

Durham E-Theses

Habitat selection and breeding ecology of three species of waders in the western isles of Scotland

David B Jackson

How to cite:

Jackson, David B (1988) Habitat selection and breeding ecology of three species of waders in the western isles of Scotland. Doctoral thesis, Durham University.

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a <https://etheses.durham.ac.uk/id/eprint/6330/> is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

HABITAT SELECTION AND BREEDING ECOLOGY OF
THREE SPECIES OF WADERS
IN THE WESTERN ISLES OF SCOTLAND

by

David B. Jackson B.Sc. (Dunelm)

The copyright of this thesis rests with the author.
No quotation from it should be published without
his prior written consent and information derived
from it should be acknowledged.

A thesis presented in candidature for the
degree of Doctor of Philosophy in the
University of Durham, September 1988.



- 4 OCT 1989

I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred upon me.

The copyright of this thesis rests with the author. No quotation from it should be published without his written consent and information derived from it should be acknowledged.

HABITAT SELECTION AND BREEDING ECOLOGY OF THREE SPECIES
OF WADERS IN THE WESTERN ISLES OF SCOTLAND

ABSTRACT

The habitat requirements and population dynamics of Redshank, Dunlin and Ringed Plover on internationally important breeding grounds in the Western Isles of Scotland were studied from 1985 to 1987 using individually colour-ringed birds.

Twenty-six habitat types were recognised at four study-sites on South Uist. The temporal and spatial use of the habitats by the three species were quantified. Redshank used a wide variety of pasture, marsh and water's-edge habitats and occurred mainly on "blackland" areas. Dunlin were largely confined to areas of old fallow machair and machair marsh. Ringed Plover occurred almost exclusively on the areas of machair used for cultivation. Redshank did not defend breeding territories and individuals ranged over wide areas. Dunlin and Ringed Plover held breeding territories within which most of their activities were confined. Late in the breeding season the seashore was an important feeding habitat for Dunlin and Ringed Plover.

Breeding densities varied markedly between major habitat divisions and appeared to be mainly determined by the availability and quality of potential nest-sites as indicated by their conspicuousness to avian predators.

Adults, especially males, nearly always returned to their previous year's nest-site or to close by. Young males bred significantly closer to their natal site than young females. Most birds settled within 4 km of their natal site.

Breeding success, first-year and adult survival, and the age of first breeding were evaluated. The data were used to predict population trends, which were compared to results from large-scale population surveys. It is concluded that Redshank and Dunlin numbers are approximately stable but that Ringed Plover are decreasing. Avian predation was the main factor limiting productivity. Both early season and well concealed/camouflaged nests were more likely to be successful. The conservation of these birds is discussed and some measures suggested that might increase their productivity.

ACKNOWLEDGEMENTS

I am especially grateful to Prof. Peter Evans for his encouragement and perceptive supervision throughout the past four years and his patience whilst criticising and discussing draft chapters. I am also indebted to Peter for his negotiations (successful and otherwise) with the Natural Environment Research Council.

I would also like to thank Dr. Mike Pienkowski for his assistance in the field and general supervision, and for making funds available from the Nature Conservancy Council to cover various expenses and the employment of a field assistant in 1987.

I would like to thank N.E.R.C. for their financial support, and the N.C.C. for additional financial help and for supplying large scale maps. The project was based at the University of Durham and I thank Prof. K. Bowler for use of facilities in the Department of Zoology.

I am grateful to the owners of South Uist Estate, the N.C.C., and the Ministry of Defence for permission to work on their land. I would also like to thank the crofters and farmers of South Uist for letting me work on their land and for their generous hospitality, in particular Jane Caytor, Norman MacAskill, Alastair MacDonald, Neil MacIntyre, Callum and Mary MacInnes, Ewan and Chirsty MacAskill, Iain and Mary MacAskill, John MacDonald, and DJ, Ann and Archie Steel. In addition I thank all the other residents in the islands who helped out in many ways and who made my stays in the islands so enjoyable, in particular Bill and Norma Neill, John and Audrey Kennedy and Donny

MacDonald. Many thanks are due to Paul Bowyer and Tim Dix for their help with bird ringing and also to Tim for his assistance in 1987 with searching for colour-ringed birds. Numerous friends have visited the islands and helped me with all aspects of the project. I am especially grateful in this respect to Anne Hudson, Richard White, Steve Percival, Jo Hughes and Clare Ditchburn. I am also very grateful to Mike Wells for his willingness to co-operate with Ringed Plover studies and for providing data on various birds.

Thanks are also due to my colleagues at the University who have helped out and given their advice. Notable amongst these are Brian Huntley who gave up much time to helping me with the vegetation classification, Hazel Taylor and her team in Data Preparation who kindly typed in the data, Nicholas Aebischer and Mark Ireland who gave computational advice and Matt Hancocks, Dave Baines, Neil Anderson, Norman Cobley and Sarah Wilson who proof read the manuscript and generally improved the english.

Mention must also be made of my appreciation of the service given by TTU 834R, CTE 865B and my constant field companion Optolyth 103563. Without these "friends" there would have been no data.

Finally, I owe special thanks to my father and mother, and my brothers and sister, for their assistance, encouragement and general involvement with all aspects of the project. Particular mention must be made of the time and skill that my father devoted to vital vehicle maintenance. I mourn his death earlier this year and am saddened that he is not able to read this thesis.

CONTENTS

	Page
CONTENTS	
ACKNOWLEDGEMENTS	
1. GENERAL INTRODUCTION	1
2. STUDY AREAS AND FIELD METHODS	5
Habitats and physiography of the coastal plain	5
Agricultural practices	8
Vegetation and classification of habitat types	11
Fieldwork methods	12
Study-sites	18
3. HABITAT USE I: HABITATS USED FOR BREEDING ACTIVITIES	27
Analysis of habitat usage data.	27
I: HABITATS USED BY REDSHANK FOR BREEDING ACTIVITIES	30
Gross habitat use by Redshank	32
Habitats used for display and courtship by Redshank	32
Habitats used for feeding by Redshank	33
Habitats usage by Redshank for chick-rearing	40
Habitats used by Redshank for comfort activities	45
Summary of Redshank habitat choice	46
II: HABITATS USED BY DUNLIN FOR BREEDING ACTIVITIES	48
Gross habitat use by Dunlin	48
Habitats used for display and courtship by Dunlin	48

Habitats used for feeding by Dunlin	50
Habitats used for chick-rearing by Dunlin	57
Habitats used for comfort activities by Dunlin	60
Summary of Dunlin habitat choice	61
III: HABITATS USED BY RINGED PLOVER FOR BREEDING ACTIVITIES	
Treatment of the data	63
Gross habitat use by Ringed Plover	65
Detailed account of habitat use by breeding Ringed Plover	65
Summary of Ringed Plover habitat choice	77
4. HABITAT USE II: DAILY MOVEMENTS DURING BREEDING SEASON	79
I: DAILY MOVEMENTS OF BREEDING REDSHANK	80
Treatment of the data	80
Movements by adult Redshank to feeding areas	81
Movements of Redshank families	86
Discussion of Redshank movements	91
II: DAILY MOVEMENTS OF BREEDING DUNLIN	94
Treatment of the data	94
Movements by adult Dunlin to feeding areas	94
Dunlin brood movements	98
Summary and discussion of Dunlin movements	100
III: DAILY MOVEMENTS OF BREEDING RINGED PLOVER	101
Treatment of the data	101
Ringed Plover movements at Stilligarry and Drimore Farm	102
Ringed Plover movements at Rubha Ardvule	105
Summary and discussion of Ringed Plover movements	105

5. NEST-SITE CHARACTERISTICS	109
Methods	110
Results	111
Redshank nest-sites	112
Dunlin nest-sites	114
Ringed Plover nest-sites	117
Factors influencing the concealment of nests	120
Associations with other species	124
6. BREEDING DENSITY	126
Methods	126
Results	127
Determinants of breeding density	131
Comparison of densities with those recorded elsewhere	137
7. BREEDING SITE FIDELITY AND NATAL PHILOPATRY	139
Methods	140
Results	140
Redshank site fidelity	144
Dunlin site fidelity	146
Ringed Plover site fidelity	147
Discussion	149
8. POPULATION DYNAMICS	150
Part 1: Breeding Performance	151
Nesting success	152
Survival of chicks to fledging	163
Summary of breeding success	170

Part 2: Survival of Full-grown Birds	170
Survival of breeding adults	170
First year survival	178
Age of first-breeding age	188
Part 3: Population Trends	192
Recruitment rate and its implications for populations	192
Population changes	196
Conclusions	199
9. GENERAL DISCUSSION	201
Determination of overall population size	201
Habitat conservation	208
Conservation measures for increasing productivity	215
SUMMARY	219
REFERENCES	229
APPENDICES	
A. Habitat classification.	240
B. Habitats used by Redshank for each activity at the northern study-sites.	254
C. Habitats used by Redshank for each activity at Rubha Ardvule.	256
D. Habitats used by Dunlin for each activity at the northern study-sites.	257
E. Habitats used by Dunlin for each activity at Rubha Ardvule.	258
F. Habitats used by Ringed Plover at each study-site.	259

G. Proportion of Redshank nests in each habitat.	260
H. Proportion of Dunlin nests in each habitat.	261
I. Proportion of Ringed Plover nests in each habitat.	262
J. Rating system for attributes of nest-sites.	263

CHAPTER 1

GENERAL INTRODUCTION

Until recently, detailed information on the distribution and abundance of waders (Charadriiformes) breeding in the British Isles and the rest of Europe was lacking. During the last two decades, there have been many extensive projects aimed at mapping the breeding distribution of birds (e.g. Sharrock 1976), and more localised censuses aimed at estimating breeding numbers and population changes. As a result of this, the approximate numbers and distribution of all wader species breeding in north-west Europe are now fairly well known and documented (e.g. Cramp and Simmons 1983, and Piersma 1986).

Studies in the mid-1970's by Wilson (1978) and by Fuller (1978) recognised that large numbers of waders breed in the Western Isles (Outer Hebrides) of Scotland. In 1983, prompted by threats of habitat changes in the islands (Cadbury and Housden 1982), a major survey of the breeding waders of the Outer Hebrides was undertaken by the Nature Conservancy Council and the Wader Study Group (Green 1983a and 1983b, Fuller *et al.* 1986). The aims of this survey were to map the distribution of all waders breeding on the coastal plain of the Southern Isles (South Uist, Benbecula, North Uist, Barra and adjacent small islands) of the Outer Hebrides and estimate their abundance.

The results from this survey (Fuller *et al.* 1986) showed that the coastal plain of the Southern Isles supports six species of breeding waders in large numbers and that some of these reach



densities greater than recorded anywhere else in north-west Europe. The approximate number of pairs of the six most common species found by the survey are as follows: Oystercatcher (*Haematopus ostralegus*) 2,700 pairs, Ringed Plover (*Charadrius hiaticula*) 2,200 pairs, Lapwing (*Vanellus vanellus*) 4,300 pairs, Dunlin (*Calidris alpina schinzii*) 3,300 pairs, Redshank (*Tringa totanus britannica*) 2,600 pairs, and Snipe (*Gallinago gallinago*) at least 1,000 pairs (based on Fuller *et al.* 1986). Comparison of these results with the numbers and densities found by surveys elsewhere in the British Isles (e.g. Smith 1983, Galbraith *et al.* 1984, Reed *et al.* 1983a) show that the Southern Isles contain at least 25% of the total number of Dunlin and Ringed Plover, and about 8% of the total number of Redshank, estimated to breed in the British Isles. The proportion of the British Isles totals for the other three species is a few percent only.

The populations of waders breeding on the Southern Isles, especially those of Dunlin, Ringed Plover and Redshank, are of considerable conservation interest. Their conservation value is likely to increase in the future because many of the wader populations breeding on mainland Britain and Ireland are decreasing due to habitat degradation, e.g. the agricultural improvement of traditional pastures and meadows by drainage and re-seeding (Baines 1988), or habitat destruction, for example, upland afforestation (Stroud *et al.* 1987). The wader populations in the Southern Isles occur predominantly on agricultural land and are therefore not free from the threats of habitat change

brought about by agricultural intensification or retrogression. Their long-term survival is dependent on the way man manages the land.

If they are to be successful, conservation policies for the waders breeding in the Southern Isles need to be based on a detailed understanding of the birds' ecology. Two key aspects of the birds' ecology that must be evaluated to this end are the habitat requirements and the population dynamics of each species. No previous studies have looked in detail at these aspects for any wader species in the Southern Isles. The aim of this study was to do so for the three species considered to be of greatest conservation value, namely Ringed Plover, Dunlin and Redshank. Although much of the work undertaken in this study was by its nature descriptive in approach, it aimed to provide quantitative descriptions and to understand the reasons behind the habitat requirements and the factors controlling the population dynamics of each species.

The habitats used by the breeding waders in the Southern Isles are in many ways unlike those found in mainland areas and their formation and character needs to be appreciated by readers of this thesis. For this reason, Chapter 2 starts with a description of the physiography, agriculture, and vegetation of the coastal plain of the Southern Isles. The remainder of Chapter 2 describes field-work methods and the study-sites. The habitat requirements of the birds during each stage of the breeding season are considered in Chapter 3. Chapter 4 deals with the spatial aspects of habitat use, such as movements to

feeding grounds, through the breeding season. Both Chapters 3 and 4 are divided into separate sections for each species. Chapter 5 considers the nest-site requirements of each species. Breeding densities and the factors that determine them constitute Chapter 6. The breeding site fidelity of adults and natal philopatry are examined briefly in Chapter 7. The population dynamics of the three species are dealt with at length in Chapter 8. This chapter considers the individual components of productivity and survival and uses these to predict population trends. These are compared with estimated population trends from surveys. The final chapter, Chapter 9, is a general discussion on the ways in which waders select their breeding sites and the processes that regulate their populations. This chapter finishes with some suggested conservation measures for the populations of waders breeding in the Southern Isles. The thesis ends with a brief summary of the important findings of the study.

CHAPTER 2

STUDY AREA AND FIELD METHODS

Habitats and physiography of the coastal plain

The coastal plain along the west side of the Southern Isles consists of a rock platform of Lewisian gneiss (Smith 1979) that is overlain by shallow deposits of glacial drift, peat, sand and water (Ritchie 1979, Glenworth 1979). The habitats found on the coastal plain fall into three broad groups: seashore, loch and terrestrial. Of these, the terrestrial habitats are the most important to breeding waders; they are also the most complex. The main factors affecting the nature of the terrestrial habitats are soil type, soil moisture and agricultural practices. Each of these is now discussed more fully.

The west of the coastal plain is dominated by the landform known as "machair". Machair is a flat dune-type land formation with a characteristic sandy soil derived from shell fragments and glacial drift (Ritchie 1979). It is confined to a few places in western Britain and Ireland where there are frequent on-shore gales, an abundant supply of sand and a low-lying coastal landform. The formation of machair occurs when large quantities of sand are swept off the beaches during westerly gales and carried some distance inland before falling to the ground. Here the sand is trapped and stabilised by vegetation and thus becomes incorporated into the soil. The vegetation protects the sandy soil from further erosion by the wind and encourages the sand to accumulate to depths of several metres. The machair of the

Southern Isles occurs as a strip, typically about 1 km. wide, along the west coast. The layout of the physiography of a typical section of the coastal plain is shown in Figure 2.1.

Along most of the machair plain there is a semi-stable sand-dune ridge between the machair proper and the beach. In places there is a well developed dune slack trough behind the dune ridge. To the east of the machair the soil is very different. It is a dark coloured peaty loam known locally as "blackland". The blackland soils have, in general, developed on areas underlain by glacial drift. Some areas are underlain solely by the bed rock of the region, Lewisian gneiss. The blackland is not flat like the machair but gently undulates to give a low hillocky landform, rising up to 10 metres in places. The blackland areas would naturally be peat bogs and scrubby forest (Ritchie 1967) but the activities of man have greatly modified the soil through drainage, removal of peat for fuel, application of shell-sand and organic fertilisers and ploughing.

The boundary between the machair and the blackland is rarely clearly defined. There is usually a transition zone about 200 metres wide with a sandy loam soil. Typically, the boundary between the machair and the blackland is obscured by a zone of marshes and lochs, the western edges of which have machair soils and are bordered to the east by blackland. As well as the extensive areas of marsh along the transition zone and around the lochs, small marshy hollows are frequent on the blackland and on some areas of machair. The marshes have waterlogged peat soils; the peat of the machair marshes is usually about 30 centimetres

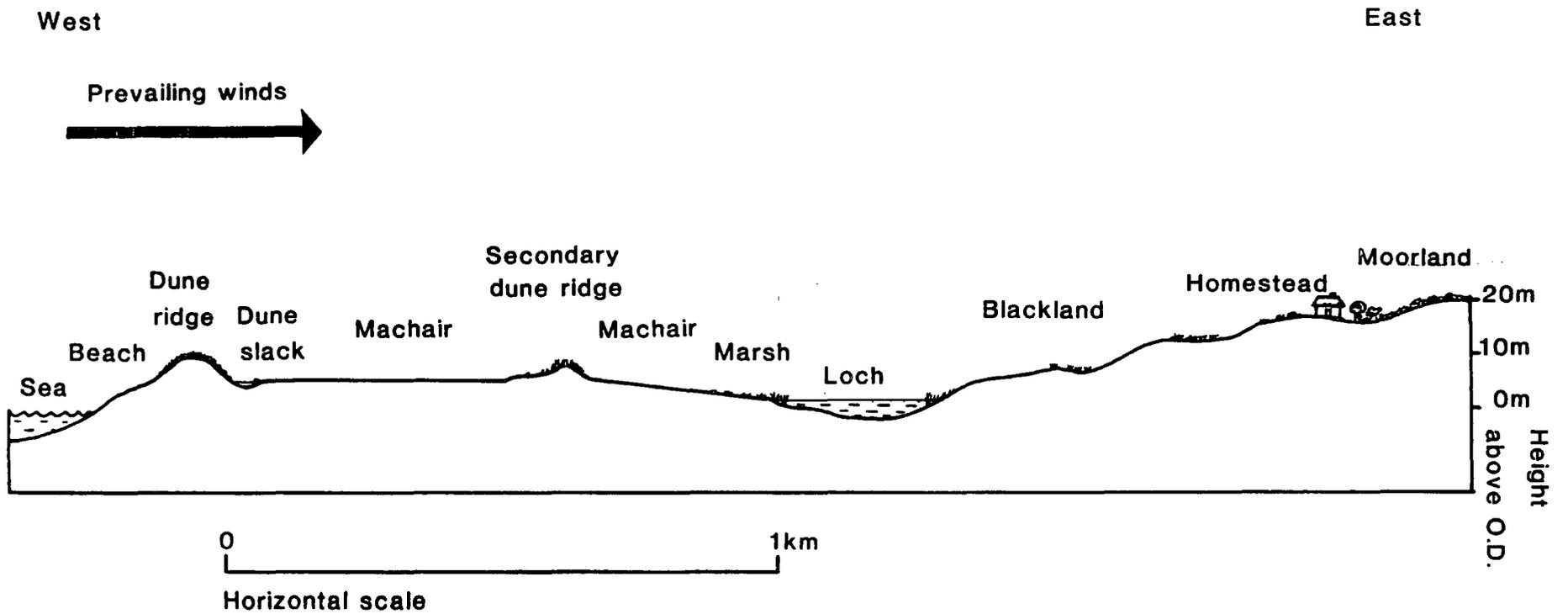


Figure 2.1: Cross-section of coastal plain

deep and is underlain by shell-sand (*pers. obs.*).

The soil chemistry of machair and blackland is very different and this has important effects on the vegetation. The machair soil is base rich and is typically pH. 8.5. The blackland soil and marshes, however, are generally base poor and are typically pH. 5-6 (*pers. obs.*).

