			Oligochaeta		36.2
			Tipula marmorata	L	64.0
			Tipulid sp.	L	52.7

[a] P = pasture, PP = permanent pasture, G = grassland
[b] includes all Cyclorraphan fly larvae: Calliphoridae, Scathophagidae etc.
[c] L = larva; A = adult

APPENDIX 4

Submitted to *Biological Conservation*

THE INFLUENCE OF HABITAT ON NEST-SITE OCCUPANCY BY RED-BILLED CHOUGHS

Pyrrhocorax pyrrhocorax

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Suggested running title: *Influence of habitat on nest-site occupancy by red-billed choughs*

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Abstract

The influence of habitat on nest-site occupancy by red-billed choughs Pyrrhocorax pyrrhocorax *was analysed in a study area comprising 155 one km national grid squares on the Rhinns of Islay, west Scotland. Because of the species' specific nesting requirements (caves, natural arches, derelict buildings and large crevices in cliffs) it was important to allow for the influence of nest-site availability on distribution of nesting pairs. To achieve this an index of nest-site occupancy was used which differentiated between areas where few pairs nested despite high nest-site availability, and where more pairs nested despite low nest-site availability. There was a positive relationship between nest-site occupancy and area of dunes, permanent pasture and coastal grassland, and a negative relationship with bog. The provision of artificial nest-sites in areas of suitable habitat where nest-site availability is limiting is recommended.*

Key words: Habitat preference, nest-site availability, red-billed chough, *Pyrrhocorax pyrrhocorax*

INTRODUCTION

The size of the breeding population of many birds has been shown to be limited by nest-site availability (Newton 1979, Charles 1972, Birkhead 1991). These include a wide variety of species which nest on cliffs or in tree cavities (see Newton 1994). The more specific a species' nesting requirements, the greater the potential influence of nest-site availability on population size and distribution. An investigation of habitat use must take into account nest-site availability, which may constrain the way that habitats are utilised.

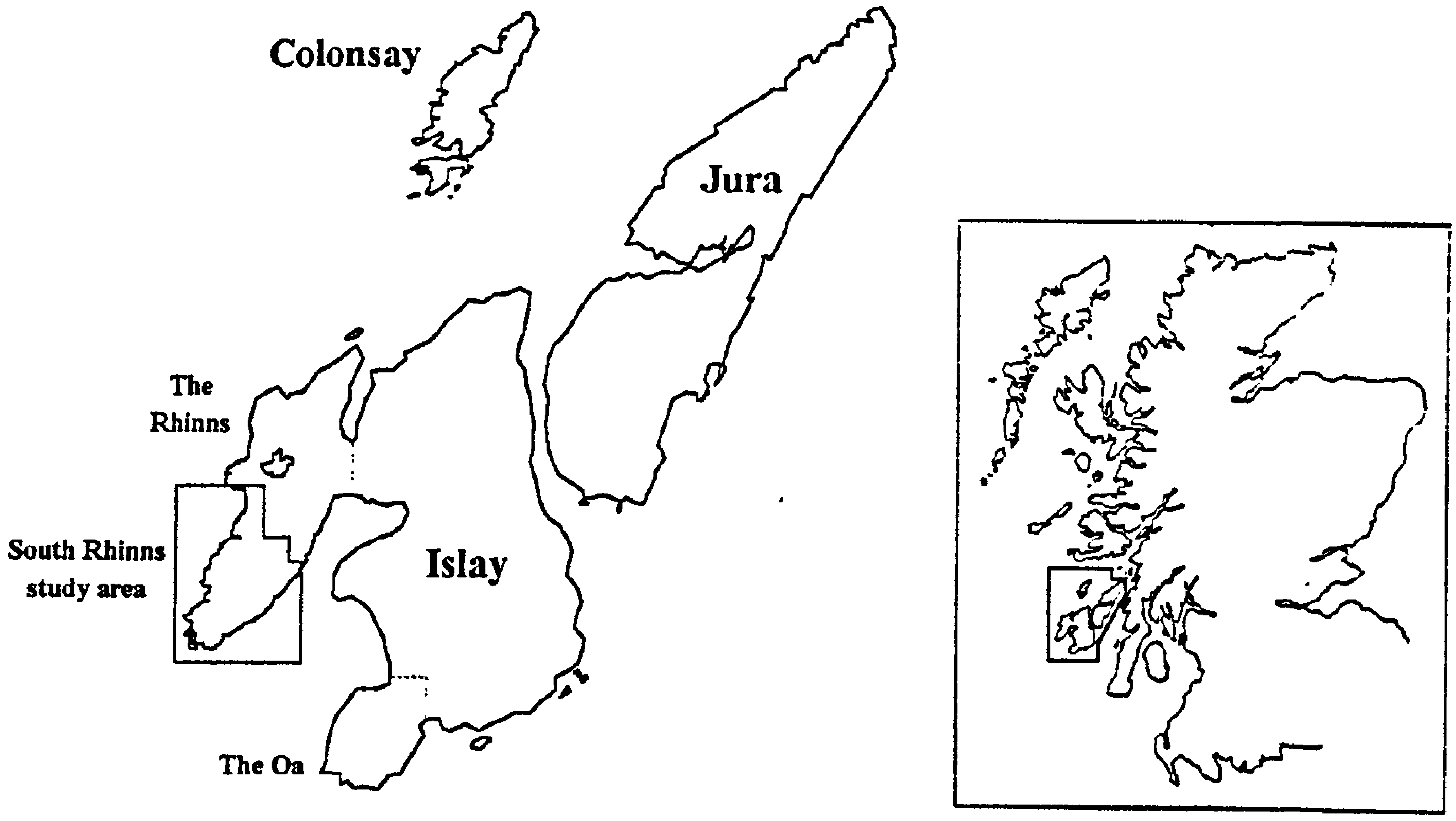
In the British Isles red-billed choughs *Pyrrhocorax pyrrhocorax* have specific nest-site requirements, usually preferring dark and sheltered sites in caves, natural arches, derelict buildings and large cavities in cliffs (Coombs 1978). Such sites may provide protection against nest predation by larger carrion/hooded crows *Corvus corone*, which Bossema *et al.* (1986) argued has been a major factor in determining the nest-site characteristics of other medium-sized corvids.