A very wide range of soil moisture conditions occur on the coastal plain. Permanently waterlogged areas of marsh occur at one extreme, and at the other are the seasonally very dry conditions of mobile dunes and dry machair. The most important factors controlling soil moisture are drainage, organic content of the soil and proximity to the water-table. The machair plain typically dips very gently towards the east. The effect of this is that the central and eastern parts of the machair are in most places close to the underlying water-table and because of this the ground rarely dries out. Also, in these places, whenever the water-table rises slightly the ground often becomes waterlogged and in parts flooded. These areas are generally known as damp machair and they usually merge on the eastern fringe into machair marsh. The western part of the machair and the dune ridge are sufficiently raised above the water table not to be at risk of flooding. They are very free draining and the soil can become very dry in the summer. This is known as dry machair. The dune slack troughs flood during the winter but are usually dry in the summer months.

The susceptibility of the soil to drying out is also influenced by the amount of organic material it contains; the

greater the amount of organic material the more water is absorbed and held by the soil and the slower it dries out. The dry machair and dunes have very small amounts of organic matter in the soil as they are almost pure shell-sand, the damp machair has moderate amounts, and the marshes and blackland have large quantities.

The degree of drainage that takes place depends on soil porosity, proximity to the water table and the slope. The very sandy soils are very porous and free draining. The less sandy soils of the damp machair and much of the blackland are also porous and free draining provided they are not already saturated with ground water. The very peaty soils are usually waterlogged and this effectively inhibits drainage through the soil. Surface run-off is probably an important component of the drainage on much of blackland where the ground is sloping.

To summarise, the coastal plain has two distinct soil types. In the west are the sandy machair soils and in the east the peaty blackland soils. Between the machair and blackland there is usually a zone of marshes and lochs. The nature of the machair and blackland is very variable particularly with regard to soil moisture, drainage and fertility. The physiographic and edaphic factors have resulted in the development of a complex mosaic of habitat types; these are discussed more fully below.

Agricultural practices

In the Southern Isles, the traditional, low intensity methods of agriculture predominate. These are different to those found

on mainland Britain in several respects.

The agriculture is based on a system of crofting (with the exception of a few farms) in which the machair and blackland of each township (village) are divided into crofts (see below) each of which is farmed (crofted) by one of the township families (Caird 1979). The agricultural economy is based on the production of lambs and store cattle which are then sold for fattening on the mainland. During the summer months the livestock is kept off much of the machair and blackland so that crops can be grown for winter fodder. The hill-land and some of the blackland is kept as common grazing for use by all the crofters of the township.

The machair land is apportioned between the crofters as strips running east-west across the width of the machair. The dry machair is cultivated on a rotational basis to grow cereals (usually a mixture of rye and oats) for winter livestock fodder (Grant 1979). Each year a crofter will normally cultivate half of his dry machair, ploughing a long strip, typically 30 metres wide and up to 500 metres long, on each of his plots of dry machair. In most townships fallow strips alternate with strips under cultivation; this is the traditional strip system. A few townships divide their machair into two parts separated by a fence, each crofter having land in both parts. The two areas alternate between cultivation and fallow every few years with the fallow half (separated from the cultivated half by the fence) being grazed during the summer. With this arrangement all the strips of fallow lie alongside each other and likewise for the

strips under cultivation resulting of this is a much more uniform habitat of large areas of either fallow or cereal. This system is generally known as the "club-machair" system.

The cereal is harvested in late summer usually using a reaper-binder. The cereal sheaves are made into stooks to dry; once dry the crop is stacked outside ready for the winter. The period of the rotation is variable but it is unusual to grow cereal on the same patch for more than four years before allowing the land to lie fallow. Fallow land is allowed to re-vegetate naturally into machair grassland. It takes about three years for the sward to become closed and it is usually at least four years before further cultivation. Each crofter normally also grows a small patch of potatoes on the dry machair for home consumption. The other main fodder crop grown is hay. Both unimproved traditional herb-rich meadows and reseeded leys are used for hay and these are mainly situated on the transition zone between the machair and blackland; this ground is difficult to plough (too wet and stony) and therefore unsuitable for cereals. The short growing season means that only one crop of hay can be taken and this is usually ready for cutting by mid July or August. The traditional method of cutting the hay by scythe and turning it by hand is still used in parts of the islands though the use of machinery for these jobs now predominates. The hay is usually heaped by hand in the fields to form haystacks; later the hay is taken back to the croft homesteads and stored for the winter. A small amount of silage is produced as an alternative fodder crop.

The Uists are fortunate in having an abundant supply of readily available natural fertiliser in the form of rotting seaweed, which accumulates in large quantities on the Atlantic beaches after storms. Many crofters spread liberal quantities of seaweed on the machair before ploughing. Manure and inorganic chemical fertilisers are also used extensively.

The economics of crofting are constantly changing (Grant 1979, Caird 1979) and have been greatly influenced in recent years by grant-aid. Historically, there have been times when crofting has been in decline and the land worked less intensively. In contrast schemes such as the Integrated Development Programme have encouraged a recent resurgence in crofting activity.

The consequences of small land units managed at different levels of intensity by many individuals and the natural physiography combine to produce an intricate and mosaic of diverse habitats.

Vegetation and classification of habitat types

The natural vegetation of machair is a herb-rich calcareous grassland in the dry areas, with marsh and fen communities in the wetter patches. The present day machair vegetation is thought to be close to the natural climatic climax community (Dickinson and Randall 1979) except for the areas under cultivation. The better drained areas of blackland originally had a covering of scrubby trees and dwarf shrubs, whilst the less well drained parts were peat bogs or marsh (Ritchie 1967). Today, after centuries of

man's farming activities, the blackland is mainly pasture land of variable quality. The poorly drained areas remain as marshes and peat bogs.

The habitat classification used in this study is largely based on the floristic composition of the vegetation. As might be expected, this closely reflects the type of physical environment and agricultural regime experienced. A phytosociological survey technique combined with multivariate analysis was used to identify different vegetation stand types; the details of the methodology are described later under "fieldwork methods".

Often the habitats merge imperceptibly from one to another so classification to a fine level must be partly subjective. Notwithstanding this inherent difficulty, it was possible to classify the habitats into many readily recognisable types. However, within the habitat types recognised, particularly the various different types of grassland, there is a certain amount of variation. The value of one of these habitat types to a wader species will therefore not necessarily always be the same.

A total of twenty four habitat types incorporating fourteen vegetation stand types (see below) were recognised. These are listed and briefly described in Appendix A.

Fieldwork methods

1) Vegetation survey and habitat classification

Field recording of the vegetation was undertaken in July and August after the waders had finished breeding. The recording

method used involved scoring the abundance, on a six point scale, of all higher plants present inside a one metre square quadrat.

The abundance scale used was as follows:

<u>Score</u>	<u>Cover</u>
1	+ (present close by)
2	1 - < 4%
3	4 - <10%
4	10 - <30%
5	30 - <70%
6	70 - 100%

Data were collected from a total of 281 quadrats covering all the major habitats present. These data were analysed using the Two-way Indicator Species Analysis classification method (TWINSpan) (Hill *et al.* 1975, Hill 1979). This is a divisive polythetic method that is well suited to producing a working classification of areas with complex vegetation assemblages.

The results from the vegetation classification are presented in Appendix A. A total of fourteen stand-types were identified and these were used as a basis for the habitat classification. Some stand-types were represented at only one study site, however it was apparent that in some cases an ecologically equivalent and floristically similar stand-type occurred at the other study-sites. Where this was the case the two stand-types have been treated as one habitat.

Classification by the floristic composition does not take account of the vegetation's structure though in most cases a given stand-type has a similar structure wherever it occurs. The chief exceptions to this are stand-types that are managed in different ways by man. For example, an area of grassland may be grazed throughout the summer and thus remain as a short sward,

or it may be left ungrazed and the grass allowed to grow tall for hay. Clearly the two management regimes produce different habitats even though the floristic composition is identical. Similarly, the changes in cereal fields from bare soil to tall, dense crops do not reflect any change in species composition but simply vegetation growth. Those stand types that undergo these fundamental seasonal changes have been subdivided into seasonal stages. Some terrestrial habitats, such as trackways and ditches, and all loch-edge and seashore habitats were not covered by the vegetation survey. These habitats are however generally clear-cut and fall into easily recognisable natural categories and therefore no special method of classification was needed. In all, 26 habitat types were recognised and these are listed and briefly described in Table A.3 of Appendix A.

ii) Field study methods on the birds

To investigate the birds' pattern of habitat usage it was necessary to find wader nests, individually mark the adult birds from these nests and to regularly locate the marked birds throughout the breeding season.

Nests were found in three ways:

- 1) by thorough ground searches of likely areas,
- 2) by walking over the nesting grounds and watching for incubating birds flushed off their nests, and
- 3) by watching from a distance for birds returning to their nests or (for Ringed Plover only) sitting on the nest.

The position of each nest was recorded in terms of a

compass-bearing and a distance in paces from one of the study-site grid posts (see below) or some other landmark, so that they could be relocated. Each nest site was described by its habitat and various physical attributes (see Chapter 5). Nests were inspected at intervals of about five days to determine their outcome and calculate egg survival. Where possible this was achieved from within a mobile canvas hide to minimise disturbance.

Adult waders were caught using heart-shaped cage-traps secured over the nest. A bird's return to the nest was usually watched; once it was back on the eggs and in the trap, the bird was left for about five minutes to warm the eggs before it was extracted from the trap. Upon capture the bird was put into a cloth bag, the trap was removed, and the vicinity vacated to minimise disturbance to the other birds breeding in the area. If, after 40 minutes (30 minutes on cold, windy days) the bird was not back on the eggs then the catching attempt was abandoned and the trap removed. To reduce the chances of causing nest desertion catching was not attempted during the first five days of incubation or during wet weather.

All the adult waders caught were ringed with a numbered metal ring and a unique combination of colour-rings. Each bird was measured, weighed and, where possible, aged and sexed (Prater *et al.* 1977) before release. Redshank could not be reliably sexed from their external characteristics and therefore, they were sexed on the basis of their display and courtship behaviour.

Observations of the colour-ringed birds were collected throughout the breeding season. Sightings of birds consisted of

spot observations made during regular surveys of the study-sites and nearby beaches. Each area was surveyed at approximately five day intervals. The details recorded for each sighting included the bird's colour-ring combination, the time and date, the position within the study-site, the bird's behaviour and the habitat type being used. After a bird was found it was watched for a short while (usually about two minutes) to collect the details necessary for the record. Normally, only one record was noted for each occasion an individual was located, however if during the time the bird was under view it changed its behaviour type, moved more than 100m or changed habitat type further records were made. This did not happen often. During a survey of an area the same bird was rarely seen more than once and only a about 60% of the individuals known to be associated with that area were seen. A bird's position was recorded as grid co-ordinates corresponding to the study-site's grid (see below). Behaviour was recorded as one of a number of predetermined behaviour types listed in Table 2.1.

Observations were made from a mobile hide or a Landrover; this allowed a moderately close approach without causing undue disturbance. The mobile hide consisted of an aluminium frame with a camouflaged canvas cover and had an internal harness allowing it to be carried on the observer's back whilst surveying the sites. The identity of birds was determined from their colour-rings using a 30X Optolyth telescope, this allowed colour-ring sequences to be read at distances up to 300m. Care was taken to minimise disturbance in areas with nests or chicks by reducing the time spent there as much as possible. Surveys

Table 2.1: Behaviour types recorded and categories used in the analyses.

BEHAVIOUR TYPE RECORDED	BEHAVIOUR CATEGORY (Chapters 3 & 4)
Display (involves male bird only)	Display
Courtship (involves a pair of birds)	Display
Mating	Display
Feeding	Feeding
Seen with chicks	Chick rearing
Giving chick danger call	Chick rearing
Standing alert or on guard	Not used unless in chick rearing stage, then Chick rearing.
Standing doing nothing	Not used
Incubating	Not used
Returning to nest	Not used
Captured in trap	Not used
Roosting	Comfort activity
Bathing and preening	Comfort activity
Miscellaneous rarely recorded activities	Not used.

were undertaken at all times through the day and in all weather conditions except heavy rain.

The observer effort was approximately uniform over each study-site; parts far away from tracks and peripheral areas (see below) were slightly under-observed. The slight variation in observer effort is of little importance because the heterogeneous habitat mosaic of the study-sites meant that the observer effort for each habitat type was proportional to its availability. Besides the work on the study-sites, checks were also made for colour-ringed birds in other areas of wader breeding habitat and on all west coast beaches on South Uist and Benbecula; this is discussed further in Chapter 8.

All information collected in the field was recorded directly on to specially designed 80 column record sheets. Recording the data in this way greatly facilitated the efficiency and accuracy of data entry onto the mainframe computer at the University.

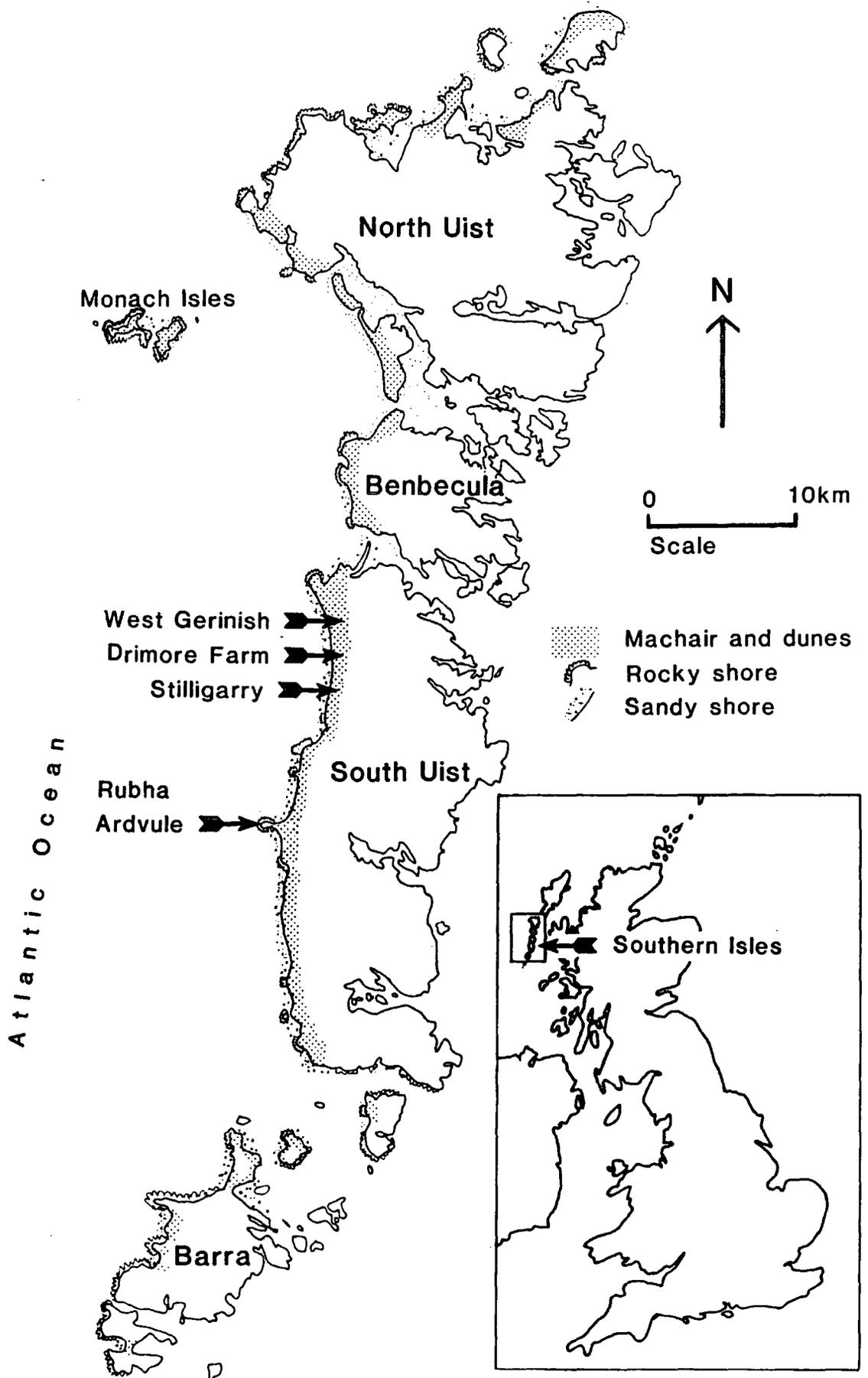
Telemetry was considered as a technique to investigate the birds' habitat use. This method would have had some advantages in reducing observer biases, but it was not used because it would have been impractical to follow the number of birds necessary to give a representative picture of habitat use by each species at each site.

Study-sites

1) Choice and design of study-sites

The fieldwork was undertaken at four study-sites on South Uist (approximately 57° 20' North, 7° 20' West), their position is shown in Figure 2.2. The sites were chosen on the basis of how

Figure 2.2: Map of the Southern Isles showing the positions of the study-sites and areas of machair habitat.



representative of the habitats they were, their range of breeding bird densities (determined from the 1983 NCC/WSG Hebridean wader survey) and their suitability for observing the birds from vehicular tracks. The study-sites contained a core area where I attempted to find all nests and colour-ring all of the breeding adults. Surrounding each core area there was a peripheral area that was regularly visited and checked for colour-ringed birds although very few adults were caught in these areas. The core area of a study-site was not always the same for each species. Habitat usage and breeding success were not studied for all three species at some sites (see species accounts).

The boundaries of the study-sites were not rigid and the size of three sites was extended in the second year, particularly at Drimore Farm, to include areas that were known to be used by birds nesting in the original area. The juxtaposition of the three northern study-sites meant that the peripheral area of one site adjoined that of the next. This had the advantage that a continuous section of the coastal plain nearly 5 km. long was regularly surveyed and thus minimised the possibilities of overlooking any birds that moved large distances on the breeding grounds.

Each study-site was divided into 50 X 50 metre squares forming a grid covering the whole site. The alignment of each study-site grid was determined by the direction of the main fence lines at the site. To aid the accurate positioning of nests and bird sightings, the corners of most grid squares were marked out using short white posts hammered into the ground or by painting

the tops of convenient fence posts white. The co-ordinates of a grid post were painted on to the post in large figures, these could easily be read through a telescope at distances up to a kilometre away.

Unlike the other three sites, the site at Rubha Ardvule could not be considered to be typical of the wader breeding grounds in the islands. For this reason much less effort was invested in this site. It was included because the site has very high breeding wader densities and the nature of the site presented many practical fieldwork advantages.

ii) Description of study-sites

A description of the four study-sites is given below. The main habitat features present at each site are shown in Table 2.2 at the end of this chapter.

1) Rubha Ardvule ($57^{\circ} 14'$ North, $7^{\circ} 27'$ West)

Area = 37ha (dry-land 22ha, loch 6ha, littoral ca.9ha)

The geography of this site is shown in Figure 2.3. The site consists of a low, rock and shingle promontory jutting out in to the Atlantic Ocean. It is approximately one kilometre long and half a kilometre wide and is surrounded by the sea on three sides. The coastline is predominantly rocky and extensive areas of intertidal rock and rock-pools are exposed at low tide. There are also several small bays of sand and shingle; after storms these usually have large amounts of rotting seaweed along the tide line. The centre of the site is occupied by Loch Ardvule, a slightly brackish loch with both stony and grassy shorelines and several vegetated islands.

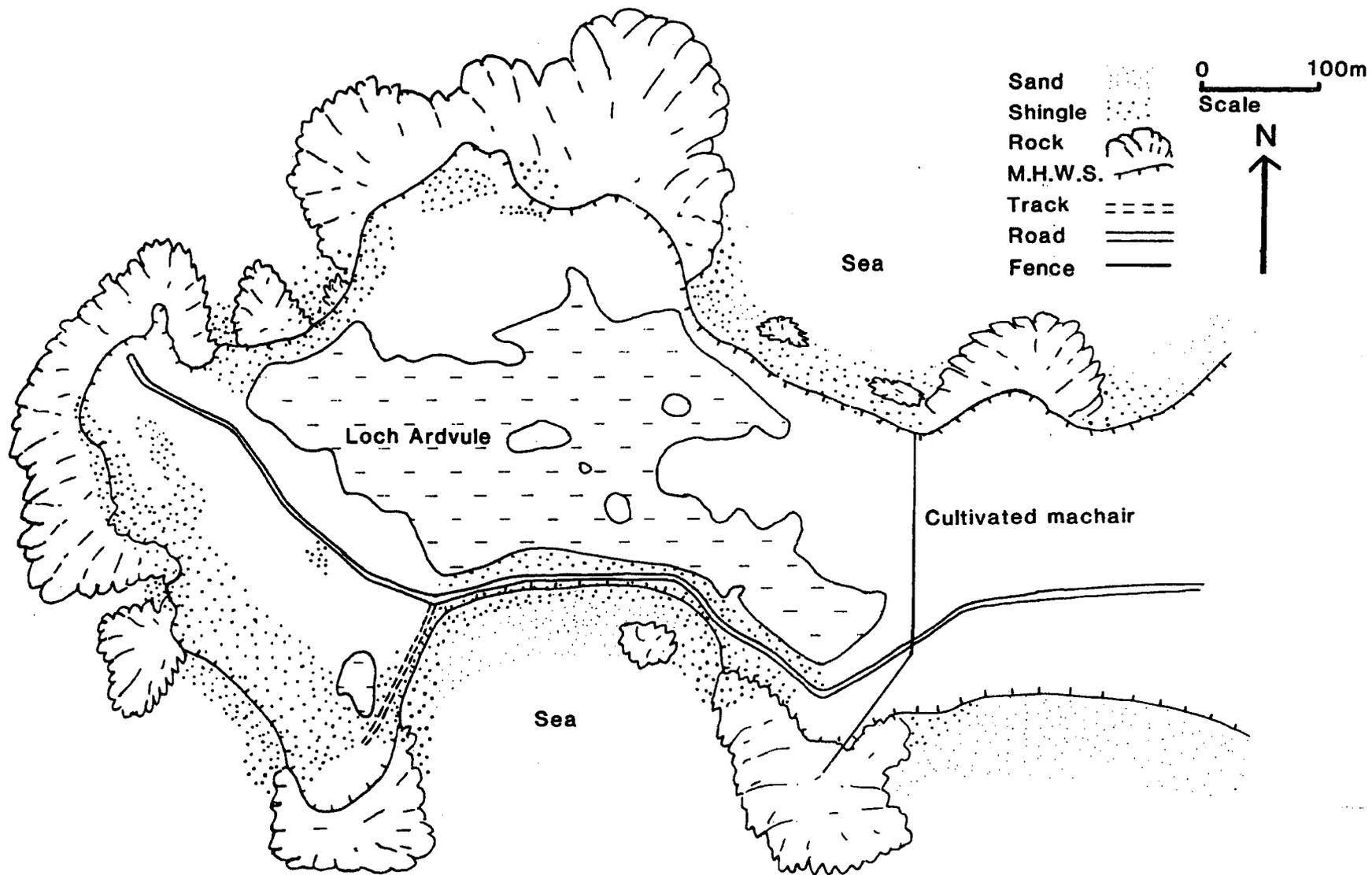


Figure 2.3: Map of Rubha Ardvule study-site.

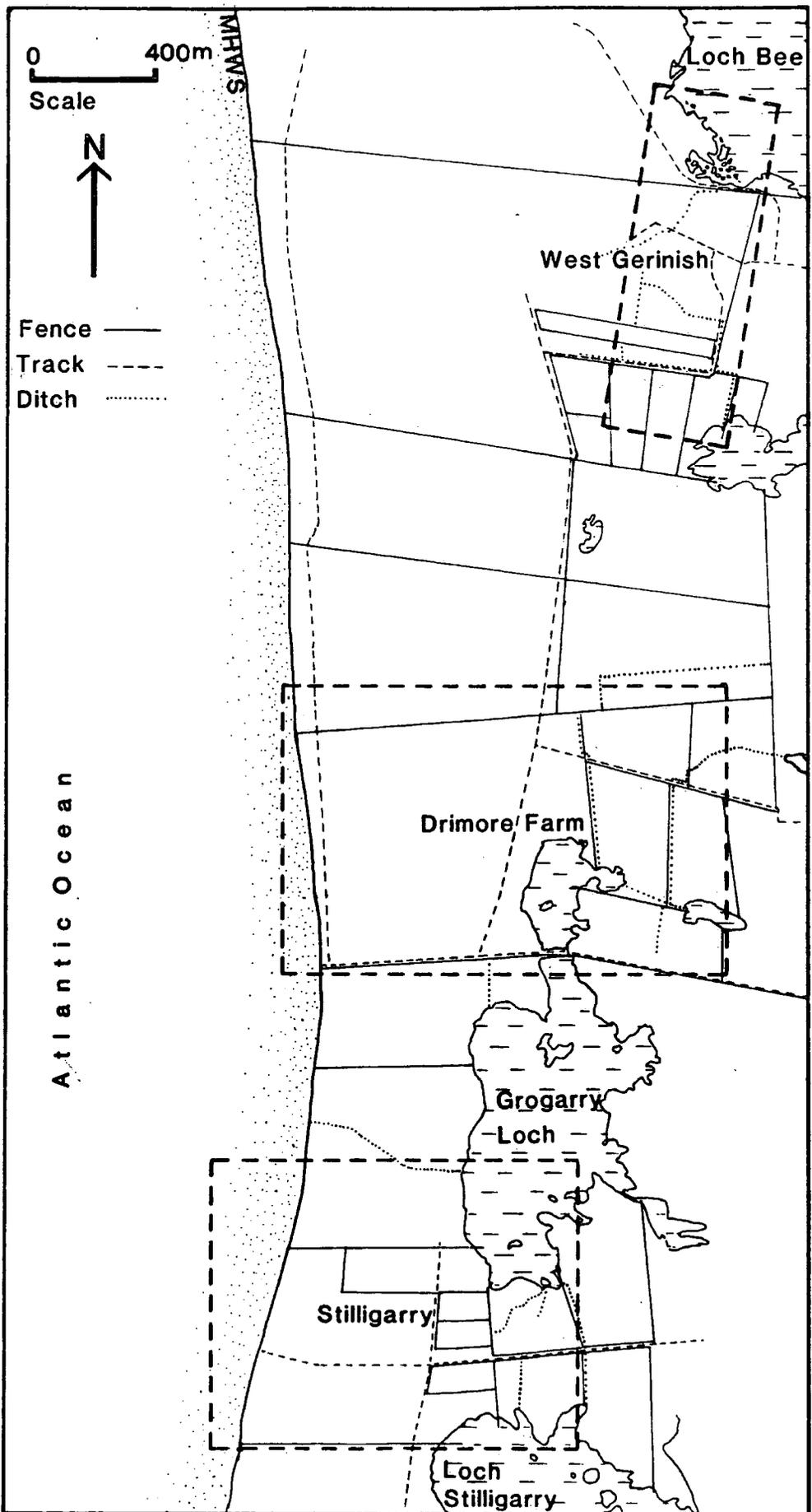
Between the loch and the seashore there are extensive areas of dry to damp grassland with patches of Yellow Iris (*Iris pseudacorus*) and Soft Rush (*Juncus effusus*) and some small marshy areas. In places there are large banks of coarse shingle, some of these are partly vegetated. The eastern edge of the site has typical dry machair grassland with cultivation strips, this is contiguous with a massive area of machair to the north and south. A metalled road runs the length of the study site and there is a small building used for military purposes. The whole site, except for the cultivated dry machair, is grazed by cattle through out the year and also by sheep in the winter.

2) Stilligarry (57° 19' North, 7° 23' West)

Core area = 99ha

The geography of the Stilligarry site, and the two other northern sites is shown in Figure 2.4. The Stilligarry site consists of a typical, traditionally crofted section of the machair plain and is part of the Druidibeg National Nature Reserve. Behind the sandy beach that forms the western boundary of the site is a dune ridge and behind this a large open area of dry to slightly damp machair. The machair extends eastwards up to, and between, the two large machair lochs, Loch Grogarry and Stilligarry Loch, which extend into the north east and south east corners of the study-site respectively. The eastern fringe of the machair proper, the area between the lochs, is divided into several small fields (each of about 2ha) by fences. Immediately east of these fields is the machair/blackland transition zone with damp to marshy grassland and this is drained by a network of ditches flowing into the lochs. Further east, this gives way to

Figure 2.4: Map of the northern study-sites.



blackland proper consisting of undulating grassland. The study-site extends for about 200 metres onto the blackland. Several strips of cereals are grown on the machair. Some crofters have not cultivated their areas of machair for many years and consequently there is a high proportion of fallow machair grassland. The better drained areas of the transition zone and the blackland are used to grow hay.

The whole site is grazed by cattle and sheep in the winter but this is reduced in the summer to a few cattle remaining in the fenced fields. The site is traversed by two rough tracks at right angles to each other crossing at the centre of the site.

3) Drimore Farm (57° 20' North, 7° 23' West)

Core area - 120ha (including 6ha of loch)

This is the largest study-site and is positioned between the Stilligarry and West Gerinish sites. Bounded on the west by a sandy beach, the site stretches eastwards across the machair and extends to cover the first 500 metres of blackland. In the southern half, between the machair and the blackland, lies the northern end of Loch Grogarry. Along the western shore of the loch there is a strip of marsh habitat and this continues as a large expanse north of the loch where it forms a transition zone between the machair and blackland. Some parts of the blackland are semi-improved pasture land and have been reseeded in the past. However, in the main the blackland is rough grazing with numerous marshy hollows and patches of Soft Rush. A network of open field-ditches extends over the blackland and these drain into Loch Grogarry. There is also a small lochan on the blackland with a patch of Phragmites reeds. The blackland is

divided by fences and stone walls into several fields each of about 6 hectares.

Between the seashore and the machair there is a well developed dune ridge and behind this a continuous dune slack trough which is flooded for most of the year. The machair at Drimore Farm is divided into three sections by east-west fences. The southern section of 16 ha mainly consists of a large, rather uniform expanse of dry to very dry machair that is cultivated each year for cereals. The central area of machair covers 40 ha, most of this is an extensive level area of dry to damp machair. Part of this area was cultivated in the first year of the study (1985); subsequently it has been left to revegetate naturally. The rest of this area is permanent natural grassland which has not been cultivated for several decades. A low, secondary dune ridge runs along the eastern flank of this area and east of this there is another area of machair. This narrow strip of machair dips slightly to the east, at first it is very dry but gradually becomes wetter, and finally merges with the marshland around Loch Grogarry. An area of small, low dune hummocks with small intervening areas of dry to damp machair occupies the remainder, the north-west part, of the central section of machair. This habitat type extends to the north and forms a large proportion of the 35 ha of the third, and northern section of machair at Drimore Farm. The rest of this section consists of a northward extension of the secondary dune ridge which flattens and widens out into a level expanse of very dry machair most of which was reseeded with a commercial grass mixture in 1984. A network of rough tracks give good access to most parts of the site.

As the name suggests, this site is a farm and not croftland. The consequences of this are more intensive land management and larger, more uniform areas of crops than found on the croftland. The large cereal fields at Drimore Farm are in many ways analogous to areas of cereals grown under the crofting "club-machair" system. The cereal crop at Drimore Farm is ensiled. No hay crop is grown. Sheep are the main livestock together with a few cattle and most of the fields are grazed throughout the year.

4) West Gerinish (57° 21' North, 7° 23' West)

Core area = 40 ha

The core area of this site lies to the east of the wide flat machair plain at West Gerinish and covers a broad machair/blackland transition zone. The site is raised somewhat above the level of this plain and has a lightly undulating surface. The machair soils extend onto the raised area and gradually merge with the typical peaty blackland soil found in the east of the site; the majority of the site has therefore a dark sandy loam. Most of the site is well drained permanent grassland, there are also a number of marshy hollows, areas of damp rough pasture and patches of Yellow Flag Iris. The land is drained by several small ditches some of which are choked with vegetation.

The south shore of Loch Bee, a very large, shallow brackish water loch, forms the northern boundary of the site. Wave action has eroded the land in this area to produce numerous low grassy islands and a rather indented and gullied shoreline of short grass and soft mud. The exact nature of the loch shore changes

with fluctuations in water level, in summer when the level falls large expanses of mud along the shore and between the islands are exposed. A small blackland loch with a stony shore is situated in the south-east corner of the site.

The site is divided into many croft strips, most of these are unfenced though in the south of the site an area of about 15 hectares has been divided into several small fields by fences. The land is mainly used to grow hay together with some cereals on the sandier soil. The area around the shore of Loch Bee is part of a military range, it is not cultivated but is grazed by sheep and cattle throughout the year. The rest of the site is grazed only during the winter months with the exception of one of the small fenced fields which is stocked with sheep all year. Two rough tracks provide access to the croftland and a fairly busy military road crosses the north of the site close to Loch Bee.

Table 2.2: Habitat types represented at each study-site.

HABITAT TYPE (CODE)	RUBHA ARUVULE	STILLIG- GARRY	DRIMORE FARM	WEST GERINISH
WATER'S EDGE				
Seashore (sand) (X)	***	***	***	.
Seashore (rock) (X)	***	.	.	.
Loch-edge (L)	***	***	***	***
Pool-edge (Z)	*	**	**	**
Ditch (D)	.	*	**	*
MARSH				
Wet marsh (N)	.	*	**	*
Damp marsh (M)	*	**	***	***
Hummock marsh (O)	.	.	**	**
BLACKLAND				
Iris beds (I)	**	*	*	*
Juncus pasture (J)	*	*	***	*
Iris & Juncus (K)	**	.	*	*
Hay (H)	.	**	.	***
Good blackland (G)	.	**	***	**
Poor blackland (W)	.	**	***	**
Rough blackland (R)	.	.	**	**
Maritime pasture (V)	***	.	.	.
MACHAIR				
Old damp fallow (E)	*	***	***	**
Old dry fallow (B)	**	***	**	.
1st year fallow (F)	**	***	***	.
2nd year fallow (S)	**	***	***	.
Plough/cereals (P,C)	**	***	***	**
Mobile dunes (A)	.	**	***	.
Reseeded machair (U)	.	.	***	.
Tracks & shingle (T)	**	**	**	**

. = Absent

* = very small area present

** = moderate area present

*** = large area present

CHAPTER 3

HABITAT USAGE I: HABITATS USED FOR BREEDING ACTIVITIES

This chapter and the following chapter use the data from sightings of the colour-ringed birds to build up a detailed picture of the habitats used by each species for different activities during the breeding cycle. The habitats chosen for nesting are dealt with separately in Chapter 5.

Analysis of habitat usage data.

The bird observation data were entered on to the mainframe computer at Durham University. The data set was analysed using a commercial statistics package (SPSS). For most colour-ringed birds, the nesting history and nest site position was known. Using this information it was, in most cases, possible to retrospectively determine the exact stage of breeding of the birds whenever they were seen. In a similar way, it was possible to calculate the distance of the birds from their nest at the time of each sighting, necessary for analysis of the birds' movements presented in Chapter 4. For the purposes of analysis, the recorded behaviours of the birds have been aggregated into four fundamental types (detailed in Table 2.1). These are: feeding, display (includes courtship), tending chicks and comfort activities (roosting, preening and bathing). Those records with behaviour types that do not fall into one of these categories, such as standing and nest activities, are excluded from this analysis.

It might have been thought valuable to calculate the area of

habitat of each type at each site but this was not done because:

1) The objective of the study was to determine the major habitat types that are used by each species for each fundamental activity. It is clear from the results that in nearly all cases the birds are very selective about the habitat they choose to use for a given activity. Although it would be interesting to investigate habitat preferences for a given activity by comparing the relative frequency of use of similar habitats corrected for availability, the results obtained would not necessarily be generally applicable. The relative value to a bird of two similar habitats may not always be the same, temporally or spatially, because the exact nature of a given habitat type may vary slightly between areas and with time (both between and within breeding seasons). For example, birds at site A may prefer old fallow over recent fallow for feeding but the reverse at site B. Such a result could easily arise from differences in soil moisture and vegetation height between habitats classified as the same, the observed inconsistency in habitat preference would then merely be a result of the limitations of the habitat classification system. There is no reason to suppose that birds breeding in one area have different preferences or requirements to those in another area.

2) Although observer effort was approximately uniform, the greater ratio of ringed to unringed birds in the core areas compared to the peripheral areas resulted in the core areas having proportionally more records. There is thus a bias in the data set in favour of the habitats in the core areas. The magnitude of this bias is unknown.

- 3) The exact area covered on different surveys within a season varied in response to the birds' behaviour, in particular the areas surveyed were extended when Redshank were rearing chicks. There was also variation between years in the size of the study sites and intensity of effort.
- 4) The area of many of the habitats is constantly changing, some pasture is left to grow into hay, plough changes to cereals and flood pools are temporary. Other habitats such as ditches and loch edges are linear and do not readily lend themselves to area calculations.
- 5) The various types of marsh and wet pasture merge gradually from one form to another and often occur in complex mosaics. Whereas it is relatively easy to determine which habitat a bird is using when seen, it is very difficult to objectively determine how much of each habitat is present.

The information on habitat use by each species in this chapter and in Chapter 4 is presented in separate sections.

CHAPTER 3: SECTION I

HABITATS USED BY REDSHANK FOR BREEDING ACTIVITIES

Data for Redshank were collected from all four study-sites. The three northern sites (Stilligarry, Drimore Farm and West Gerinish) have broadly similar habitats (Table 2.2) and have therefore been analysed together. The Rubha Ardvule study-site has a very different habitat composition and is analysed separately. The number of records of each activity at each site is shown in Table 3.1.

The number of records from each habitat for each of the four activities are tabulated in Appendices B and C, for the northern study-sites and Rubha Ardvule respectively. With the exception of comfort activities, the results in these appendices are illustrated using barcharts in Figures 3.1 and 3.2; habitats that had less than 2% of the total records are excluded from these figures. These results have to be interpreted with caution because they are influenced in part by the amount of each type of habitat available and the detectability of the birds in each habitat (see later discussion on ditch use). Nevertheless, they show the types of habitat that are of importance for each activity and those which are of little or no value. For the reasons discussed earlier the available area of each habitat is not given. However, except where indicated, all the habitat types listed in the relevant table were well represented at the site(s) concerned.

Table 3.1: Number of records of adult Redshank in each behaviour category at each study-site.

STUDY-SITE	NUMBER OF RECORDS ¹				ROW TOTAL
	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	
Rubha	45	262	103	14	424
Ardvule	10.6%	61.8%	24.3%	3.3%	20.1%
Stilli-garry	31	156	71	1	259
	12.0%	60.2%	27.4%	0.4%	12.3%
Drimore Farm	63	431	504	19	1017
	6.2%	42.4%	49.6%	1.9%	48.1%
West Gerinish	34	262	108	10	414
	8.2%	63.3%	26.1%	2.4%	19.6%
Total	173	1111	786	44	2114
%	8.1%	52.5%	37.2%	2.1%	100%

¹This table is included to show the amount of data available for use in the subsequent analyses from each study-site for each behaviour type . It is not possible to use this information to show time-budgets for each activity, either between or within sites, because the effort spent in obtaining observations was not equally spread temporally at all sites, and the detectability of the birds varied according the behaviour type. In particular, the high proportion of chick-rearing records at Drimore Farm reflects a combination of higher breeding success and a higher level of observer effort than at the other sites.