The chough is on Annex 1 of EC directive 79/409/EEC, which requires member states to conserve the species and its habitat, and it is a British *Red Data Book* species (Batten *et al.* 1990). It is important that we understand the factors which influence its population size. The aims of this paper are to examine the pattern of nest-site availability and use by choughs, and to assess the influence of habitat on chough nest distribution after taking into account the potentially confounding influence of nest-site availability. This was achieved by devising an index of nest-site occupancy for use as the dependent variable in habitat analyses, rather than using simple number of nesting pairs. Results from this study on the Rhinns of Islay are compared with nest-site availability and nest-site occupancy on the nearby Inner Hebridean islands of Jura and Colonsay.

STUDY AREA

The main study area comprised 155 one km^2 Ordnance Survey (O.S.) national grid squares on the Rhinns of the island of Islay, west Scotland (55°43' N, 6°26' W) (Figure 1), with a total land area (after subtraction of open water) of 122.2 km^2. The 93 km coastline includes rocky low (<10m) and high (up to 50 m) cliffs, deeply eroded sea-gullies, low-lying coast and dunes. Many former 'coastal' cliffs and caves are raised above the high water mark due to uplifting since the last ice-age, and may

Figure 1. Location of study area in west Scotland.



be found up to 1 km inland. The Rhinns supports a wide range of semi-natural habitats (Table 1). Agriculturally, it is primarily pastoral, with most unenclosed areas (including dune systems) being extensively grazed by beef cattle and sheep. In the mid 1980s approximately 1100 ha of bog and heath on the south Rhinns was planted with alien conifers, mostly sitka spruce *Picea sitchensis*.

METHODS

Nest-sites

The number of pairs of choughs building or refurbishing nests was counted in a census of 155 one km study squares in 1988. For the calculation of the nest-site availability index (see below) more intensive observations were made in 72 one km squares in the south Rhinns study area over a 3 year period (1987-89). To minimise disturbance, observations of nesting birds were made away from the immediate vicinity of the nest-site. Nest presence was confirmed by sightings of birds nest-building or of the female returning to the nest after being fed by the male. Nest-sites were categorised as follows: **Natural sites**: Low cliff (< 10 m high), High cliff (> 10 m high), Cave, Natural arch, Rockfall; **Man-made sites**: Buildings.

Calculation of an *Index of Nest-site Availability*

It was not possible to identify and count all potential nest-sites in the field (except for barn sites). Many natural sites are mere crevices in cliffs, and to find and classify all these would have involved climbing and surveying all cliffs in the study area, which, even if possible, would have been exceptionally time-consuming. Instead, an index of nest-site availability was used, based on the number of nests built per unit length of cliff (high or low) or per nesting feature (cave, natural arch or building). Because the index was based on known nests it was likely to under-estimate actual nest-site availability. In an attempt to overcome this the index was calculated in such a way as to maximise the estimated number of nest-sites per unit area. Firstly, it was based on an area of high nesting density (the south Rhinns study area); secondly, it was calculated only from 1 km squares within this area in which nesting attempts were made (*n*=28); and thirdly, data from 3 years' (1987-89) intensive observations within this study area were used (to allow for between-year changes in nest-site use).

Table 1. **Combined habitats used in this study and the NCC/RSNC habitat categories from which they were derived.**

Habitat in this study	Area (ha)	NCC/RSNC Habitat code & categories	
Woodland	1252	A.	Woodland, plantation & scrub
Permanent pasture	1826	B.1.1	Acid grassland unimproved
		B.1.2	Acid grassland semi-improved
		B.2.1	Neutral grassland unimproved
		B.2.2	Neutral grassland semi-improved
Marsh	605	B.1.3	Acidic marshy grassland
		E.2	Flush
		F.1.2	Tall fen
Imp'd pasture/Arable	1718	B.4	Improved grassland
		J.1	Arable
Tall Herb & Fern	64	C.1	*Pteridium* (bracken)
		C.2	Upland species rich vegetation
		C.3	Other Tall Herb or Fern
Heath	2383	D.1	Dry heath
		D.2	Wet heath
		D.5	Dry heath/acid grassland mosaic
		D.6	Wet heath/acid grassland mosaic
Bog	3769	E.1	Bog
Open water	85	G.1	Open water
Dunes	375	H.6	Sand dune
			Fore dune
			Grey dune
			Dune pasture
			Beach
Coastal grassland	144	H.8.4	Coastal grassland
Rock outcrop	linear	I.1	Rock outcrop
Built up	64	I.3	Building
Boundary	linear	J.2	Boundary
			Dyke/earth bank
			Fence
			Wall
TOTAL	12200		

The total length/number of nesting features was recorded using 1:25 000 O.S. *Pathfinder* series maps. Length of high and low cliff was measured to the nearest 0.01 km: cliff height was determined from map contours. The number of caves, arches and suitable buildings (see below) was counted. Several caves not marked on the map in English were identified by their Gaelic name "*uamh*"; the existence of these sites was verified in the field and added to the total cave count. Buildings were checked in the field to ascertain their suitability for nesting choughs: buildings deemed 'suitable' contained a potential nest-ledge or crevice in a fairly dark situation, with easy chough access (e.g. through a roof hole, broken window or open doorway). Most were semi-derelict ruins or farm out-houses. Rockfalls are not marked on O.S. maps, so nests in this category were assigned to the cliff type (high or low) in which the rockfall was found.

A total of 40 nest-sites were used in the south Rhinns study area during 1987-89. The number of nests in each land feature is shown in Table 2. The land feature (cliff, cave etc.) in which 36 (90%) of the 40 nests were built was accurately depicted on 1:25 000 O.S. maps. At the four remaining sites, the land feature depicted on the map was incorrect, but in all cases another suitable nesting feature was shown at the site (two natural arch sites were depicted as high cliff, one cave site as low cliff, and one low cliff site as a cave). The maps were therefore considered sufficiently accurate to justify the computation of a nest-site availability index based on map-depicted features alone. In the calculation of the index, the four incorrectly map-depicted nest-sites were assigned to the map feature shown at that site (see Results, Table 2). Nests built by the same pair in different years within 20m of their previous nest were not considered independent: this was the minimum recorded nearest neighbour distance for nests occupied by different pairs in the same year in this study.