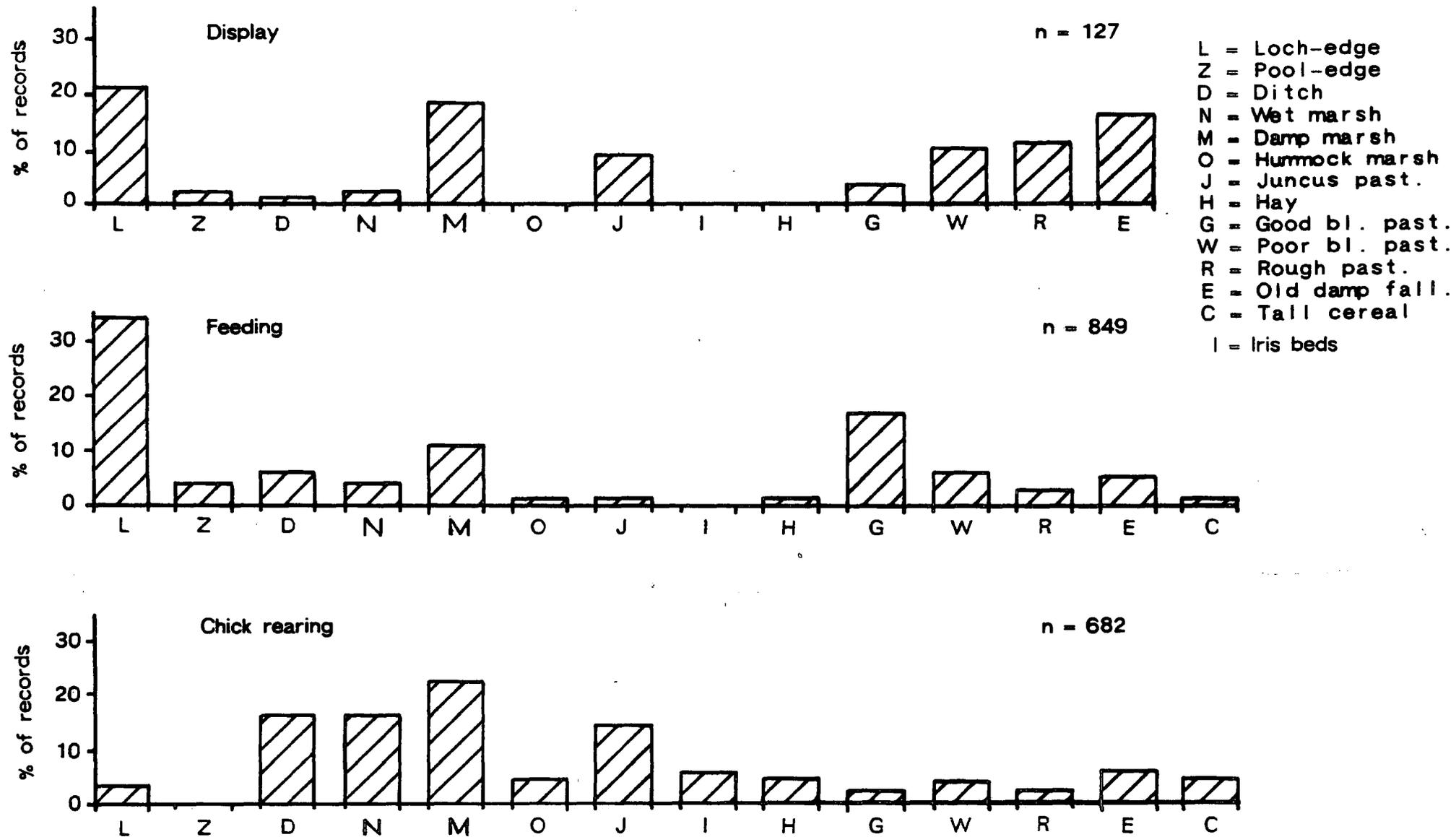
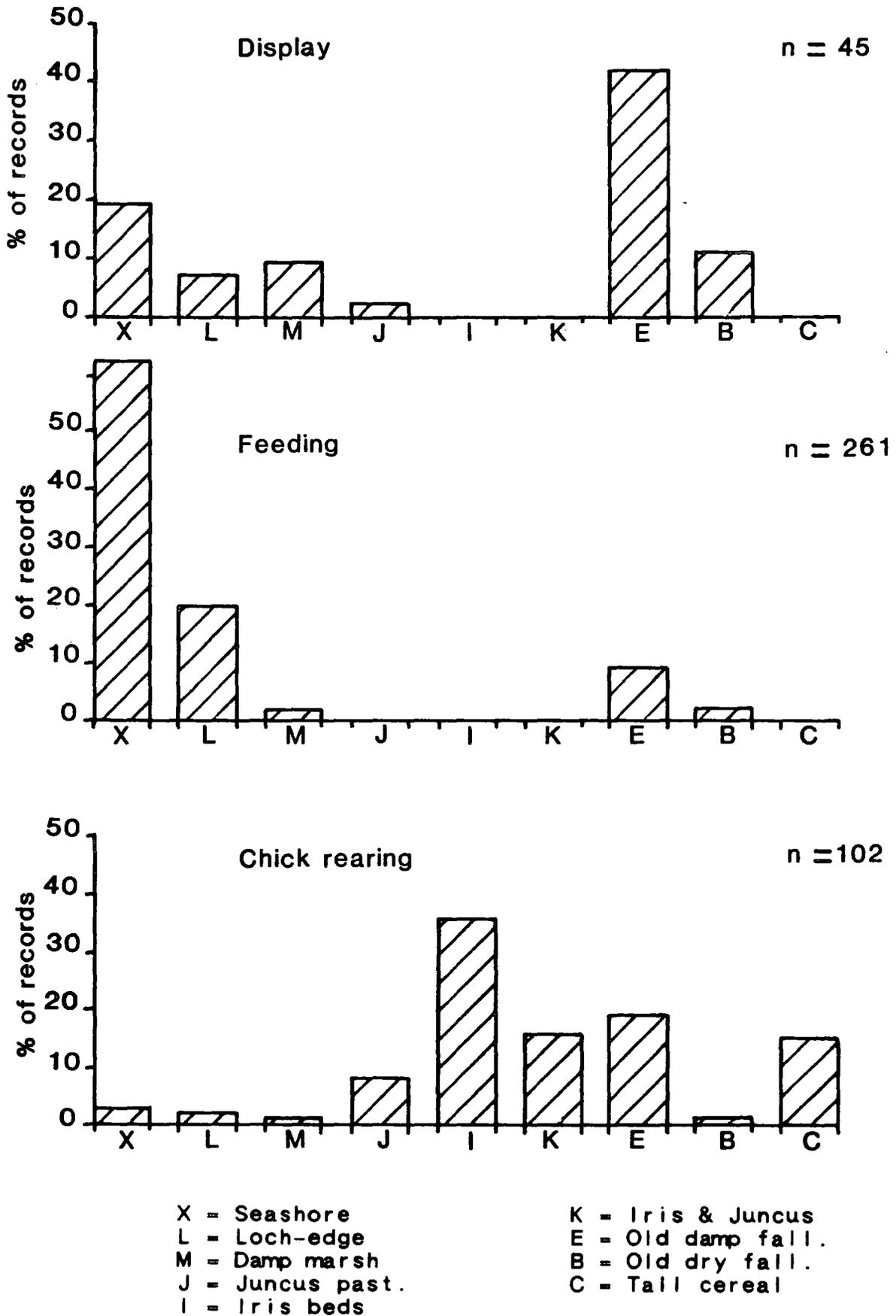


Figure 3.1: Percentage of records from the northern study-sites of adult Redshank from each habitat for three types of behaviour.

Figure 3.2: Percentage of records from Rubha Ardvule of adult Redshank from each habitat for three types of behaviour.



Habitats with < 2% of all records are excluded.

Gross habitat use by Redshank

Appendices B and C include almost all the habitat types present on the study-sites but many of these were used only infrequently. The most important habitats for Redshank were blackland pastures, all types of marshes and freshwater margins. The habitats of cultivated machair and dunes were generally of little importance. The seashore was used very rarely except at Rubha Ardvule which is surrounded by rocky shore habitat.

Habitats used for display and courtship by Redshank

On the ground, display and courtship behaviour by Redshank mainly occurs on and around the areas used for feeding and in the nesting areas (*pers. obs.*). The most frequent component of these behaviours are ground chases involving two or three birds. These chases usually last for 1-2 minutes (Cramp and Simmons 1983) and frequently cover distances in excess of 200 metres (*pers. obs.*). Ground chases take place in open spaces; the value of openness is probably to give the birds good all round visibility; this may be especially important at the start of the breeding season when Redshank are frequently taken by birds of prey (Chapter 8).

The most important habitats used for ground display behaviour were open, short, damp grassland habitats such as old damp fallow, damp marsh, and blackland pastures. Loch-edge and pool-edge habitats and, at Rubha Ardvule, the seashore, were the next most important group of habitats used for display behaviour. The number of records from loch-edge and seashore habitats is not as high as would be expected if the usage of these habitats for

display and courtship was proportional to their use for feeding. This is probably because some parts of these habitats, particularly rocky areas, were not open or flat enough. Similarly, ditches which were commonly used for feeding were used extremely rarely for display or courtship.

The types of habitats used for ground display and courtship were similar at Rubha Ardvule and the northern study-sites except for the high frequency of use of the seashore at Rubha Ardvule and a corresponding lower use of loch edges. This is explained by differences in the habitats used for feeding between the two areas (see below).

Records of aerial displays are not included in this analysis. The display flights of the male Redshank occurred over all types of habitat and often involved flights of over 500m covering a wide range of habitat types (*pers. obs.*).

Habitats used for feeding by Redshank

The habitats used by Redshank for feeding fall into two major groups: damp grasslands and marshes and, water's-edge habitats (loch-edges, pool-edges, ditches and, at Rubha Ardvule only, seashore).

1) Use of terrestrial feeding habitats.

Damp grasslands and marshes account for 47% of all feeding records at the northern study-sites. The important qualities of these habitats appear to be relatively short vegetation and a soil that is not too dry and hard for probing. In general, the nesting areas themselves were little used for feeding. There appears to be a consistent avoidance of the nest area (Chapter

4.I) possibly to reduce nest predation rates.

Well drained, "good" blackland pasture (17% of feeding records), was of particular importance especially early on in the season when the grass was short. Later on, unless heavily grazed, the grass grows too tall and, in some places, the soil may become too dry. At Stilligarry and West Gerinish most of this pasture type was fenced off and grown on for hay. Marsh habitats combined account for a further 16% of feeding records at the northern sites. Flat damp marsh was especially important probably because the vegetation generally remains short late into the season and because little use was made of this habitat for nesting; wet marsh tends to have taller vegetation and hummock marsh is an important nesting habitat. The areas of poorly drained "unimproved" blackland pasture, rough blackland pasture and old damp fallow machair were sometimes used for feeding though not as much as might be expected considering the large areas of these habitats present. This is may be because of inferior food resources in these habitats. At Rubha Ardvule, only 14% of feeding records were from grassland habitats, the most important of which were old fallow and marsh. At all study-sites, very dry habitats, such as first and second year fallow machair, bare plough, cereals, reseeded machair, dune sward and tracks, and habitats with tall cover such as Iris, Juncus, hay and tall cereals were used only rarely for feeding.

ii) Use of shoreline feeding habitats

Freshwater margins in the form of loch-edges, pool-edges and ditches were a very important feeding habitat; at the northern

study-sites they form 44% of feeding records and 21% at Rubha Ardvule. Redshank feeding in ditches are easily overlooked because they are often hidden from view by banks. The recorded frequency of ditch use at the northern study-sites (there are no ditches at Rubha Ardvule) is therefore almost certainly an under representation of their actual use. It is likely that ditches and loch edges (where suitable) have approximately equal value as feeding habitats when compared on a length for length basis. The comparatively low frequency of pool-edge records is mainly due to the transitory nature of the pools and their comparative scarcity. When flood pools were present they were much favoured by feeding Redshank and this habitat is probably of equal, if not greater, intrinsic value than loch-edges and ditches. Redshanks feeding along freshwater margins either wade in the water, often to the tops of their legs, submerging their head to feed off the bottom, or, they forage on soft mud, wet turf and sand at or close to the water's-edge.

The major difference in the choice of feeding habitat between Rubha Ardvule and the northern study-sites was in the use made of the seashore. At Rubha Ardvule, 63% of all feeding records were from the seashore. On the seashore, Redshank fed mainly at the tide-edge on rocky areas and on shingle beaches. The rocky areas used were mainly covered with seaweeds (especially *Fucus vesiculosus*) and had many shallow rock pools. The favoured parts of the shingle beaches were along the tide edge where there was wrack and detritus, and higher up the beach on heaps of rotting wrack left along the strand lines.

In marked contrast to Rubha Ardvule, at the northern

study-sites the seashore was used extremely rarely for feeding; all records were either early or late in the season and involved newly arrived or departing birds. The reason for the difference between the levels of use of seashore habitats lies in the distance from the nesting grounds to suitable seashore habitats. The seashore flanking the northern study-sites is a sandy beach, the nearest rocky shore was at least 2 km away. The very extensive areas of sandy beach at both Rubha Ardvule and all along the northern study-sites were used extremely rarely and are of no importance to breeding Redshank. The habit of using the seashore for feeding by breeding Redshank in the Southern Isles is not confined to Rubha Ardvule. There are several other rocky shore areas along the west coast all of which are commonly used by Redshank during the breeding season (*pers. obs.*), presumably these are birds nesting nearby. However, for the majority of the Redshank population in the Southern Isles the seashore is of negligible importance during the breeding season..

iii) Seasonal variation in the use of feeding habitats

The account given above of the habitats used for feeding by adult breeding Redshank does not consider whether the habitat preference changes through the breeding season. To look at this aspect of habitat use the feeding records have been aggregated into stages through the breeding season and the habitats have been grouped, where necessary, to increase sample sizes. At the northern study-sites, the breeding season is divided into the following stages: pre-laying period, incubation period (includes laying period) and chick rearing period. At Rubha Ardvule, there

are very few feeding observations in the chick rearing stage, the records are therefore aggregated into two stages only: pre-laying and post-laying . For the northern study-sites, the habitats have been aggregated into five categories: dry pasture, damp pasture, marsh, freshwater margins and nesting habitats... At Rubha Ardvule, the habitats are grouped into three categories: seashore, freshwater margins and "pasture" (all other habitats). Each habitat category contains habitat types that are similar, both in nature and in value for feeding. The results are presented in Tables 3.2 and 3.3 for the northern study-sites and Rubha Ardvule respectively. There is no evidence to suggest that the relative detectability of birds in different habitats changed markedly through the breeding season and therefore the observed seasonal variations in habitat use are believed to be genuine.

For the northern study-sites, there is a highly significant difference in the proportional usage of the various habitat categories between the pre-laying stage and the incubation stage ($\text{Chi}^2 = 41, 4 \text{ d.f.}, P < 0.001$). The most important change is a large decrease in the use of freshwater margins (from 54% to 34%) and a corresponding increase in the use of pastures. The increase in the use of pastures was not uniform across the three pasture categories; the percentage increase was largest for dry pasture and smallest for wet pasture. The differences between the incubation stage and the chick rearing stage are not significant ($\text{Chi}^2 = 2.4, 4 \text{ d. f.}, P > 0.5$).

A Chi^2 test comparing the pre-laying and post-laying periods at Rubha Ardvule shows no significant difference in the proportions that the habitat categories were used ($\text{Chi}^2 = 4.9, 2$

Table 3.2: Seasonal usage of feeding habitats by adult Redshank at the northern study-sites.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS			ROW TOTAL
	PRE-LAY STAGE (1)	INCUBT STAGE (2)	CHICK STAGE (3)	
Dry pasture (B,F,S,P,Q,C,V)	15 3.8%	29 11.9%	5 10.0%	49 7.2%
Damp pasture (E,W,H,G)	65 16.6%	67 27.6%	19 38.0%	151 22.1%
Marsh (M,N)	57 14.6%	40 16.5%	6 12.0%	103 15.1%
Nesting habitats (J,I,K,O,R)	42 10.7%	31 12.8%	6 12.0%	79 11.5%
Freshwater margins (D,L,Z)	212 54.2%	76 31.3%	14 28.0%	302 44.2%
Total %	391 57.2%	243 35.5%	50 7.3%	684 100%

Stage 1 vs. 2 $\text{Chi}^2 = 41.0$, 4 d.f., $P < 0.001$ SIGNIFICANT

Stage 1 vs. 3 $\text{Chi}^2 = 20.6$, 4 d.f., $P < 0.001$ SIGNIFICANT

Stage 2 vs. 3 $\text{Chi}^2 = 2.36$, 4 d.f., $P > 0.05$ NOT SIGNIFICANT

For details of habitat codes see Appendix A

Table 3.3: Seasonal usage of feeding habitats by adult Redshank at Rubha Ardvule.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS		
	PRE-LAY STAGE	INCUBT & CHICK STAGES	ROW TOTAL
Pasture (B,E,U,F,S,M,I,J,K)	15 11.0%	14 22.6%	29 14.6%
Seashore (X)	89 65.4%	33 53.2%	122 61.6%
Freshwater margins (L,Z)	32 23.5%	15 24.2%	47 23.7%
Total %	136 68.7%	62 31.3%	198 100%

Chi² = 4.9, 2 d.f., P > 0.05 NOT SIGNIFICANT

For details of habitat codes see Appendix A

d.f., $P > 0.05$). However, there is a significant trend to feed less on the seashore and more on pasture habitats after laying ($\text{Chi}^2 = 4.9$, 1 d.f., $P < 0.05$).

The changes in habitat choice were probably caused by a general shift in food selection from probing in wet places for sub-surface invertebrates to surface pecking for surface active invertebrates on pasture. The shift is probably in response to an increase in the abundance and activity of surface active invertebrates resulting in more profitable feeding conditions. Baines (1988a) working on upland grasslands in northern England found that the total number of invertebrates caught in pitfall-traps increased from April to June and, Williams (1959) showed that carabid beetle activity increased from March to July.

Habitats usage by Redshank for chick-rearing

1) Habitats used for chick-rearing

Redshank chicks are usually led from the nest a few hours after hatching to suitable feeding grounds. Redshank families frequently cover comparatively large distances during the chick rearing stage often visiting several areas with different or similar habitat types each day (Walker & Chandler 1985, Chapter 4). The chicks themselves are normally very difficult to observe because they are obscured from view by vegetation, however the adults with broods are extremely obvious; they stand on guard nearby, often on a raised object such as a fence post, boulder or mound. From the adults' behaviour, it is therefore usually apparent as to where the chicks are feeding and, because of this,

differences in detectability between habitats are thought to be negligible.

Marsh habitats, especially wet marsh were the most frequently used for chick rearing at the northern study-sites, together they account for 41% of records. Redshank chicks must have some form of cover in which to hide when danger threatens. Marshes were especially valuable because they usually have rather uneven and coarse vegetation, often with hummocks and tussocks, that give chicks good hiding opportunities. In general, Redshank chicks either use areas where the vegetation is quite tall and coarse such as wet marshes or composed of short vegetation suitable for feeding, such as damp marsh, together with patches of taller vegetation that can be used for hiding. Two species of plant, Yellow Flag Iris (*Iris pseudacorus*) and Soft Rush (*Juncus effusus*) are of considerable importance for providing cover for Redshank chicks in the Uists. At Rubha Ardvule, 59% of records were from Iris or Juncus and at the northern study-sites, 18% of records were from these habitats, (excluding ditches which were frequently flanked by these plants). Ditches are a very important chick rearing habitat, particularly if they have tall vegetation along the banks and marsh vegetation and mud in the bottom. Ditches with predominantly short vegetation on the banks or with deep water are of little value (this type of ditch was however uncommon on the study-sites). The recorded frequency of ditch usage is not considered to be an under-representation because of the high detectability of the adult birds at this stage.

Use is also made for chick rearing of areas with no tall vegetation but where the ground has been puddled by cattle

leaving a pocked and broken surface. This provides a multitude of depressions for chicks to hide in. Such a surface invariably only forms on wet soils (especially damp marsh) where there is a high concentration of cattle. In general, the sward of good blackland pasture and fallow machair is short and even and provides insufficient cover for Redshank chicks, however these habitats were used where good cover was sufficiently close (e.g. nearby *Juncus* clumps and *Iris* beds) or where the surface was broken. Loch edges were used only occasionally, nearly all the records of loch edge use were from Loch Bee at the West Gerinish study-site where the broken-up muddy areas between the undercut banks of the shore and small islands provided excellent hiding opportunities.