By quantifying the length/number of the equivalent nesting feature for all sample squares in the rest of the study area, it was possible to predict the number of nest-sites that they should support. The same methods were used to quantify predicted nest-site availability on the nearby islands of Colonsay and Jura, except that the analysis was restricted to natural nest-sites only, as suitability of buildings on these islands was not checked in the field. [When comparisons are made between these islands and the Rhinns of Islay, data from the Rhinns are also restricted to natural nest-sites only (see Results)].

Table 2. Number of nests in each land feature, and total length/number of corresponding map-depicted land features in the 28 occupied 1 km squares, south Rhinns of Islay study area, 1987-89.

Land feature	Length or no. of map features in occupied squares (A)	No. of nests used in 1987-89 (n=40)	Nests after reassigning to map-depicted feature[1] (B)	Length/number of nest features per nest (A/B)
High cliff	3.85 km	10	12	1 nest/.321 km high cliff
Low cliff	7.03 km	12	12	1 nest/.586 km low cliff
Caves+arches	17	9	7	1 nest/2.429 caves+arches
Suitable barns	16	9	9	1 nest/1.78 buildings

[1] For the calculation of the index, nests at sites incorrectly depicted on the map were reassigned to the map feature shown at that site (see Methods).

Nest-site occupancy

An index of *nest-site occupancy* was calculated for all sample squares which contained potential nest features. The index was the difference between the number of nesting pairs in the 1988 census and the number of potential nest-sites as predicted from the index of nest-site availability. Negative values represent under-occupancy of sample squares, whilst positive values represent over-occupancy of sample squares. In this way it was possible to distinguish quantitatively between areas where few choughs nested despite a high availability of nest-sites, and areas where more choughs nested despite a limited availability of nest-sites. Hence it was possible to assess the influence of habitat availability on nest-site occupancy over and above the influence of nest-site availability. For Jura and Colonsay nest-site occupancy was analysed at the whole island level, by comparing total nest-site availability with number of nesting pairs in natural sites based on the results of the 1986 Scottish chough census (Monaghan *et al.* 1989).

Nest spacing

An important factor to consider when using nest distribution as a dependent variable is whether nest-spacing might be so regular as to over-ride the influence of environmental parameters. Nearest neighbour distances were measured for the 47 nests used in the Rhinns study area in 1988. Distances were measured to the nearest 100 m, except for nests less than 100 m apart, which were measured to the nearest 10m.

Habitat measurement

Habitat data were taken from the 1988 Nature Conservancy Council (NCC) habitat survey of the Rhinns of Islay Site of Special Scientific Interest, which used the NCC/Royal Society for Nature Conservation habitat mapping system (NCC/RSNC 1984). Habitats were mapped in the field to a resolution of 0.1 ha (c.30x30 m) on 1:10 000 O.S. maps by NCC staff. Areas outwith the SSSI were mapped by C.R.M. Linear habitats (field boundaries and rock outcrops) were mapped to the nearest 10m. Over 30 NCC/RSNC habitat categories were recorded in the Rhinns study area A number of these were combined for use in this study (see Table 1), giving the following 12 habitat categories: *Woodland*, *Permanent Pasture*, *Improved pasture/Arable*, *Coastal Grassland*, *Marsh*, *Tall Herb & Fern*, *Heath*, *Bog*, *Dunes*, *Rock outcrop*, *Built up* and *Boundary*. Correlation matrices were constructed for all environmental variables (i.e. the *index of nest-site availability* and all habitat variables).

Aggregation and scale of sample squares

The basic assumption in this analysis is that habitats close to potential nest-sites are more likely to influence nest-site occupancy than those further away. However, some coastal 1 km squares contained mainly sea: 29 one km grid squares had land areas of less than 0.5 km^2, and the minimum recorded area was only .05 km^2. This could result in a lower habitat diversity and/or an over-representation of coastal habitats in these squares. Such bias would heavily influence results because these coastal squares were the ones in which most chough nests were found. To overcome this bias, squares with land areas less than 0.5 km^2 were aggregated with the next adjacent 1 km square perpendicular to the coast, so that aggregated 1 km sample square areas ranged from 0.5-1.5 km^2.

A second sampling problem was scale. Observations of nesting choughs have shown that pairs may forage at distances of 1 km or more from the nest (Bullock *et al.* 1985, *pers. obs.*), such that a 1 km square sampling unit might under-represent their potential foraging range. To investigate this the study area was resampled using tetrads (2x2 km squares); a similar process of aggregation of coastal tetrads with land areas of less than half a 'normal' tetrad (i.e. < 2 km^2) was employed, giving aggregated tetrad areas of 2-6 km^2. Because of the difficulties of the standard tetrad grid producing either very large or very small land areas when overlaid on coastal squares, coastal tetrads were positioned in such a way as to produce square areas as close to 4km^2 as possible. This neccessitated some deviation from the standard tetrad grid. The aggregation procedures produced samples of 125 aggregated 1 km squares, and 33 aggregated tetrads (Figure 2).

Statistical analysis

The influence of environmental parameters on nest-site occupancy was analysed by means of stepwise multiple regression analysis using *SPSS/PC+ v4.0* (Norusis/SPSS Inc. 1990). The analyses were repeated on both sizes of sampling unit (aggregated 1 km squares and aggregated tetrads). Sample squares with no potential nest-sites (i.e. index of nest-site availability = 0) were excluded from the analyses, which reduced the sample size of aggregated 1 km squares to 56 (total land area of 54.8 km^2), and aggregated tetrads to 31 (total land area 110.4 km^2). Note the greater land area sampled when using tetrads.

Two habitat variables were dropped prior to analysis due to their limited extent (*Tall herb & Fern* and *Built up*) (see Table 1). The correlation matrix for the remaining variables showed that *Improved pasture* and *Boundary* were inter-correlated at $r>.7$, so the *Boundary* variable was dropped (after Tabachnik & Fidell 1989). This gave a total of 10 environmental variables for entry in the regression analysis at the 1 km^2 scale: the *Index of nest-site availability* and 9 habitat variables (*Woodland, Permanent pasture, Improved pasture/Arable, Coastal grassland, Marsh, Heath, Bog, Dunes,* and *Rock outcrop*).

Because of the smaller sample size available for analysis at the tetrad scale (n=31) it was desirable to enter only 6 independent variables in the analysis (to maintain the minimum cases to independent variables ratio of 5:1, see Tabachnik & Fidell 1989). To achieve this 3 allied pastoral

Figure 2a. Aggregated 1 km squares (n=125). Rhinns study area. Figures on the x and y axes represent the national 1 km grid.

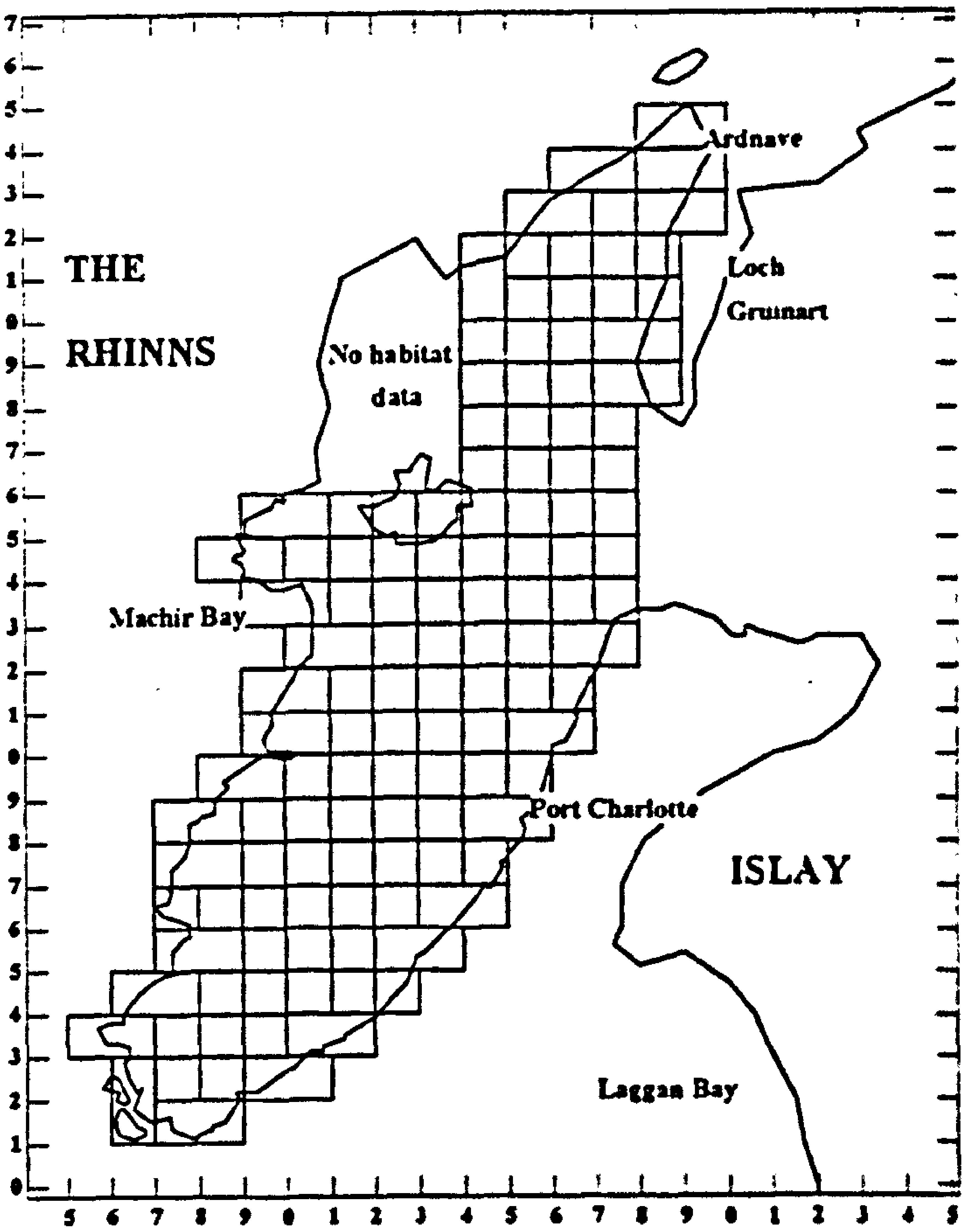
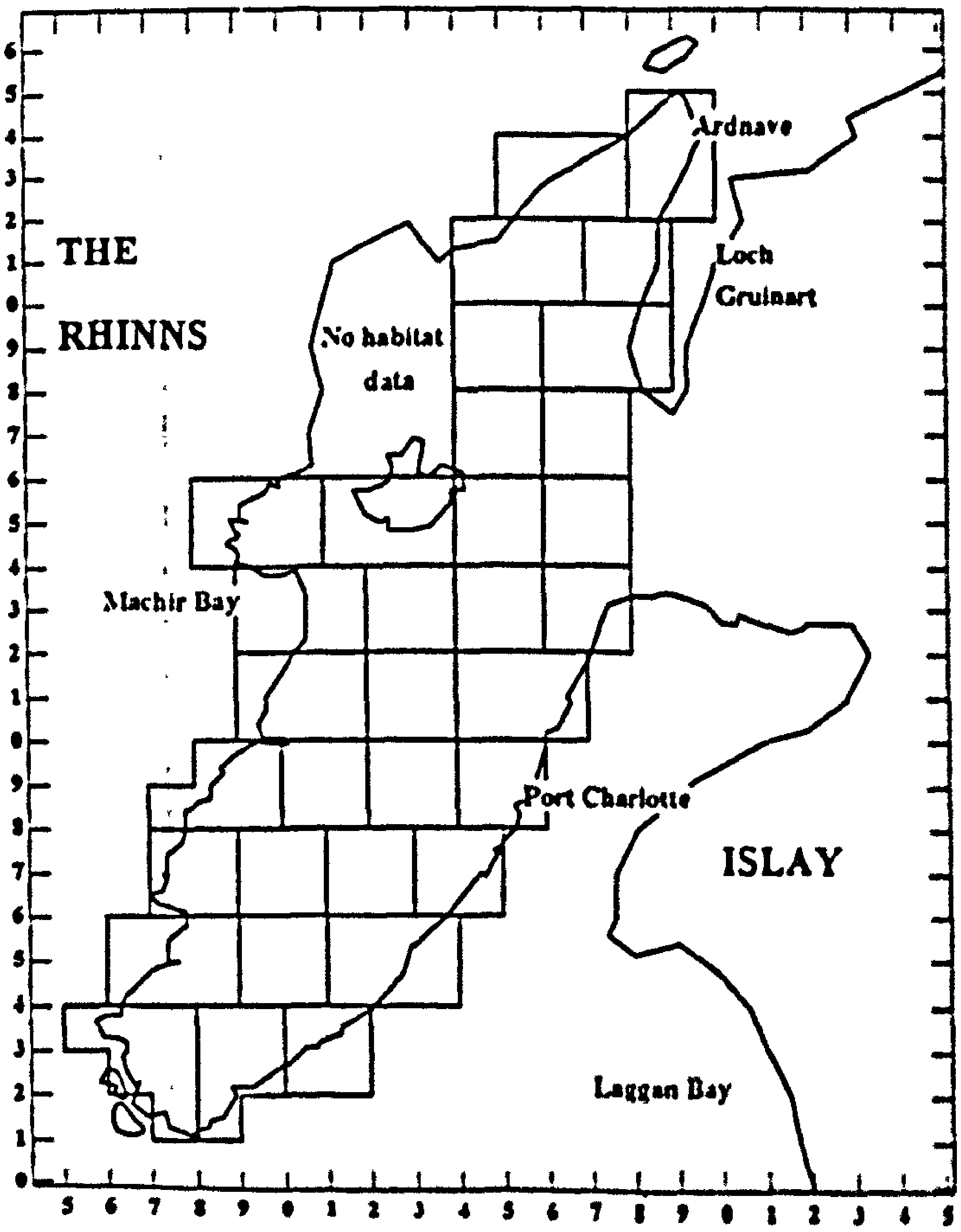