The extent to which Redshank chick rearing habitats need to be wet or damp is unclear. That most of the chick rearing takes place in damp and wet habitats may be a consequence of these habitats having superior cover rather than better food supplies, there is certainly a general paucity of suitable cover on most of the dryer habitats. Many late Redshank broods were reared almost entirely in growing cereal crops which have a dry substrate. However, some of these broods were known to make occasional visits to adjacent wet and damp habitats.

Hay fields were used surprisingly little (4% of records) considering that they have excellent cover and a damp soil. Compared to marsh vegetation, *Iris* beds and cereals (where the plants are in distinct drill rows), the vegetation of hay fields is much thicker and this may impede the mobility of the chicks especially late in the season. Despite the very dense growth

form of *Juncus*, chick mobility in *Juncus* pasture is not seriously impeded because the clumped arrangement of the rushes with shorter grassland in between allows the chicks to move through the habitat easily.

At Rubha Ardvule, occasional use was made of rocky seashore habitat by Redshank chicks, in all cases the chicks were large.

ii) Temporal changes in the use of chick-rearing habitats.

As chicks grow their requirements in terms of food and cover are likely to change. To investigate the influence of chick age upon habitat requirements in Redshank, the chick rearing period has been divided into three periods and the habitat use in each period compared. The three periods are: first week, second week and post-second week of the chick rearing stage. The habitats have been aggregated into six categories: dry pasture, damp pasture, marsh, *Juncus* and *Iris*, ditches and loch-edges, and cereals. Each habitat category contains habitat types that are similar in their nature and chick rearing value. The results for the northern study-sites are summarised in Table 3.4. Due to the smaller amount of observer effort expended at Rubha Ardvule, there are too few records to investigate the seasonal variation in the use of chick-rearing habitats at this site.

At the northern study-sites there is a highly significant difference in the proportional usage of the various chick rearing habitats between each of the three chick rearing periods (Table 3.4). The main changes in habitat usage through the chick rearing stage were as follows:

Table 3.4: Seasonal usage of chick-rearing habitats by Redshank at the northern study-sites.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS			
	WEEK 1	WEEK 2	POST WEEK 2	ROW TOTAL
Dry pasture (B,V,F,S)	3 1.5%	2 1.0%	8 3.5%	13 2.1%
Damp pasture (E,W)	26 12.9%	10 5.2%	25 10.8%	61 9.8%
Marsh (M,N,O)	91 45.0%	93 48.4%	85 36.8%	269 43.0%
Freshwater margins (D,L,Z)	24 11.9%	32 16.7%	56 24.2%	112 17.9%
Juncus and Iris (I,J,K)	56 27.7%	42 21.9%	46 19.9%	144 23.0%
Cereals (C,Q)	2 1.0%	13 6.8%	11 4.8%	26 4.2%
Total %	202 32.3%	192 30.7%	231 37.0%	625 100%

WEEK 1 vs. 2 $\text{Chi}^2 = 18.2$, 4 d.f., $P < 0.01$ SIGNIFICANT
(Dry pasture excluded)

WEEK 1 vs. 2 $\text{Chi}^2 = 20.7$, 5 d.f., $P < 0.001$ SIGNIFICANT

WEEK 2 vs. 2+ $\text{Chi}^2 = 13.8$, 5 d.f., $P < 0.05$ SIGNIFICANT
(1 of 12 expected values < 5 (4.5))

For details of habitat codes see Appendix A

- i) A steady increase in the use of ditches (and loch edges at West Gerinish) from 12% of records in the first week to 24% after the second week.
- ii) A small decrease in the use of Juncus and Iris after the first week from 28% to 22% of records.
- iii) A small decrease in the use of marshes after the second week from 47% in the first two weeks to 37% of records.
- iv) An increase in the use of cereals after the first week from 1% to about 6% of records after the first week.

The reason for these differences may be partly due to a general drift away from the habitats close to nesting areas (Chapter 5), such as marshes and Juncus pasture, to dryer areas such as cereal fields. It is not clear why ditches become so important later on, one possible explanation is that late in the season marshes often start to dry out while ditch bottoms remain wet.

Habitats used by Redshank for comfort activities

Adult Redshank spend a small part of their time preening, bathing and roosting. By far the most important habitat for these activities were loch-edges, which account for 59% of all records and include all the records of actual bathing. The permanent presence of some clean, standing freshwater near to the breeding area may be very important for Redshank. The rest of the records of comfort activities refer to preening or roosting birds and were mainly from the damp grassland habitats that were favoured for feeding.

Summary of Redshank habitat choice

The most important habitats for Redshank breeding in the Southern Isles are blackland pastures and marshes. The areas of cultivated machair, although used a little, are of little overall importance.

During the breeding season adult Redshank feed in two principal habitat types: freshwater margins (loch-edges, pasture and old fallow). "Good" blackland pasture with a short sward is a particularly valuable feeding habitat. Habitats with tall vegetation (*Juncus* pasture, *Iris* beds, hay and cereals) are of negligible value as feeding habitats for adult Redshank. There is a significant difference in the proportional usage of different feeding habitats between the pre-laying stage and the incubation stage; this is due to a shift from freshwater margin habitats to pasture and marsh habitats. There is no significant difference in the proportional use of the feeding habitats between the incubation and chick rearing stages.

At sites where areas of suitable rocky seashore occur in close proximity (>1 km) to the breeding grounds, such as at Rubha Ardvule, the adult Redshank feed extensively within rocky parts of the littoral zone. For the majority of Redshank breeding in the Southern Isles the seashore is of negligible importance.

Redshank chicks are reared in habitats that can provide them with adequate cover to hide in, this can be in the form of tall vegetation (especially *Juncus effusus*, *Iris pseudacorus* and wet marsh) or broken ground. Although most of the chick rearing habitats are in damp or wet places it is not clear whether the soil wetness is important in some other way besides promoting the

development of suitable cover; cereal fields which are generally very dry are used commonly in some places. The proportional use of the various habitats used for chick rearing between weeks 1 and 2, and between week 2 and post week 2, of chick rearing are significantly different. The main change in habitat use as the chicks get older is an increase in the use of ditches and cereal fields and a decrease in the use of marshes and *Juncus* pasture. Despite its apparent suitability, the tall vegetation of maturing hay fields is used little by Redshank chicks. It is thought that this may be because the very thick vegetation impedes chick mobility.

Redshank ground displays take place both on the feeding and nesting areas on all types of open habitats. Besides their importance for feeding, loch-edges are also used for bathing and preening by adult and juvenile Redshank.

This study did not cover the whole range of habitats used by breeding Redshank in the Southern Isles, a small proportion of the population breed on the blackland-moorland fringe, improved moorland (Pienkowski *et al.* 1986, Chandler and Walker 1985) and on saltmarsh (Fuller *et al.* 1986).

CHAPTER 3: SECTION II

HABITATS USED BY DUNLIN FOR BREEDING ACTIVITIES

Data on habitat usage by breeding Dunlin were collected from two study-sites, Stilligarry and Drimore Farm. The habitat usage at the two sites was very different and therefore the two sites are treated separately. The proportion of records in each behaviour category at the two sites is shown in Table 3.5.

The proportion of records in each behaviour category is similar at both study-sites. The higher breeding success at Drimore Farm (Chapter 8) explains the greater proportion of records in the chick-rearing stage at this site.

The habitats used for each behaviour type are tabulated in Appendices D and E; habitats with less than two records have been excluded from these tables. The main details of these appendices are illustrated using barcharts in Figures 3.3 and 3.4.

Gross habitat use by Dunlin

Figures 3.3 and 3.4 show that in the Southern Isles Dunlin are largely restricted to machair habitats, especially the damper ones, and the adjacent marshes. Many habitats types are of little or no value to Dunlin, these are: all types of blackland pasture, all habitats with tall vegetation (Juncus pasture, Iris beds, hay, and tall cereals) and ditches.

Habitats used for display and courtship by Dunlin

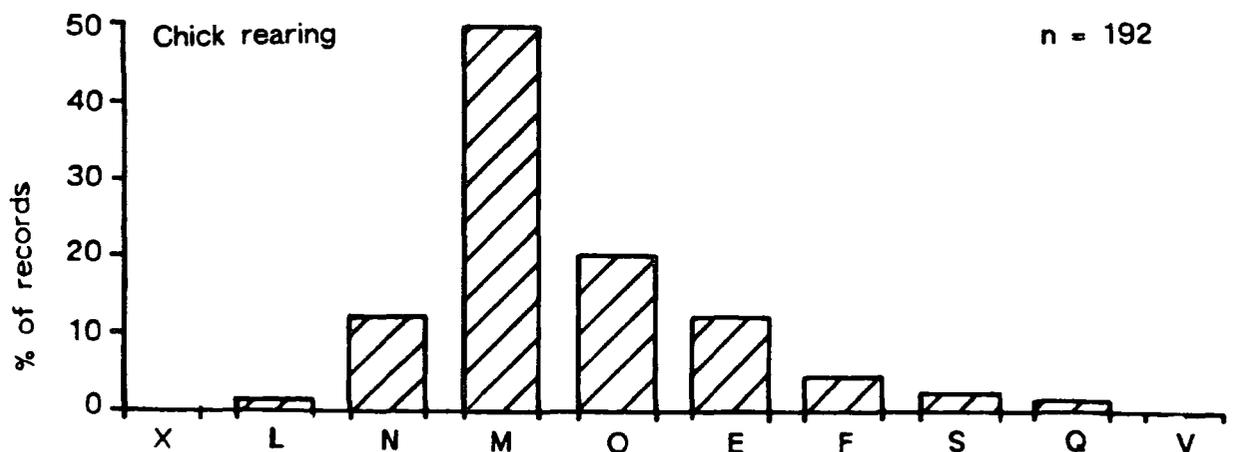
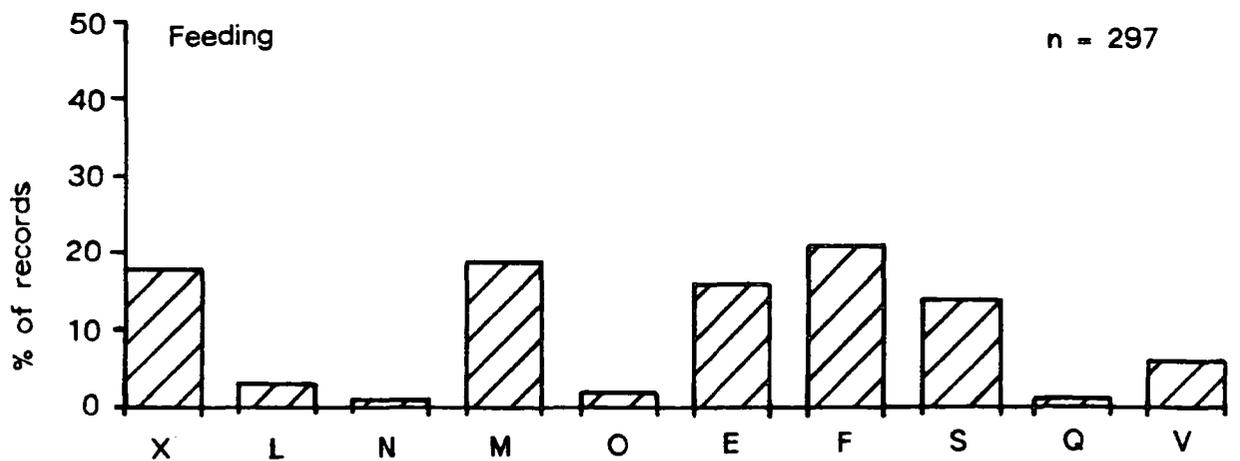
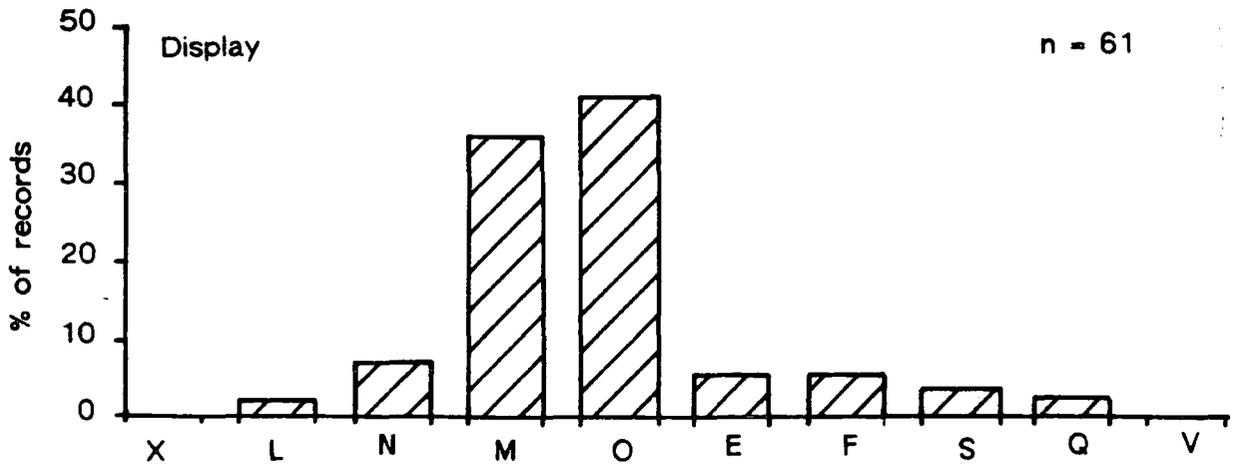
Male Dunlin display almost exclusively over and on their nesting territories (*pers obs.*). The difference in the use of habitats for display between the two sites is entirely due to

Table 3.5: Dunlin: Number of records in each behaviour category at each study-site.

STUDY-SITE	NUMBER OF RECORDS ¹				ROW TOTAL
	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	
Stilligarry	55 12.6%	254 58.1%	117 26.8%	11 2.5%	437 43.2%
Drimore Farm	61 10.6%	297 51.7%	192 33.4%	25 4.3%	575 56.8%
Total	116 %	551 54.4%	309 30.5%	36 3.6%	1012 100%

¹This table is included to show the amount of data available for use in the subsequent analyses from each study-site for each behaviour type . It is not possible to use this information to show time-budgets for each activity, either between or within sites, because the effort spent in obtaining observations was not equally spread temporally at all sites, and the detectability of the birds varied according the behaviour type.

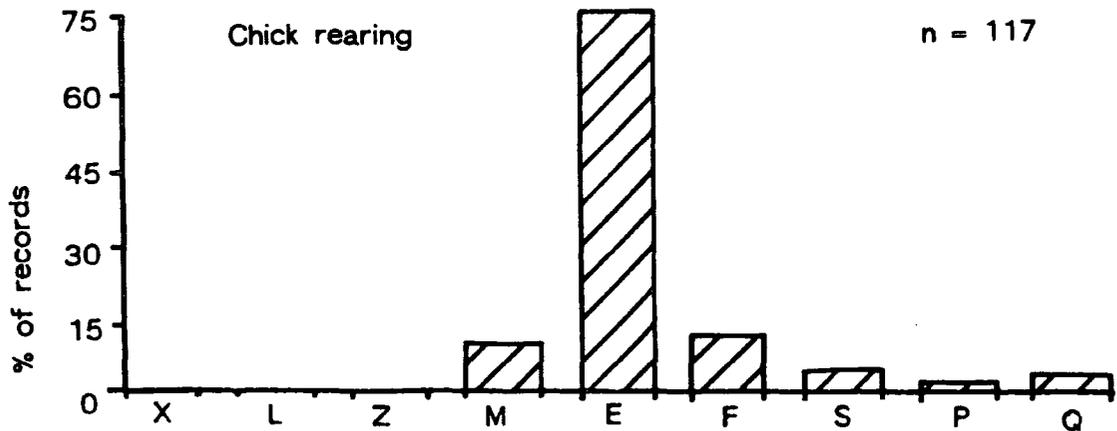
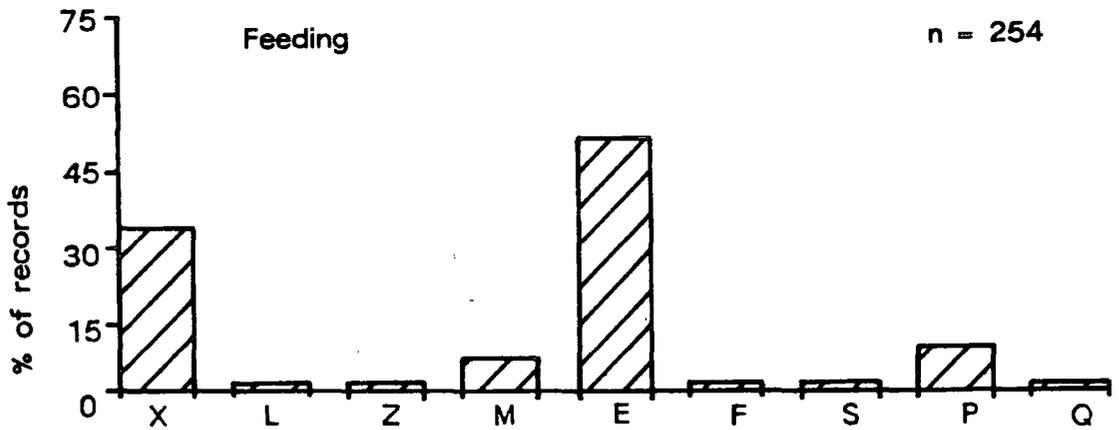
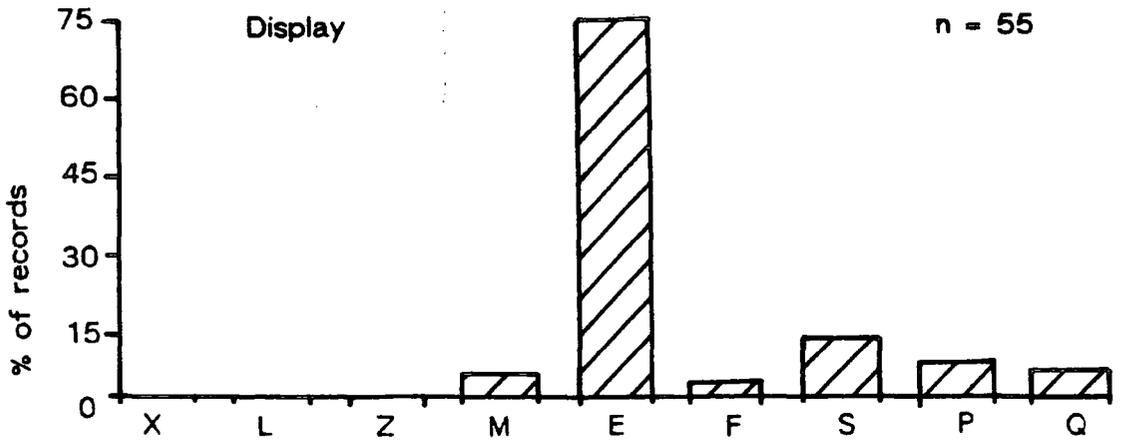
Figure 3.3: Percentage of records from Drimore Farm of adult Dunlin from each habitat for three types of behaviour.



- | | |
|--------------------|--------------------|
| X = Seashore | F = 1st year fall. |
| L = Loch-edge | S = 2nd year fall. |
| N = Wet marsh | P = Plough |
| M = Damp marsh | Q = Short cereal |
| O = Hummock marsh | V = Reseeded mach. |
| E = Old damp fall. | |

Habitats with < 2% of all records are excluded.

Figure 3.4: Percentage of records from Stilligarry of adult Dunlin from each habitat for three types of behaviour.



- | | |
|--------------------|--------------------|
| X = Seashore | F = 1st year fall. |
| L = Loch-edge | S = 2nd year fall. |
| Z = Pool-edge | P = Plough |
| M = Damp marsh | Q = Short cereal |
| E = Old damp fall. | |

Habitats with < 2% of all records are excluded.

the differences in the habitats used for nesting. At Stilligarry nearly all the records of displaying Dunlin were on old fallow whereas at Drimore they were nearly all from marsh habitats, especially hummock marsh. The proportion of display records from each habitat closely reflects the the proportional use of each habitat for nesting (see Figure 5.1). Occasionally Dunlin displayed from habitat unsuitable for nesting, such as plough, but in these cases suitable nesting habitat was always nearby (<50 metres away).