Figure 2b. Aggregated tetrads (n=33), Rhinns study area. Figures on the x and y axes represent the national 1 km grid.



habitats were combined (*Permanent pasture*, *Improved pasture/Arable* and *Coastal grassland*), and 2 variables considered from previous work (Holyoak 1972, Bullock *et al.* 1983) to be unlikely chough feeding habitats (*Marsh* and *Woodland*)were dropped. None of the variables used in the tetrad analysis were inter-correlated at $r>.7$. Prior to analysis variables with skewed distributions were transformed using square root, log (x+1) or inverse transformations, as appropriate.

RESULTS

Calculation of the *Index of nest-site availability* (south Rhinns data only).

The index of nest-site availability was calculated as follows (see Table 2 for data):

Index of Nest-site Availability = (High cliff/0.321)+(Low cliff/0.586)+(Caves+Arches/2.429)+ (Barns[1]).

[1] As it was possible to check the suitability of barns directly one suitable barn was assumed to represent one potential nest-site.

Considering the original data (before reassigning nests to their map-depicted features, see column 2 Table 2), there were more nests per unit length of high cliff (1 nest/.321 km) as compared to low cliff (1 nest/.586 km). Of the discrete nest features, buildings had a similar occupancy rate (1 nest/1.78 suitable barns) to caves+arches (1 nest/1.89 caves+arches).

Nest-sites

In the 1988 census 47 pairs of nesting choughs were located in the Rhinns study area. The land features in which the nests were sited are given in Table 3. Using the index of nest-site availability the same area contained 84.2 predicted nest-sites, therefore 55.8% of available sites were occupied. Twenty eight (59.6%) nests were in natural sites, all but one of which were at coastal sites or on former sea cliffs within 1 km of the coast. There were 19 (40.4%) nests in buildings. These occurred in 18 aggregated 1 km squares, 13 (72.2%) of which contained no natural nest-sites.

Of the 125 aggregated one km study squares, 69 (55.2%) contained no potential nest-sites; of the remaining 56 aggregated squares, 21 (37.5%) contained potential nest-sites but no nesting choughs in 1988. In squares with potential nest-sites there was a significant positive relationship between nest-site availability and number of nesting pairs (aggregated 1 km squares, r=.369, r^2=.136, P<.01, n=56).

Table 3. Land features used by 47 pairs of nesting Choughs, Rhinns study area, 1988.

Crevice					
High cliff	Low cliff	Rockfall	Cave	Natural Arch	Building
6	8	2	8	4	19

Nearest neighbour distances (n=47) ranged from 20 m to 3.50 km. Their frequency distribution (Figure 3) was slightly positively skewed, with a median distance of 0.80 km, and a mean of 1.02 km (s.e.=.124). Both number of nest-sites and number of nesting pairs per aggregated 1 km square had variances roughly similar to the mean (*nest-sites* mean = 1.50, variance 1.23; *nesting pairs* mean = .84, variance = .76), suggesting that both had a near random distribution (Sokal & Rohlf 1981).

Comparison of the Rhinns of Islay with Jura and Colonsay

Calculated values for nest-site availability and nest-site occupancy at natural nest-sites in 1986 on Jura, Colonsay and the Rhinns of Islay are given in Table 4. Jura had the highest number of nest-sites (143.8), but the lowest nest-site occupancy (2.1%), with only 3 nesting pairs in 1986. Colonsay had the lowest number of nest-sites (34.5) but intermediate nest-site occupancy (17.4%) with 6 nesting pairs. The Rhinns of Islay had intermediate numbers of nest-sites (64.3) and the highest nest-site occupancy (57.5%) with 37 nesting pairs. Figure 4 shows nest-site availability on Colonsay on a 1 km square basis. Most nest-sites are clumped on the north-west coast of the island, and there are large areas with less than 1 predicted natural nest-site per km square.

Figure 3. Frequency distribution of nearest neighbour distances for 47 nest-sites used in 1988, Rhinns study area. Values on x axis are mid-points.

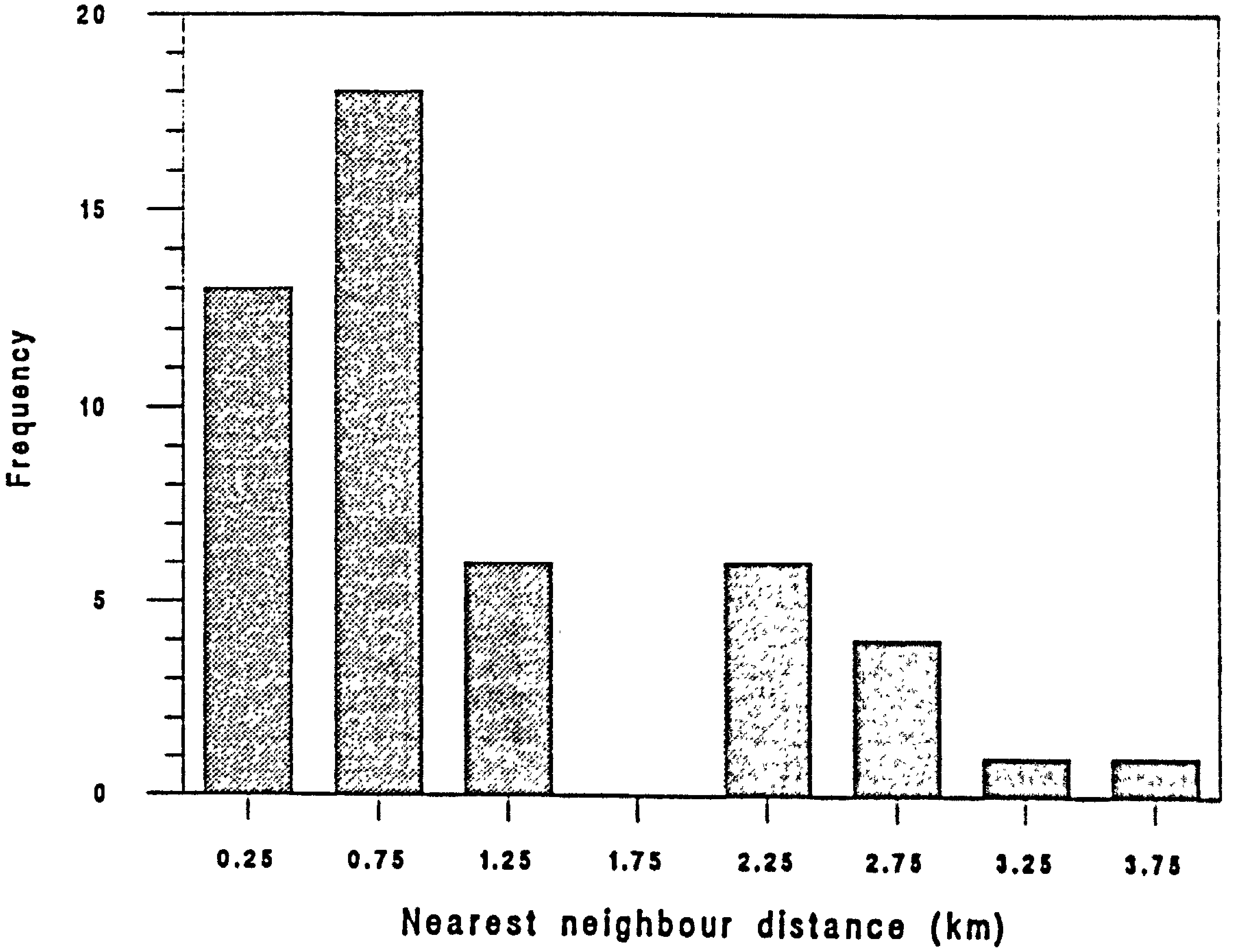


Figure 4. Predicted nest-site availability on Colonsay by 1 km square. Figures on the *x* and *y* axes represent the national 1 km grid.

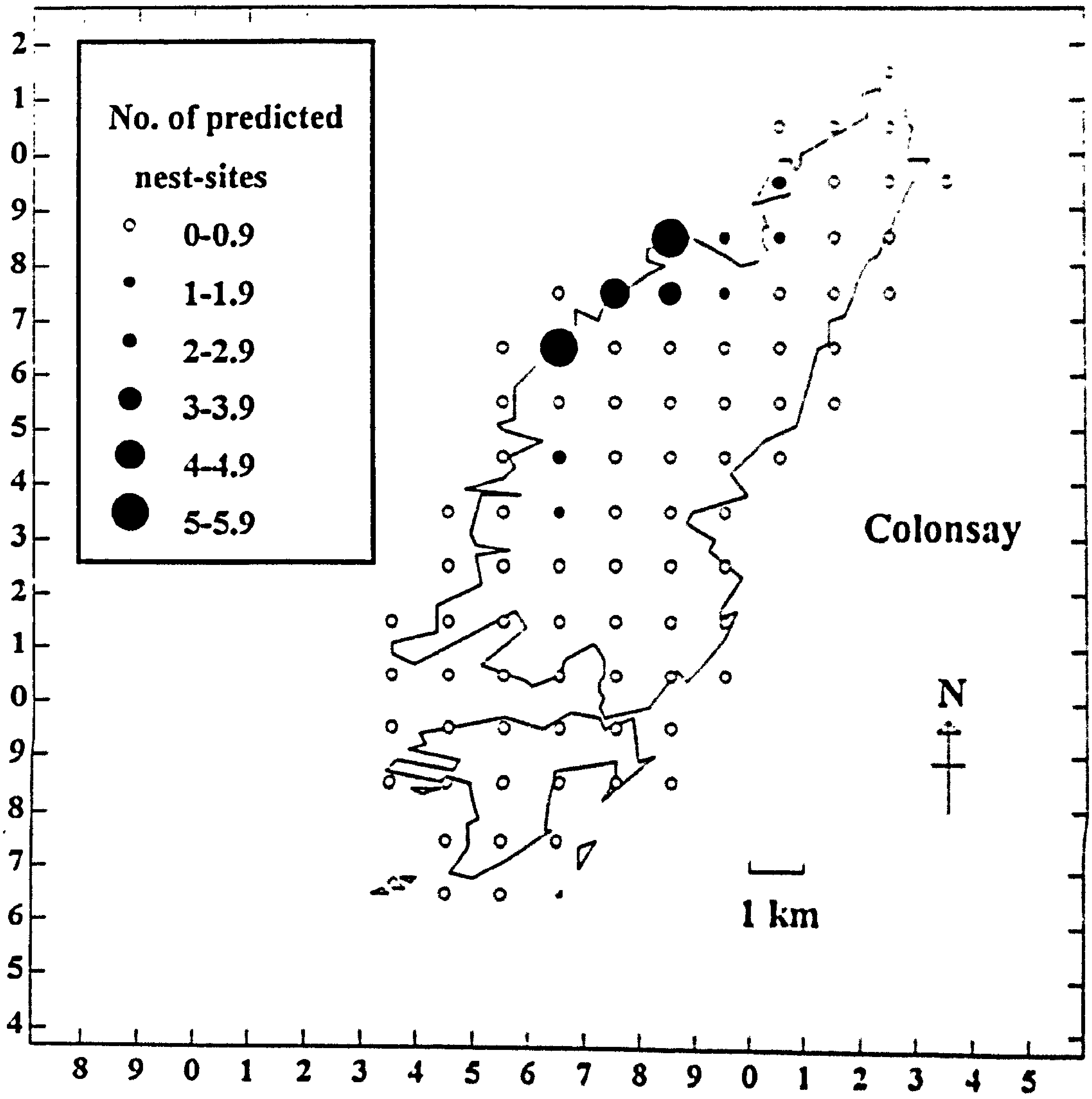


Table 4 **Predicted number of natural nest-sites, and nest-site occupancy in 1986, Islay, Jura and Colonsay.**