Habitats used for feeding by Dunlin

1) Major seasonal variations

In the breeding season adult Dunlin fed mainly in areas with a short sward and damp soil; the most important habitats were damp marsh, old fallow and recent fallow. They also used the seashore.

Before discussing the usage of the feeding habitats in greater detail it is helpful to consider any major seasonal variations. To investigate the seasonal variation in feeding habitat usage the records for each stage of the breeding season are compared. The habitats have been aggregated into categories each containing similar habitats for the site concerned. The results are given in Tables 3.6 and 3.7. From the results in these tables, it is clear that for both sites there was one major change in habitat usage during the season, viz a large increase in the use of the seashore as the season progresses. Chi^2 tests for heterogeneity show that at Drimore Farm (Table 3.7) there was no significant difference in the proportional use of habitat

Table 3.6: Seasonal usage of feeding habitats by adult Dunlin at Stilligarry.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS				ROW TOTAL
	PRE-LAY STAGE	INCUBT STAGE	CHICK STAGE	AFTER STAGE	
	(1)	(2)	(3)	(4)	
Seashore (X)	5 6.2%	9 14.8%	7 46.7%	54 83.1%	75 33.8%
Wet habitats (L,M,Z)	15 18.5%	4 6.6%	0 0.0%	0 0.0%	19 8.6%
Old fallow mach. (E,B)	52 64.2%	39 63.9%	5 33.3%	5 7.7%	101 45.5%
Dry machair (F,S,P,Q)	9 11.1%	9 14.8%	3 20.0%	6 9.2%	27 12.2%
Total %	81 36.5%	61 27.5%	15 6.8%	65 29.3%	222 100%

Stage 1 vs. 2 $\text{Chi}^2 = 6.68$, 3 d.f., $P > .05$ NOT SIGNIFICANT

Stage 1 vs. 3 $\text{Chi}^2 = 15.5$, 1 d.f., $P > 0.01$ SIGNIFICANT
(all terrestrial habitats grouped, 1 expt. value < 5)

Stage 1 vs. 4 $\text{Chi}^2 = 94.4$, 3 d.f., $P < .0001$ SIGNIFICANT

Stage 2 vs. 3 $\text{Chi}^2 = 4.89$, 1 d.f. (Y), $P < .05$ SIGNIFICANT
(All terrestrial habitats grouped, 1 expt. value < 5)

Stage 2 vs. 4 $\text{Chi}^2 = 58.7$, 2 d.f., $P < .0001$ SIGNIFICANT
(Wet habitats excluded)

Stage 3 vs. 4 $\text{Chi}^2 = 7.02$, 1 d.f. (Y), $P < .001$ SIGNIFICANT
(All terrestrial habitats grouped, 1 expt. value < 5)

Stage 1 vs. 2+3 $\text{Chi}^2 = 13.1$, 3 d.f., $P < .005$ SIGNIFICANT

(Y) = YATES CORRECTION APPLIED

Table 3.7: Seasonal usage of feeding habitats by adult Dunlin at Drimore Farm.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS				ROW TOTAL
	PRELAY STAGE	INCUBT STAGE	CHICK STAGE	AFTER STAGE	
Seashore (X)	0 0.0%	2 3.2%	0 0.0%	46 48.4%	48 22.0%
Wet habitats (L,Z,N,M,O)	8 23.5%	28 44.4%	5 19.2%	12 12.6%	53 24.3%
Old fallow mach. (E,W)	7 20.6%	12 19.0%	7 26.9%	12 12.6%	38 17.4%
Dry machair (B,F,S,V)	19 55.9%	21 33.3%	14 53.8%	25 26.3%	79 36.2%
Total %	34 15.6%	63 28.9%	26 11.9%	95 43.6%	218 100%

Stage 1 vs. 2 $\text{Chi}^2 = 5.28$, 3 d.f., $P > 0.05$ NOT SIGNIFICANT
(Excludes seashore)

Stage 1 vs. 3 $\text{Chi}^2 = 0.39$, 2 d.f., $P > 0.05$ NOT SIGNIFICANT
(Excludes seashore)

Stage 1 vs. 4 $\text{Chi}^2 = 25.9$, 3 d.f., $P < 0.001$ SIGNIFICANT

Stage 2 vs. 3 $\text{Chi}^2 = 5.56$, 2 d.f., $P > 0.05$ NOT SIGNIFICANT
(Excludes seashore)

Stage 2 vs. 4 $\text{Chi}^2 = 42.3$, 3 d.f., $P < 0.001$ SIGNIFICANT

Stage 3 vs. 4 $\text{Chi}^2 = 20.7$, 3 d.f., $P < .0001$ SIGNIFICANT
(minimum expected value = 3.65, 2 expected values of 8 < 5)

categories between the pre-laying, incubation or chick rearing periods yet each of these stages is significantly different ($P < 0.001$) from the post-breeding stage. At Stilligarry, use of the seashore started earlier (Figure 3.3), there were several records of birds still with unfledged chicks on the machair visiting the shore to feed. The difference in the usage of the feeding habitats during the pre-laying period and the incubation period at Stilligarry is not significant. The low number of feeding records from the chick rearing period at Stilligarry necessitates further aggregation of the habitats for the Chi^2 tests involving this stage. The differences between all other pairs of stages at Stilligarry are significant (Table 3.6). It is the difference in seashore use between the stages that is the most important change.

ii) Use of terrestrial habitats by feeding Dunlin

At Stilligarry, there are few records of feeding adults from the chick-rearing and post-breeding stages and consequently the sample sizes for most categories are too small to use statistical significance tests. There appears to be a seasonal pattern involving a reduction in the use of wet habitats and a corresponding increase in the use of dry machair as the season progresses. If these differences are real they are probably caused by changes in the condition and availability of the habitats; the exact nature of the habitats is constantly changing, particularly through vegetation growth and variation in the soil moisture. The drier machair may be favoured more later on because the vegetation remains shorter. A meaningful Chi^2 test is possible between the pre-laying and incubation stages;

the result is not significant ($\text{Chi}^2 = 3.86$, 2 d.f., $P > 0.05$). At Drimore Farm the sample sizes are larger and it is apparent that there are no significant differences in the proportional use of terrestrial feeding habitats between the stages.

At Stilligarry, old damp fallow (49% of all feeding records) was by far the most important feeding habitat for most of the breeding season. Plough habitats (9% of the records) and, considering the small amount present, damp marsh (6%) were also important feeding habitats. Surprisingly, recent fallow was used very little (2%) at Stilligarry despite the appreciable areas present. This contrasts to the situation at Drimore Farm where recent fallow was the most important feeding habitat accounting for 35% of the records. The reason for this difference probably lies in the dampness of the ground. At Stilligarry the areas of recent fallow tended to be far drier than those at Drimore Farm, where much of the recent fallow was prone to flooding, especially early in the season, and the soil then remained moist for the rest of the season. Damp marsh (19% of records) and old fallow (16%) were the other two very important feeding habitats at Drimore Farm. Wet marsh and hummock marsh were little used for feeding, possibly because the vegetation is too tall. During the incubation and chick-rearing stages usually only one adult tends the nest or young, the off-duty bird normally leaves the territory to visit feeding and loafing areas up to 1 km away (Chapter 4). The reason why hummock marsh was so little used for feeding despite its apparent suitability (it generally has a short damp sward) may be because the birds were actively avoiding the nesting and chick-rearing areas as a means of reducing the

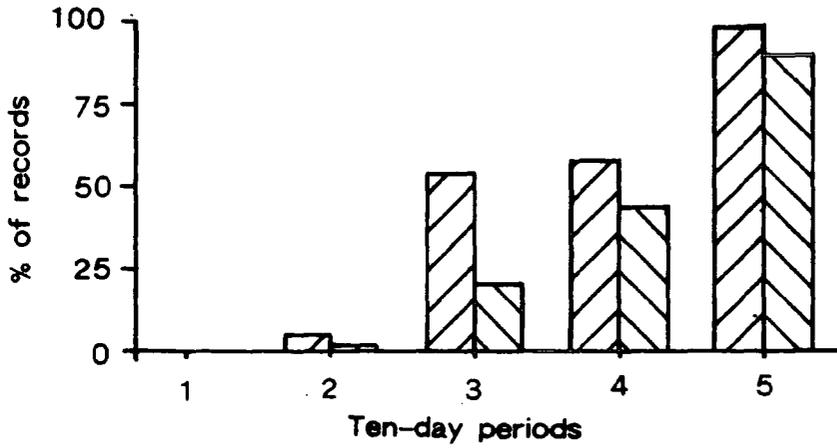
chances of attracting nest predators or, but perhaps less likely, to reduce depletion of food reserves in the chick-rearing areas.

iii) Use of shore-line habitats by feeding Dunlin

At both sites loch-edge and pool-edges were occasionally used for feeding (3% of all feeding records). When using freshwater margins exposed or shallowly covered areas of mud or wet sward were selected. At The West Gerinish study-site, quite large areas of mud become available whenever the water level of Loch Bee recedes, usually towards the end of the breeding season. When this happened, the mud was used by many Dunlin from nearby nesting areas and later by juvenile birds also. For the nationally important concentration of Dunlin breeding on the marshy machair along the west shore of Loch Bee (Fuller *et al.* 1986) the loch-edge is probably a far more important feeding habitat than it is at Stilligarry or Drimore Farm.

The seashore was used as a feeding habitat only towards the end of the breeding season when it was of considerable importance. The increase in the use of the seashore was mainly governed by date rather than stage of breeding; all the records of birds at Stilligarry using the seashore during the incubation and chick rearing stages were late in the season and involved replacement nests. Figure 3.5 illustrates the percentage of feeding records from the seashore for ten day periods at the end of the breeding season for the two study-sites. It clearly shows that there was a shift to seashore feeding starting in mid June and rapidly increasing so that by early July almost all feeding takes place on the seashore.

Figure 3.5: Percentage of Dunlin feeding records from the seashore during the final part of the breeding season divided into ten-day periods.



= Stilligarry



= Drimore Farm

1 = 31/5 - 9/6 (ST n = 15, DF n = 104)
 2 = 10/6 - 19/6 (ST n = 97, DF n = 82)
 3 = 20/6 - 29/6 (ST n = 82, DF n = 200)
 4 = 30/6 - 9/7 (ST n = 77, DF n = 119)
 5 = 10/7 - 19/7 (ST n = 37, DF n = 41)

The proportion of seashore feeding records in the post-breeding stage (see Tables 3.6 and 3.7) is significantly greater at Stilligarry (83%) than at Drimore Farm (48%) ($\text{Chi}^2 = 17.2$, 1 d.f., $P < 0.01$). The shift towards seashore feeding late in the season at the two sites is illustrated in Figure 3.5 using the percentage of feeding records from the seashore in ten-day periods. From Figure 3.5, it appears that the difference in seashore use between the two sites was caused by a time lag, the Drimore Farm birds generally not using the shore until later in the year. Two contributory factors may explain the difference in the level of seashore use between the two sites. Firstly, the height of the machair vegetation was considerably greater at Stilligarry late on in the season than at Drimore Farm because only the latter was grazed through the summer. Most of the machair vegetation at Stilligarry was therefore too tall for adult Dunlin to feed in after late June whereas at Drimore Farm this was not so. Secondly, the distance to the nearest suitable seashore feeding site was approximately twice as far for the birds from Drimore Farm. Birds from both sites used the same areas of seashore for feeding; this was approximately 1.2 km from Stilligarry and 2.2 km from Drimore Farm (see Chapter 4.II)

On the seashore Dunlin fed on areas of intertidal sand and amongst rotting seaweed left along the strand line. Only certain areas of intertidal sand were used, these were in general the same areas used by Ringed Plover. The proximate factor controlling the areas of sandy shore selected for feeding is almost undoubtedly the food resource. However, the ultimate factor is thought to be the supply of nutrients from rotting

seaweed released into the sand from higher up the beach which presumably form the basis of the food chain. The seaweed nearly always accumulates in the same parts of a beach (*pers. obs.*) and so the distribution of the birds' invertebrate food along a beach is very localised. Dunlin also occasionally fed amongst seaweed covered boulders and cobbles.

Habitats used for chick-rearing by Dunlin

1) Comparison of Drimore Farm and Stilligarry

The results in Figures 3.3 and 3.4 show that old fallow and marsh habitats were by far the most important habitats used for chick rearing. At Stilligarry, the emphasis was on old fallow (76% of records), this was also the main nesting habitat at this site. At Drimore Farm, marsh habitats were the most important and together make up 81% of the chick-rearing records there. This marked difference between the two study-sites reflects the relative amounts of habitat available and the nesting habitats (see Chapter 5). Dunlin chicks are usually reared in the immediate vicinity of the nest; rarely do they move more than 250 metres from the nest site (Chapter 4).

To look at changes in habitat usage through the chick-rearing stage the frequency of usage of the habitats during the first week, second week and third week of chick rearing are compared. The habitats have been aggregated into categories each containing similar habitats for the site concerned. Because of the small sample sizes, the records from Stilligarry are aggregated into two habitat groups only: old fallow and all other habitats. The results are given in Tables 3.8 and 3.9.

Table 3.8: Seasonal usage of Dunlin chick rearing habitats at Stilligarry

HABITAT CATEGORY (HABITATS)	N U M B E R O F R E C O R D S		ROW TOTAL
	A g e o f b r o o d WEEK 1	WEEKS 2 & 3	
Closed sward (B,E,M)	64 91.4%	21 55.3%	85 78.7%
Open sward (F,S,P,Q)	6 8.6%	17 44.7%	23 21.3%
Total %	70 64.8%	38 35.2%	108 100%

Chi² = 17.1, 1 d.f., P <.001 SIGNIFICANT Yates correction used

Table 3.9: Seasonal usage of Dunlin chick-rearing habitats at Drimore Farm.

HABITAT CATEGORY (HABITATS)	N U M B E R O F R E C O R D S			ROW TOTAL
	A g e o f b r o o d WEEK 1	WEEK 2	WEEK 3	
Wet marsh & Loch-edge (N,L)	7 10.6%	8 14.5%	8 16.0%	23 13.5%
Damp marsh (M,O)	45 68.2%	40 72.7%	35 70.0%	120 70.2%
Machair (all types) (B,E,F,S,V)	14 21.2%	7 12.7%	7 14.0%	28 16.4%
Total %	66 38.6%	55 32.2%	50 29.2%	171 100%

Week 1 vs. 2 Chi² = 1.7, 2 d.f., P >0.05 NOT SIGNIFICANT

Week 1 vs. 3 Chi² = 1.5, 2 d.f., P >0.05 NOT SIGNIFICANT

Week 2 vs. 3 Chi² = 0.1, 2 d.f., P >0.05 NOT SIGNIFICANT

For details of habitat codes see Appendix A

For Drimore Farm (Table 3.9), there was no significant difference in habitat use through the chick rearing period ($\text{Chi}^2 = 2.3$, 4 d.f., $P > 0.05$). At Stilligarry (Table 3.8), there was a highly significant difference in the use of the two habitat groups between the first week and the following two weeks ($\text{Chi}^2 = 17.1$, 1 d.f., $P < 0.01$). The cause of this difference is mainly due to an increase in the proportion of records from marsh habitats after the first week. However, this is not thought to represent a shift in habitat selection but is probably a consequence of greater chick survival in the marsh habitats (Chapter 8).

ii) Habitat requirements of Dunlin during chick-rearing

Dunlin chicks require a certain amount of cover to conceal themselves when danger threatens. Their small size combined with excellent camouflage means that they can hide effectively in only moderately tall vegetation or lightly broken ground. In fact, Dunlin chicks did not use areas with tall vegetation or very broken ground, possibly because the parents could not effectively watch the chicks in such habitats or because these habitats present too many physical obstacles to the movement of small chicks. The type of cover required by Dunlin chicks contrasts markedly to that required by Redshank chicks (this chapter, Section I). The areas used for chick rearing usually had taller and coarser vegetation than the areas preferred by the adults for feeding which have a short, even sward. Two species of plant, namely Silverweed (*Potentilla anserina*) on old damp fallow and Baltic Rush (*Juncus balticus*) on damp marsh and hummock marsh,

appeared to be good indicators of suitable chick rearing areas. The differences in the recorded levels of use of the three types of marsh habitat at Drimore Farm was largely caused by the amount of habitat available; damp marsh covers larger areas than the other two types combined. The intrinsic value of each of the marsh types for chick-rearing is therefore approximately equal. From the results at Stilligarry, it is clear that Dunlin chicks do not have an obligate requirement for marsh, but marsh is almost certainly a superior habitat to dry, fallow grassland for two reasons. Firstly, at Drimore Farm a large marsh used by many Dunlin for chick rearing was flanked by an area of old fallow yet only rarely did Dunlin chicks use it. Secondly, the survival rate of Dunlin chicks on marsh habitats was approximately twice that of chicks on old fallow (ca. 0.56 compared to ca. 0.24, see Table 8.5 Chapter 8).

Habitats used for comfort activities by Dunlin

For most of the breeding season Dunlin spend little time roosting, bathing or preening. The only time when these activities occurred commonly was on hot days late in the breeding season. At such times Dunlin frequently visited loch-edges where they would bathe and preen, and then often roost for a while on a nearby rock. At Drimore Farm, one small area of loch-edge with a sand and shingle shore and with adjacent rocks was particularly favoured. On hot days in late June and early July this area of loch shore was used by a succession of birds, up to ten at once, and during the course of a day was probably visited by a large proportion of the Dunlin still present on the study-site. At Stilligarry, there was a similar situation with the Dunlin

focussing their activity on the shore of a small island in Loch Grogarry. Unfortunately, it was rarely possible to read the birds' colour-ring combinations when they were on this island and so few observations were recorded. However, those birds whose ring combinations were read confirm that the island was used by birds breeding at Stilligarry and also that it was used as a roost site at high tide by birds that were using the seashore for feeding.

Summary of Dunlin habitat choice

At both sites where Dunlin habitat use was investigated, almost all activities were restricted to areas of marsh and fallow machair; blackland pastures and habitats with tall vegetation were of little importance. Display activity was confined to the nesting areas; mainly old fallow at Stilligarry and marsh at Drimore Farm. During the breeding season adult Dunlin feed mainly in habitats with a short sward and damp soil, such as old fallow, recent fallow and damp marsh. At some other sites exposed loch-edge mud was an important feeding habitat. From mid June onwards intertidal sand and wrack were increasingly important feeding habitats; by the end of the breeding season almost all feeding was done on the seashore. The timing of the switch to seashore feeding was different at the two study-sites; it is suggested that this may have been due to the length of the vegetation at alternative feeding grounds (i.e. the machair). There was no significant change in the proportional use of the terrestrial feeding habitats at either site between the pre-laying, incubation or chick rearing periods.

Chick-rearing usually occurred close to the nest (Chapter 4.II) on either old fallow or marsh habitats (all types). In general, the chicks were reared in slightly taller vegetation than that used by the adults for feeding, but habitats with tall vegetation were not used by chicks. There was no significant change in the proportional usage of the chick-rearing habitats as chicks grew older at Drimore Farm, a predominantly marshy breeding area. However, at Stilligarry a significant increase in the proportional use of marsh in the latter half of chick rearing probably reflects superior chick survival in marsh habitats than fallow machair, and not a genuine shift in habitat choice.

Late in the breeding season certain small areas of loch shore were used by a large proportion of the locally breeding Dunlin for bathing, preening and roosting.