Locality	Total coast length[1] (*km*)	Total high cliff (*km*)	Total low cliff (*km*)	Caves+ Arches (*n*)	Pred-icted nest-sites (*n*)	Breeding pairs in 1986[2] (*n*)	% nest-site occupancy (*prs/sites*)
Jura	174.6	11.7	29.2	140	143.8	3	2.1
Colonsay[3]	62.9	4.6	10.0	8	34.5	6	17.4
Islay, Rhinns[4]	92.6	4.9	19.7	38	64.3	37	57.5
Islay, S. Rhinns study area only[5]	42.3	3.9	7.0	17	37.3	25	67.0

[1] Measured on O.S. 1:25 000 *Pathfinder Series* maps.

[2] Data from Monaghan *et al.* (1989), except for S. Rhinns study area, which is the maximum no. of breeding pairs using natural sites 1987-89.

[3] Including Oronsay.

[4] Includes the whole Rhinns peninsula, west of O.S. easting NR29, for details see Monaghan *et al.* 1989.

[5] This study.

The influence of nest-site availability and habitat on nest-site occupancy

The results of stepwise multiple regression analyses of environmental variables on nest-site occupancy are presented in Table 5. Only those regression coefficients which differed significantly from 0 (at $P \leq .05$) entered the equation. At the aggregated 1 km square scale, four variables were entered in the analysis - *nest-site availability*, *dunes*, *permanent pasture* and *coastal grassland* ($F=35.53$, $r^2=.56$, $P<.001$), with *nest-site availability* accounting for most of the variation (46%). At the aggregated tetrad scale two variables were entered, *nest-site availability* and *bog* ($F=20.75$, $r^2=.60$, $P<.001$), with *nest-site availability* again accounting for the greatest proportion of the variation (54%).

Table 5 Results of stepwise multiple regression analyses of nest-site occupancy on nest-site availability and habitat for aggregated 1 km squares n=56) and aggregated tetrads (n=31).

Independent variables	B	Beta	F	P	Multiple r	r^2 (incremental)
Aggregated 1 km sqs						
Nest-site avail (log)	-3.235	-.853	97.54	<.001	.46	.46
Dunes (log)	.312	.091	58.88	<.001	.51	.05
Coastal grass (sqrt)	.304	.192	44.15	<.01	.54	.03
Permanent grass (log)	.031	.150	35.53	<.05	.56	.02
Intercept	-.101					
Aggregated tetrads						
Nest-site avail (sqrt)	-2.321	-.787	33.38	<.001	.54	.54
Bog (sqrt)	-0.051	-.255	20.75	<.05	.60	.06
Intercept	3.252					

DISCUSSION

It is not always possible to quantify nest-site availability in birds (Newton 1994). However, since choughs use specific types of nest-sites which are also depicted on maps, it was possible in this study to devise an index of nest-site availability. Consequently it was also possible to devise an index of nest-site occupancy which should provide a more sensitive measure of preference/avoidance of areas than simple number of nesting pairs. For example, only 56 (45%) of the 125 aggregated 1 km squares used in this study contained potential nest-sites. The absence of nesting choughs in the remaining 55% of study squares can be explained in terms of absence of nest-sites alone. However, within squares with potential nest-sites the number of nesting pairs ranged from 0-4, and in this paper we have attempted to assess the influence of habitat types on this variation after taking into account nest-site availability.

Nest-sites

Most chough nests were in natural sites (caves, arches, rockfalls and crevices in high and low cliffs) along the coast. Barn nest-sites were used in areas where natural nest-sites were scarce or absent (mostly away from the coast). Barns are presumably analogous to caves/arches for nesting choughs; both shared similar occupancy rates. Islay is unique in Britain in the high proportion of pairs nesting in buildings (Warnes 1983). The use of buildings increased the number of inland sample squares available for analysis in this study, and reduced the potential bias towards coastal squares where most natural nest-sites are found.

It is hard to know how accurately the nest-site availability index reflects the number of potential crevice nest-sites in high and low cliff. It is assumed that even within occupied squares a number of crevice sites existed which remained undetected by us during this study because they were not used by nesting choughs. This assumption is supported by the fact that 3 pairs whose nests were flooded or washed out over-winter switched to nearby but previously unknown sites in the following year. It seems likely therefore that the index gives a conservative estimate of the number of crevice nest-sites, even though it was calculated from an area (the south Rhinns) where nesting density was high.

In sample 1 km squares <u>with</u> potential nest-sites (n=56) there was a significant positive relationship between number of nesting pairs and nest-site availability. Of the 47 nest-sites used in the study area in 1988, 33 (70.2%) were in sites which could be categorised as 'spacious cavities' (greater than 0.5 m x 0.5 m x 0.5 m: caves, natural arches, rockfalls and barns) rather than in smaller cliff crevices, despite the fact that the latter were presumably proportionally much more numerous. This suggests that spaciousness may be an important prerequisite of chough nest-sites. Bullock *et al.* (1983) noted that even crevice nest-sites used by choughs are generally more spacious than those used by jackdaws *Corvus monedula*. Interestingly, in Britain at least, natural inland cliffs are rarely used by nesting choughs: Bullock *et al.* (1985) reported only 3 natural nest-sites out of 45 inland sites in Wales, the rest being in man-made mine-shafts, mine caverns and quarries. It seems probable that inland cliffs do not provide large enough cavities for choughs, at least within those areas currently occupied in Britain. [It should be noted that this potential difference between nest-site availability in coastal *vs.* inland cliffs will have had negligible influence on the results of the current study since inland cliffs were extremely scarce in the study area]. Elsewhere in Europe, choughs occupy areas where large nesting cavities are probably readily available, such as in the mountain ranges of the Pyrenees and the Alps, and in the calcareous karst landscape of the Iberian peninsula where water-eroded pot-holes and caverns are abundant (Dory 1983).