CHAPTER 3: SECTION III

HABITATS USED BY RINGED PLOVER FOR BREEDING ACTIVITIES

Treatment of the data

Data on habitat usage by breeding Ringed Plover were collected from three study-sites: Rubha Ardvule, Stilligarry and Drimore Farm. Nearly all the records are of birds feeding. Ground display and comfort activities were rarely seen, and when they were the habitats used were the same as for feeding, therefore, individual accounts of habitat usage for these two activities are not given. The very poor nest survival of the Ringed Plovers (Chapter 8) resulted in few pairs rearing chicks and so there are relatively few records of birds in the chick-rearing stage. During chick-rearing both parents stay close to the chicks and normally feed in the same habitats as the chicks (*pers obs.*). A comparison between the proportional use of habitats of adults recorded as tending broods and adults recorded as feeding during the chick-rearing stage is made in Table 3.10. The results in this table show that there is no significant difference in the use of habitats between the two types of activity ($\text{Chi}^2 = 3.9$, 4 d.f., $P > 0.05$). Therefore, for the chick-rearing stage, the records of adults feeding and adults tending chicks are aggregated and analysed together.

The habitats available and their arrangement were different for each study-site, the data from each site are therefore analysed separately. The number of records from each stage of the breeding season for each study-site are shown in Table 3.11. The uneven distribution of records between the three sites

Table 3.10: Habitat usage by Ringed Plover during chick-rearing stage. Comparison between adults feeding and tending chicks.

HABITAT CATEGORY (HABITAT)	NUMBER OF RECORDS		
	FEEDING	CHICK REARING	ROW TOTAL
Old damp fallow m. (E)	11 22.9%	27 19.1%	38 20.1%
Old dry fallow m. (E)	2 4.2%	11 7.8%	13 6.9%
1st year fallow m. (F)	15 31.3%	48 34.0%	63 33.3%
2nd year fallow m. (S)	3 6.3%	19 13.5%	22 11.6%
Plough and tracks (P,T)	17 35.4%	36 25.5%	53 28.0%
Total %	48 25.4%	141 74.6%	189 100.0%

Chi² = 3.9, 4 d.f., P > 0.05 NOT SIGNIFICANT
 (1 expected value of 10 is <5 (3.3))
 For details of habitat codes see Appendix A

Table 3.11: Number of records of adult Ringed Plover from each breeding stage at each site.

STUDY- SITE	NUMBER OF RECORDS					ROW TOTAL
	PRELAY STAGE	INCUBT STAGE	CHICK STAGE	AFTER STAGE	UNKNOWN STAGE	
Drimore Farm	43 5.8%	131 17.6%	135 18.1%	110 14.8%	326 43.8%	745 27.3%
Rubha Ardvule	94 13.7%	142 20.7%	47 6.9%	104 15.2%	299 43.6%	686 25.1%
Stilli- garry	187 14.4%	308 23.7%	188 14.5%	199 15.3%	417 32.1%	1299 47.6%
Total %	324 11.9%	581 21.3%	370 13.6%	413 15.1%	1042 38.2%	2730 100%

reflects the amount of observation effort. Rubha Ardvule is atypical of the breeding grounds used by Ringed Plover in the Southern Isles, therefore, the gathering of information from this site was considered to be of least importance and visits to Rubha Ardvule were made less often than to the other sites. Data on habitat usage were not collected from Drimore Farm in 1985.

The number of records from each habitat type at each site is tabulated in Appendix F. The results in this table are summarised for the important habitats in Figure 3.6.

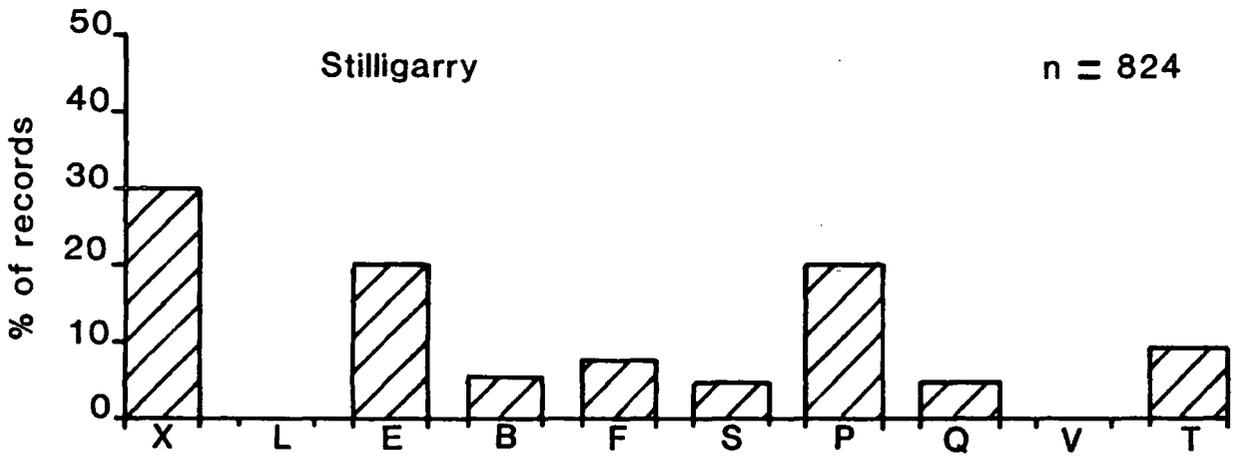
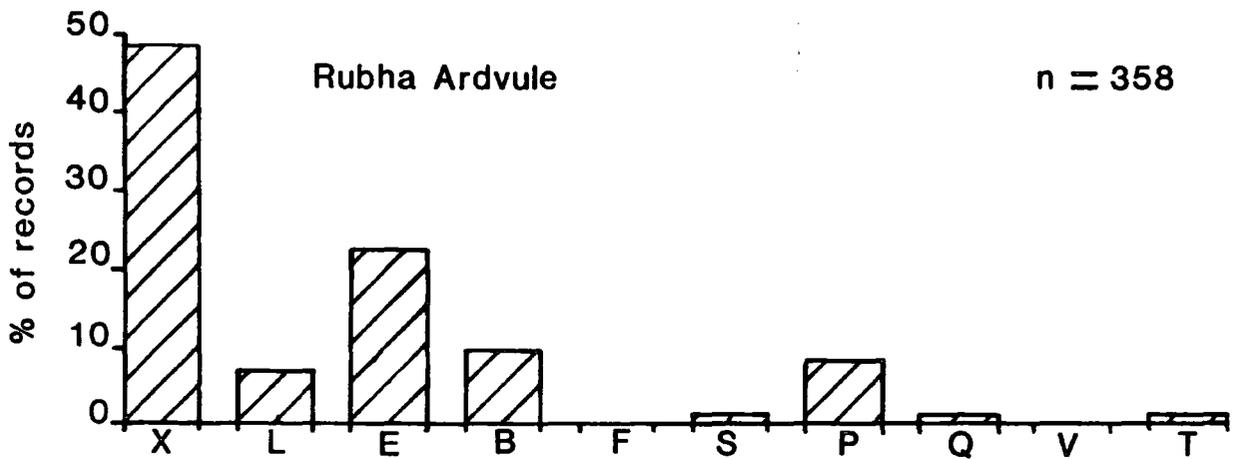
Gross habitat use by breeding Ringed Plover

The results in Figure 3.6 clearly show that during the breeding season Ringed Plover use a very limited range of habitats. blackland pastures, marshes, all habitats with tall vegetation and freshwater margins are very rarely used, together they represent only 5% of the records. The remaining 95% of the records are split between the seashore (29%), and machair (66%). In general the seashore is used for feeding by adults and not for nesting (Chapter 5) or chick rearing. The breeding habitats proper of Ringed Plover in the Southern Isles are almost entirely confined to the areas of machair used for cereal cultivation.

Detailed account of habitat use by breeding Ringed Plover

Stilligarry can be considered as representing a typical area of strip cultivated machair, whereas the cultivation system at Drimore Farm, although not strictly crofting itself, closely resembles the other main cultivation pattern to be found in the Southern Isles, the club machair system. The differences between

Figure 3.6: Percentage of records of adult Ringed Plover from each habitat at each study-site.



- | | |
|--------------------|--------------------|
| X = Seashore | S = 2nd year fall. |
| L = Loch-edge | P = Plough |
| E = Old damp fall. | Q = Short cereal |
| B = Old dry fall. | V = Reseeded mach. |
| F = 1st year fall. | T = Track |

Habitats with < 2% of all records are excluded.

the two systems are explained in Chapter 2. As explained above, Rubha Ardvule is not typical, it does however represent a more natural situation because the birds are not dependent on cultivation habitats.

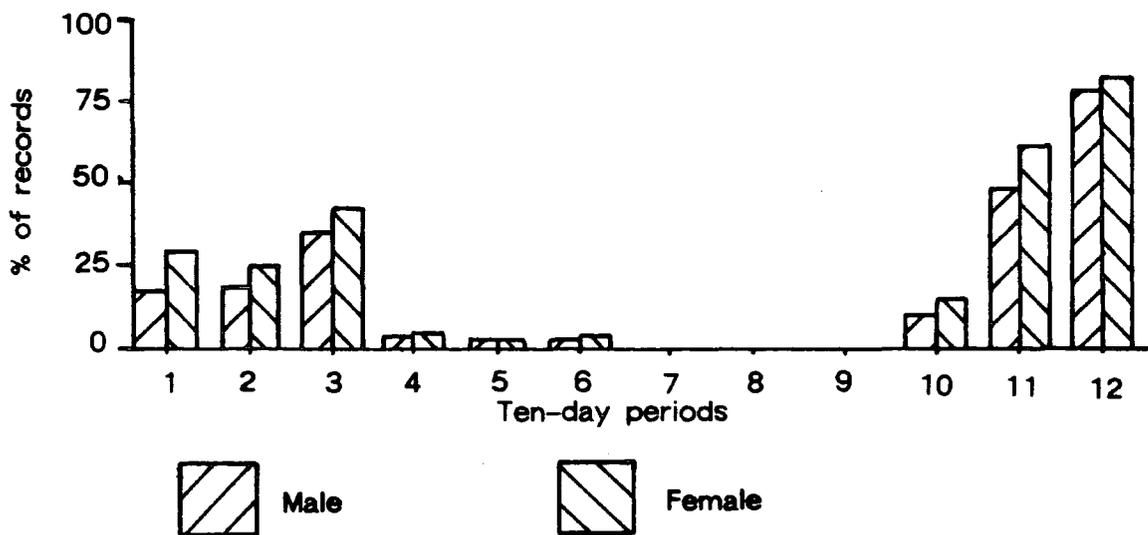
The account is split into three parts. The first two parts consider the habitat usage at Stilligarry and Drimore Farm only, and deal with use of the seashore, and use of the machair respectively. The third part describes briefly the habitat use at Rubha Ardvule.

1) Use of the seashore at Stilligarry and Drimore Farm.

The importance of the seashore as a feeding habitat varies greatly through the breeding season. The majority of the Ringed Plover breeding in the Southern Isles are resident and mainly spend the non-breeding season on the west coast beaches (*pers obs.*). Before and after the breeding season almost all feeding was done on the seashore. The relative importance of the seashore during the breeding season can be evaluated by comparing the proportion of feeding records from seashore and machair habitats for different periods. This comparison is illustrated, for males and females separately, in two ways. Firstly, Figure 3.7 shows the proportion of feeding records from the seashore through the breeding season divided into ten-day periods. Secondly, Figure 3.8 shows the proportion of feeding records from the seashore for each stage of the breeding cycle.

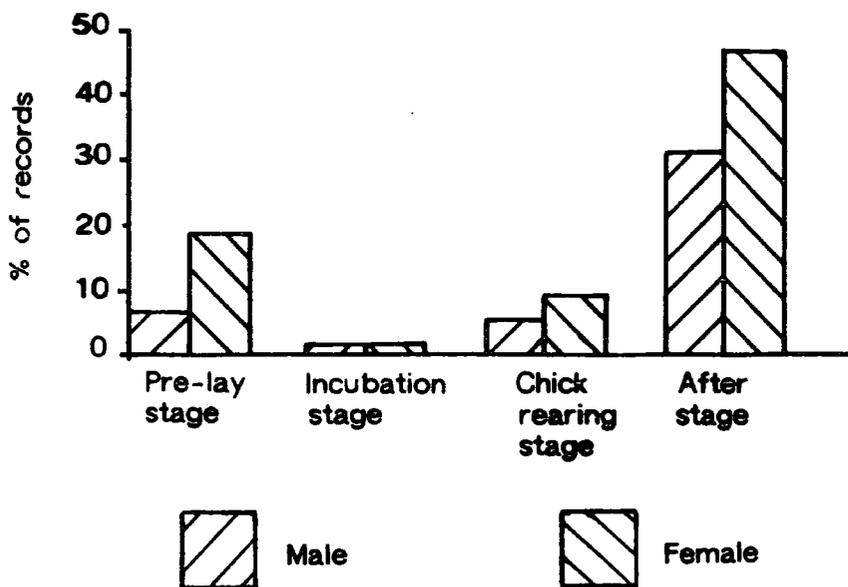
Figure 3.7 shows a much stronger relationship than Figure 4.8 and this suggests that use of the shore is largely determined by the date and not the stage of breeding. The reason why the

Figure 3.7: Ringed Plover: percentage of records from the seashore for ten-day periods through the breeding season. Stilligarry and Drimore Farm study-sites only



1	=	22/3	-	31/3	(M	n=	21,	F	n=	21)
2	=	1/4	-	10/4	(M	n=	48,	F	n=	56)
3	=	11/4	-	20/4	(M	n=	34,	F	n=	33)
4	=	21/4	-	30/4	(M	n=	64,	F	n=	52)
5	=	1/5	-	10/5	(M	n=	83,	F	n=	82)
6	=	11/5	-	20/5	(M	n=	95,	F	n=	121)
7	=	21/5	-	30/5	(M	n=	93,	F	n=	85)
8	=	31/5	-	9/6	(M	n=	102,	F	n=	83)
9	=	10/6	-	19/6	(M	n=	104,	F	n=	114)
10	=	20/6	-	29/6	(M	n=	129,	F	n=	110)
11	=	30/6	-	9/7	(M	n=	165,	F	n=	178)
12	=	10/7	-	19/7	(M	n=	164,	F	n=	216)

Figure 3.8: Ringed Plover; percentage of records from the seashore during each stage of the breeding season. Stilligarry and Drimore Farm tites only.



Pre-lay: male n = 123, female n = 111
 Incubation: male n = 199, female n = 222
 Chick rearing: male n = 157, female n = 149
 After stage: male n = 151, female n = 165

relationship with breeding stage is not as strong as that each stage extends over a long period. Although the start of egg laying in Ringed Plover is well synchronised, the synchrony between pairs through the season lessens as birds repeatedly fail and relay. Ringed Plover will continue to replace clutches until early July (*pers. obs.*).

Ringed Plover return to their breeding grounds from February onwards (*pers obs.*) and then proceed to establish their territories. During February, March and early April, before the onset of egg laying, Ringed Plover frequently visit the shore to feed. Just before the onset of laying (ten-day period 3) there was an apparent increase in the use of the shore, this may be connected with greater food requirements necessary for egg production in females. It is not clear why this increase should occur for the males. In late April there was a rapid decline in the use of the shore and from early May through to late June the shore was only very seldom used. The reason why the shore was virtually abandoned as a feeding habitat for two months is probably largely explained by the amount of invertebrate food available on the machair. The number of surface active invertebrates, measured by pit-fall trapping, is known to rise in the spring (e.g. Baines 1988). Presumably once the abundance of this food supply rises above a certain threshold level feeding on the machair becomes more profitable than feeding on the seashore. It is not known how the availability of the seashore invertebrate food supply varies through the year. A further advantage in feeding on the machair is that the birds can remain on (or close to) their territory and be close to their nest or chicks. If the

latter reason were the only advantage in feeding on the machair during May and June then one would expect females which had recently failed and not yet relayed to frequently feed on the shore but this was not the case.

Seashore feeding started again at the end of June, there was then a steady and rapid increase in the use of the shore and by mid July almost all the Ringed Plover have deserted their breeding grounds and moved to the beaches. The uptake of shore feeding again does not start solely with birds that have given up attempting to breed for that season but involves birds from all breeding stages, though by this time there were comparatively few pairs with eggs. Pairs with broods in July usually moved the chicks to the nearest beach. The underlying factors which initiate the rapid exodus from the machair to the beaches are not known but are probably connected with feeding. To feed successfully adult Ringed Plover require either bare ground or very short vegetation. The movement to the shore may be induced by the vegetation of the machair becoming too tall for the birds to feed in. However, if this was the sole reason then one would expect the birds from Drimore Farm to move to the shore later because the vegetation at Drimore Farm was grazed through the summer and was therefore generally shorter than at Stilligarry. However, there was no difference in the timing of the birds' adoption of shore feeding between the two sites. Alternatively, the movement to the seashore may be triggered by a reduction in abundance or availability of machair invertebrates.

For all the ten-day periods and breeding stages, female Ringed Plover make slightly greater use of the seashore. This is

probably because the males have to defend the breeding territory and cannot therefore so readily afford to be away from the territory feeding on the shore.

ii) Use of the machair at Stilligarry and Drimore Farm.

Although the range of habitats at Drimore Farm and Stilligarry was similar, the spatial arrangement of the habitats at the two sites was very different (see description of study-sites in Chapter 2). At Drimore Farm nearly all the Ringed Plover were breeding on a large area of recent fallow and the majority of the territories included no other habitat types, some territories, for example those around the edge of the area of recent fallow, also had old fallow and small amounts of various other habitats. In contrast to this, at Stilligarry the strip arrangement of the machair habitats meant that most territories contained a mixture of old fallow and plough, and to a lesser extent, recent fallow. Therefore, the birds at Stilligarry had much greater opportunity to choose between different habitat types without leaving their territory.

The use of the machair habitats at the two sites is summarised for each stage of the breeding season in Tables 3.12 and 3.13., and by ten-day periods through the breeding season in Tables 3.14 and 3.15. To give large enough samples for a χ^2 test it has been necessary to group together some similar habitat types. Some habitats with less than 3% of the records for a site, such as loch-edge habitats are excluded from Tables 3.12 and 3.13.

At Drimore Farm there is no significant variation in habitat

Table 3.12: Use of machair habitats by Ringed Plover during each stage of the breeding season at Stilligarry.

N U M B E R O F R E C O R D S					
HABITAT CATEGORY (HABITATS)	PRELAY STAGE (1)	INCUBT STAGE (2)	CHICK STAGE (3)	AFTER STAGE (4)	ROW TOTAL
Old fallow mach. (E,B)	66 60.0%	59 48.4%	29 32.2%	20 34.5%	174 45.8%
Recent fallow (F,S)	27 24.5%	23 18.9%	8 8.9%	2 3.4%	60 15.8%
Plough (P,Q)	17 15.5%	40 32.8%	53 58.9%	36 62.1%	146 38.4%
Total %	110 28.9%	122 32.1%	90 23.7%	58 15.3%	380 100%

Stage 1 vs. 2	$\text{Chi}^2 = 13.7, 2 \text{ d.f.}, P < 0.001$	SIGNIFICANT
Stage 1 vs. 3	$\text{Chi}^2 = 45.1, 2 \text{ d.f.}, P < 0.0001$	SIGNIFICANT
Stage 2 vs. 3	$\text{Chi}^2 = 13.8, 2 \text{ d.f.}, P < 0.001$	SIGNIFICANT
Stage 2 vs. 4	$\text{Chi}^2 = 16.4, 2 \text{ d.f.}, P < 0.001$	SIGNIFICANT
Stage 3 vs. 4	$\text{Chi}^2 = 1.66, 2 \text{ d.f.}, P > 0.05$ (1 expected value of 6 is < 5 (3.9))	NOT SIGNIFICANT
Stage 1 vs. 4	$\text{Chi}^2 = 38.4, 2 \text{ d.f.}, P < 0.0001$	SIGNIFICANT

For details of habitat codes see Appendix A

Table 3.13: Use of machair habitats by Ringed Plover during each stage of the breeding season at Drimore Farm.