Nest-site occupancy in relation to nest-site availability and habitat

In stepwise multiple regression analyses at both the 1 km and tetrad scale there was a significant negative relationship between nest-site occupancy and nest-site availability: where nest-sites were scarce a high proportion was occupied, but where nest-sites were abundant a lower proportion was occupied, though by a larger number of nesting pairs in absolute terms. This suggests that factors other then nest-site availability must be involved in determining nest-site occupancy. One such factor could be territorial behaviour which can limit population size to a level below that which the number of nest-sites could support (Watson & Moss 1970, Newton 1979). However, within the Rhinns study area the distribution of occupied chough nests was close to random, with a wide range of nearest neighbour distances (20 m - 3.5 km). Thus the possibility that regular nest-spacing might over-ride the influence of environmental parameters on nest distribution can be discounted.

A second factor which might influence nest-site occupancy is habitat availability. At the aggregated 1 km scale, 3 pastoral habitat variables were selected for entry in the regression (after *nest-site availability* had been entered, see above): *permanent /semi-improved pasture*, *dunes* and *coastal grassland.* All of these had a positive relationship with nest-site occupancy, suggesting that they were preferred feeding habitats. This finding concurs with results from other studies which have shown that choughs feed primarily in pastoral habitats (Bullock *et al.* 1983, Roberts 1983, Meyer 1990). It is notable that these habitats are all semi-natural habitats whose soil structure will not have been destroyed by, for example, ploughing or other agricultural practices; semi-improved pastures on the Rhinns of Islay have usually only been 'improved' by the addition of lime to the pasture surface. choughs feed primarily on invertebrates (Holyoak, 1972, Roberts, 1982, McCracken & Foster 1993) and unimproved pastures, coastal grassland and dunes are likely to support a diverse assemblage of these (Fowles 1994). Moreover, within the study area these habitats were extensively grazed by sheep and cattle, producing the close-cropped sward favoured by foraging choughs (Bullock *et al.* 1983), and providing herbivore dung, an important chough feeding 'habitat' in its own right (Warnes 1982, Roberts 1982, Meyer 1990).

At the tetrad scale, the only habitat variable entered in the regression (after *nest-site availability*) was *bog*, this being a negative relationship. Because the dependent variable in this analysis was *nest-site occupancy* rather than simple *number of nesting pairs*, this relationship cannot simply be a result of limited nest-site availability in areas dominated by bog (which would otherwise be a reasonable hypothesis). Rather it suggests that *bog* is a non-favoured feeding habitat for choughs. Interestingly, *bog* had the largest extent of cover of any single habitat in the study area. This relationship has not been shown by previous studies, which may be a result of the fact that chough nest-sites and bog rarely occur in close proximity.

Comparisons between areas

It is interesting to compare levels of nest-site occupancy between the Rhinns of Islay and the nearby Inner Hebridean islands of Jura and Colonsay (see Table 5). Jura has a long and rugged coastline and a large number (143.8) of predicted nest-sites, yet in 1986 it supported only 3 pairs of nesting choughs (Monaghan *et al.* 1989). [That the predicted nest-sites actually existed was shown by a foot-survey by CRM along most of the Jura coast in 1986 which confirmed that there was a large number of caves and arches containing suitable nesting ledges for choughs]. This extreme under-occupancy of sites can be explained by the fact that Jura is dominated by blanket bog and supports virtually no areas of pastoral or dune habitat. The few areas of pasture which do exist are on the east coast of the island where nest-sites are few.

In contrast, Colonsay has a wide range of pastoral habitats, several dune systems and similar land uses to the Rhinns of Islay, suggesting that nest-site occupancy should be high. However, of the 34.5 predicted natural nest-sites on Colonsay, only 6 (17.4%) were occupied in 1986, a much lower occupancy rate than on the Rhinns of Islay (57.5%). This under-occupancy may be due to the clumped distribution of nest-sites on Colonsay (see Figure 3): most nest-sites were on a restricted section of the north-west coast of the island adjacent to areas dominated by heath and bog, whereas in other parts of the island where more suitable foraging habitats were present natural nest-sites were scarce. It is perhaps as a result of this that, as on Islay, choughs on Colonsay have recently started to nest in buildings (Monaghan *et al.* 1989).

Provision of artificial nest-sites

These results highlight the importance to breeding choughs of the proximity of suitable nesting sites to favoured feeding habitats. The nest-site availability index devised here can be used to determine nest-site availability in any given area. In conjunction with the results of the habitat analysis it should be possible to identify those areas where suitable feeding areas exist (pastoral and dune habitats) but where nest-site availability is limiting. Provision of artificial nest-sites in areas with these characteristics is likely to be beneficial to choughs, as well as being an efficient use of resources from the conservationist's standpoint.

One such area was identified on Colonsay in 1994 - a small cliff lacking suitable nesting crevices adjacent to a dune system within a mixed pastoral farming unit (with sheep and out-wintered beef cattle). In association with the landowner an artificial nest-site was erected on this cliff by the Royal Society for the Protection of Birds in the autumn of 1994; choughs occupied the site in the following spring and bred successfully (Dr. D. Beaumont & M. Peacock RSPB, *pers. comm.*). This area had been devoid of breeding choughs since a nest-site in a barn had been inadvertently made inaccessible by building work 5 years earlier.

Artificial nest-sites provided in similar situations in Wales have also been adopted by choughs (Cross *et al.* 1993), and on Islay, steps have been taken to halt the decay of derelict barn nest-sites which limits the duration of their suitability to nesting choughs (Bignal and Bignal 1987). Provision of artificial nest-sites in areas of low nest-site availability and suitable habitat is a simple and cost-effective way of consolidating or increasing the size of chough breeding populations. Within appropriate areas, occupancy rates of artificial sites are likely to be highest if they are regularly spaced (*c.* 1/km^2) rather than clumped, and if the artificial sites themselves are spacious (preferably not less than 0.5 m x 0.5 m x 0.5 m).

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