HABITAT CATEGORY (HABITAT)	NUMBER OF RECORDS				ROW TOTAL
	PRELAY STAGE	INCUBT STAGE	CHICK STAGE	AFTER STAGE	
Old fallow (B,E,W,M)	4 14.3%	6 11.1%	25 22.7%	4 9.8%	39 16.7%
Recent fallow (F,S,V)	24 85.7%	48 88.9%	85 77.3%	37 90.2%	194 83.3%
Total %	28 12.0%	54 23.2%	110 47.2%	41 17.6%	233 100%

Whole table

$\text{Chi}^2 = 5.61, 3 \text{ d.f.}, P > 0.05$ NOT SIGNIFICANT

No two pairs of stages are significantly different.

For details of habitat codes see Appendix A

Table 3.14: Use of machair habitats by Ringed Plover during calendar periods through the breeding season at Stilligarry.

HABITAT CATG. (HABITATS)	NUMBER OF RECORDS					ROW TOTAL
	CALENDAR PERIODS ¹					
	1	2	3	4	5	
Old fallow (E,B)	29 70.7%	36 59.0%	39 52.7%	22 36.1%	9 14.5%	135 45.2%
Recent fall. (F,S)	12 29.3%	9 14.8%	14 18.9%	4 6.6%	3 4.8%	42 14.0%
Plough (P)	0	16 26.2%	21 28.4%	35 57.4%	50 80.6%	122 40.8%
Total %	41 13.7%	61 20.4%	74 24.7%	61 20.4%	62 20.7%	299 100%

Period 1 vs. 2 $\text{Chi}^2 = 0.56$, 1 d.f., $P > 0.05$ NOT SIGNIFICANT
(Plough excluded)

Period 1 vs. 3 $\text{Chi}^2 = 0.01$, 1 d.f., $P > 0.05$ NOT SIGNIFICANT
(Plough excluded)

Period 1 vs. 4 $\text{Chi}^2 = 1.01$, 1 d.f., $P > 0.05$ NOT SIGNIFICANT
(Plough excluded)

Period 1 vs. 5 $\text{Chi}^2 = 0.01$, 1 d.f., $P > 0.05$ NOT SIGNIFICANT
(Plough excluded)

Period 2 vs. 3 $\text{Chi}^2 = 0.64$, 2 d.f., $P > 0.05$ NOT SIGNIFICANT

Period 2 vs. 4 $\text{Chi}^2 = 12.4$, 2 d.f., $P < 0.001$ SIGNIFICANT

Period 2 vs. 5 $\text{Chi}^2 = 36.7$, 2 d.f., $P < 0.001$ SIGNIFICANT

Period 3 vs. 4 $\text{Chi}^2 = 12.7$, 2 d.f., $P < 0.001$ SIGNIFICANT

Period 3 vs. 5 $\text{Chi}^2 = 36.9$, 2 d.f., $P < 0.0001$ SIGNIFICANT

Period 4 vs. 5 $\text{Chi}^2 = 8.23$, 2 d.f., $P < 0.05$ NOT SIGNIFICANT
(1 of 6 expected values is < 5 (3.5))

¹Calendar Periods

1 = before 30th April

2 = 1st May - 20th May

3 = 21st May - 9th June

4 = 10th June - 29th June

5 = 30th June - 19th July

For details of habitat codes see Appendix A

Table 3.15: Use of machair habitats by Ringed Plover during calendar periods through the breeding season at Drimore Farm.

HABITAT CATEGORY (HABITATS)	NUMBER OF RECORDS				ROW TOTAL
	1 + 2	CALENDAR PERIODS ¹			
	3	4	5		
OLD FALLOW (E,B,M,W,V)	4 12.5%	9 20.5%	10 18.9%	9 18.8%	32 18.1%
RECENT FALLOW (F,S)	28 87.5%	35 79.5%	43 81.1%	39 81.3%	145 81.9%
TOTAL %	32 18.1%	44 24.9%	53 29.9%	48 27.1%	177 100%

Whole table

$\chi^2 = 0.88$ 3 d.f., $P > 0.05$ NOT SIGNIFICANT

No two pairs of stages are significantly different.

Calendar Periods

- 1 = before 30th April
- 2 = 1st May - 20th May
- 3 = 21st May - 9th June
- 4 = 10th June - 29th June
- 5 = 30th June - 19th July

For details of habitat codes see Appendix A

use through the season, when tested using either breeding stage (Table 3.13) or ten-day period (Table 3.15). The Chi^2 test statistics are shown below the table concerned.

This result is not surprising for two reasons. Firstly, the uniform nature of most of the Ringed Plover territories at Drimore Farm means the birds had little in the way of habitat choice unless they left their territories. Secondly, compared to the situation at Stilligarry (see below), the nature of the habitats at Drimore Farm remained largely unchanged through the breeding season; there was no ploughing on the main area studied and sheep were present throughout the season which kept the vegetation short.

There was a marked seasonal variation in the use of machair habitats at Stilligarry. The seasonal differences are clearer when the records are grouped into ten-day periods (Table 3.12) than when they are grouped into different breeding stages (Table 3.14). This suggests that the change in habitat use occurs independent of breeding stage. Ploughing usually took place in late April and early May, before this no plough habitat was available. Before ploughing the birds use both old and recent fallow. Although old fallow accounts for 71% of the records it covered approximately five times the area of recent fallow and therefore it can be concluded that recent fallow is of greater intrinsic value. During the years of the study most of the ploughing at Stilligarry was of recent fallow, ploughing therefore brought about a large reduction in the amount of recent fallow available. The difference in habitat use between period 1 (late March to 30th April) and period 2 (1st May to 20th May) was

almost entirely due to the creation of plough habitat and a corresponding reduction in fallow. However, plough was used more than would be expected based on the area available, accounting for 26% of the records while occupying only about 16% of the area of machair. The proportional use of each habitat during period 3 (21st May to 9th June) is not significantly different to that in period 2 ($\text{Chi}^2 = 0.64$, 2 d.f., $P > 0.05$). This is perhaps not surprising because during periods 2 and 3 the fundamental nature of the machair habitats changed little mainly because livestock continue to graze the machair until late May. In period 4 (10th to 29th June) and period 5 (30th June to 19th July) the plough became increasingly important; by period 5 it accounts for 81% of all non-seashore records, but it must be remembered that by this time most birds were feeding on the seashore. As the use of the plough increases, there was a corresponding and approximately equal decrease in the use of old and recent fallow. By about mid June most of the cereals had reached a height of about 15cm at which point they become too tall for adult Ringed Plover (chicks will occasionally use slightly higher cereals). During periods 4 and 5, as the cereals grew taller, the amount of suitable plough habitat became progressively less, eventually diminishing to a small fraction of the amount originally available.

There are two reasons why suitable plough habitat continues to exist through to the end of the season. Firstly there is a large spread in ploughing dates from mid April up until late May. This results in the strips of cereals being at different stages of development at any one time. Secondly, and more importantly, it is not uncommon for patches of the cereals to fail leaving

areas of predominantly bare ground. This type of crop failure is caused either by flooding soon after sowing which can prevent germination, or by drought conditions and drying winds which kill the young plants. Bare patches among the cereals are therefore usually found either in hollows or on slight mounds, and their occurrence largely depends on the weather conditions in May. Late in the season, when the cereals fields and fallow machair are largely covered in tall vegetation, all remaining areas with either bare ground or short vegetation become important for Ringed Plover; beside patches of failed cereals these include the machair tracks, dry dune turf and drying-up dune slack pools.

Although bare or only partly vegetated areas may have some small advantages over short sward as feeding habitats for adult Ringed Plover, it is clear that all these habitat types are very frequently used for feeding and, therefore, all must be of high value for feeding. For nesting and chick rearing however, the value of bare and partly vegetated habitats is far greater than that of a short closed sward (Chapter 5). The reason for this lies in the far superior camouflage of nests and chicks on the former habitats. When Ringed Plover do use old fallow for nesting or chick rearing they normally use an area that has a higher potential for camouflaging nests or chicks, this may be in the form of: broken ground, old cowpats, rabbit warrens, stones, an adjacent gravel track or an abundance of Daises (*Bellis perrenis*).

iii) Use of habitats at Rubha Ardvule.

Habitat usage at Rubha Ardvule by breeding Ringed Plover is

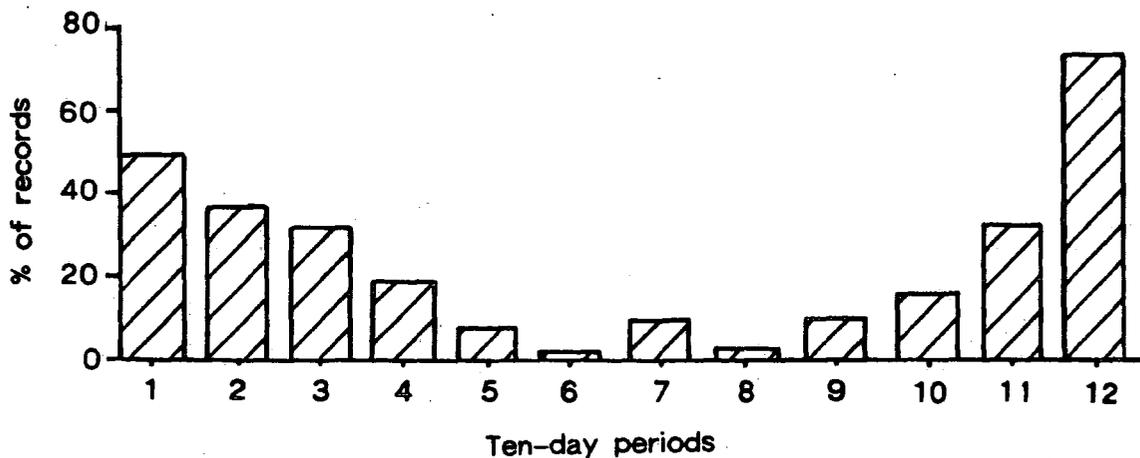
only discussed briefly because of this sites atypical nature. Plough and recent fallow habitats were relatively unimportant habitats, only occurring on the eastern fringe of the site and were only used by the few pairs of Ringed Plover in that area. The majority of Ringed Plovers at Rubha Ardvule confined their activities to the areas of permanent pasture that predominate on the site, both damp and dry, and the seashore. The pasture at Rubha Ardvule generally remained short through the season because it was grazed by cattle, and because in places the soil is very thin and prone to drying out. Around the edge of the site much of the pasture is strewn with cobbles and shingle from the extensive coarse shingle banks. (see description of site in Chapter 2).

These areas of mixed grass and shingle were particularly favoured for nesting (see chapter 5) and chick rearing presumably because of the excellent camouflage afforded by the shingle. The use of the seashore at Rubha Ardvule is illustrated in Figure 3.9. Although there was a large decrease in its use during May and June, the shore never stopped been used altogether as it was at Stilligarry and Drimore Farm. The reason for this was that many of the territories at Rubha Ardvule incorporated, or were adjacent to, areas of seashore feeding habitat thus in many cases the adults could visit the shore without leaving their territories.

Summary of Ringed Plover habitat choice

In the Southern Isles Ringed Plover breed almost exclusively on areas of cultivated machair. All habitats produced by the

Figure 3.9: Ringed Plover: percentage of records from the seashore for ten-day periods through the breeding season. Rubha Ardvule study-site only.



1	=	22/3	-	31/3	(n= 26)
2	=	1/4	-	10/4	(n= 55)
3	=	11/4	-	20/4	(n= 22)
4	=	21/4	-	30/4	(n= 70)
5	=	1/5	-	10/5	(n= 78)
6	=	11/5	-	20/5	(n= 59)
7	=	21/5	-	30/5	(n= 41)
8	=	31/5	-	9/6	(n= 42)
9	=	10/6	-	19/6	(n= 71)
10	=	20/6	-	29/6	(n= 65)
11	=	30/6	-	9/7	(n= 67)
12	=	10/7	-	19/7	(n= 90)

cultivation cycle, except tall cereals are extensively used during all stages of the breeding season. At sites where there are strips of cultivation habitats at different stages in the cycle adjacent to each other the Ringed plover show a significant seasonal change in the proportional use of the each habitat type. As the season progresses, habitats with bare ground such as plough become increasingly important for feeding, this is probably because as the vegetation of the fallow habitats grows taller it increasingly interferes with the birds' feeding technique. At sites where there are large homogeneous areas of the cultivation habitats (i.e. the club-machair system) there is no significant change in the proportional use of the machair habitats through the breeding season. Plough and recent fallow are particularly valuable habitats for chick rearing because they give the chicks better opportunities for concealment from predators. Large expanses of close-sward fallow machair are of limited value as a breeding habitat unless they incorporate some areas of bare ground such as gravel tracks or dried out pools.

The use of the seashore for feeding follows a marked seasonal pattern. There is a rapid decrease in seashore feeding in late April. From May to late June shore feeding is of negligible importance, there is then a rapid increase and by mid July nearly all Ringed Plover have deserted the machair and moved to the beaches for the non-breeding season.

CHAPTER 4

HABITAT USAGE II: DAILY MOVEMENTS DURING BREEDING

The previous chapter considered the types of habitats chosen for each breeding activity but it did not consider the spatial aspects of their use such as the distances travelled to feeding grounds or the size of area used by broods. This is the subject of this chapter. The previous chapter shows that Redshank, Dunlin and Ringed Plover each have distinct habitat preferences for each activity and it is thus apparent that these species require a range of habitats. The degree to which an area will fulfil a species' habitat requirements will not only depend on the presence of suitable habitats but also on the appropriate spatial arrangement of these habitats. By investigating the daily movements of the breeding waders, some measure of the appropriate spatial arrangement of the habitats can be obtained. This type of information has important implications for the conservation of the birds, for example in determining the optimal spatial scale of habitat heterogeneity for each species, and in deciding how large to make nature reserves in order to encompass the birds' movements.

As discussed at the beginning of Chapter 3, the data used for this chapter are from the sightings of colour-ringed birds for which it has been possible to retrospectively calculate a bird's distance from its nest-site each time it was seen, and also its exact stage of breeding. In common with the previous chapter, the information for each species is presented in a separate section.

CHAPTER 4: SECTION I

DAILY MOVEMENTS OF BREEDING REDSHANK

Treatment of the data

All records of adults feeding and of family parties are used in the following analysis. The data from the three northern study-sites are analysed together because of their broadly similar nature. The data from the Rubha Ardvule study-site are treated separately because the nature of this site restricts the opportunity for large movements and because the habitat usage is atypical of that generally found in the Southern Isles (Chapter 3.I). The breeding season has been divided into six periods defined as follows:

- Early pre-laying: Arrival back on breeding grounds to 20 days before laying.
- Late pre-laying: From 20 days before laying to laying of the first egg.
- Early incubation: From laying of the first egg to 16 days later.
- Late incubation: From 16 days after laying of the first egg up to hatching.
- Week 1 chicks: From hatching to 8 days later.
- Week 2 chicks: From 8 days after hatching to 15 days after hatching.
- Week 3+ chicks: From 15 days after hatching to fledging (approximately 30 days after hatching).

Some family parties were recorded more frequently than others, in particular broods that wandered outside the cores of the study-sites tended to be seen less often than those that remained within the core areas. To reduce the bias against broods that were seen less frequently, each brood is given equal

weighting by using the mean of the distance from the nest for all observations of a brood during each of the three chick-rearing periods.

Movements by adult Redshank to feeding areas

The distances travelled from the nest-site to feeding areas by adult Redshank are summarised for the pre-laying and incubation stages in Tables 4.1 and 4.2, for the northern study-sites and Rubha Ardvule respectively. The distances moved to feeding grounds during the chick-rearing stage are not included in these tables. Because adult Redshank always stayed near their chicks (usually within 50 metres) (*pers. obs.*), their feeding movements at this stage are practically the same as the movements of the brood and these are considered separately. The significance of the seasonal differences in feeding movements are tested using the Mann-Whitney U-test; the results of these tests are shown in Table 4.3.

1) Feeding movements at the northern study-sites

The general pattern of distances travelled from the nest-site to feeding areas by adult Redshank at the northern study-sites was broadly similar throughout the pre-laying and incubation stages (Table 4.1). During these stages 66% of all records were within 210 metres of the nest-site; within this distance the distribution of records is approximately equal. Beyond 210 metres from the nest the number of records drops gradually as the distance increases up to 400 m. Only 10% of records are further than 400 m from the nest site, the furthest was 1.1 km.

During the early pre-laying and late incubation stages the

Table 4.1: Distances moved by adult Redshank from nest-site to feeding areas at the northern study-sites during the pre-laying and incubation stages.

DISTANCE FROM NEST-SITE	N U M B E R O F R E C O R D S				ROW TOTAL
	S t a g e o f b r e e d i n g s				
	EARLY ¹ PRE-LAY	LATE ² PRE-LAY	EARLY ³ INCBT.	LATE ⁴ INCBT.	
<70m	38 19.8%	41 27.9%	32 27.6%	15 16.7%	126 23.1%
70-140m	33 17.2%	32 21.8%	27 23.3%	15 16.7%	107 19.6%
141-210m	49 25.5%	31 21.1%	27 23.3%	21 23.3%	128 23.5%
211-400m	47 24.5%	28 19.0%	24 20.7%	28 31.1%	127 23.3%
>400m	25 13.0%	15 10.2%	6 5.2%	11 12.2%	57 10.5%
TOTAL	192 35.2%	147 27.0%	116 21.3%	90 16.5%	545 100.0%

- ¹ Arrival back on breeding grounds to 20 days before laying.
- ² From 20 days before laying to laying of the first egg.
- ³ From laying of the first egg to 16 days later.
- ⁴ From 16 days after laying of the first egg to hatching.

Table 4.2: Distances moved by adult Redshank from nest-site to feeding areas at Rubha Ardvule study site during the pre-laying and incubation stages.

DISTANCE FROM NEST-SITE	NUMBER OF RECORDS				ROW TOTAL
	Stage of breeding ⁴				
	EARLY ¹ PRE-LAY	LATE ² PRE LAY	EARLY ³ INCBT	LATE ⁴ INCBT	
<70m	13 17.8%	11 25.0%	16 36.4%	2 14.3%	42 24.0%
70-140m	20 27.4%	20 45.5%	12 27.3%	7 50.0%	59 33.7%
141-210m	32 43.8%	11 25.0%	12 27.3%	3 21.4%	58 33.1%
211-400m	7 9.6%	2 4.5%	3 6.8%	2 14.3%	14 8.0%
>400m	1 1.4%	0	1 2.3%	0	2 1.1%
TOTAL %	73 41.7%	44 25.1%	44 25.1%	14 8.0%	175 100.0%

- ¹ Arrival back on breeding grounds to 20 days before laying.
- ² From 20 days before laying to laying of the first egg.
- ³ From laying of the first egg to 16 days later.
- ⁴ From 16 days after laying of the first egg to hatching.

distances travelled to feeding areas are generally greater than those in the late pre-laying and early incubation stages. Mann-Whitney U-tests show that these differences are significant (Table 4.3). There is no significant difference in the distances moved between the early pre-laying and late incubation periods or between the late pre-laying or early incubation periods (Table 4.3). At the start of the season many individuals had not chosen their exact nest-site and it is therefore not surprising that their feeding movements are more wide ranging than when they have a nest. It is not clear why Redshank tend to forage further away from the nest in the second half of the incubation period than in the first half; it may be connected with minimising the risk of nest predation. The birds may have to balance between foraging sufficiently close to the nest to be able to see and react to predators that threaten the nest's survival and preventing attracting predators to the nesting area by not feeding near the nest; the birds' optimal solution to this dilemma may change through the incubation stage.

ii) Feeding Movements at Rubha Ardvule

The pattern of feeding movements at Rubha Ardvule is similar to that at the northern study-sites, the only major difference is that the distances moved are generally shorter; 91% of records are within 210 m of the nest and no records are further than 500 m away. This result is not surprising considering the peninsular nature of the site which effectively restricts the birds' movements in most directions. The seasonal variation in the distances moved is also similar to that at the northern

study-sites though in only one case (early pre-lay vs. late pre-lay) is the difference between two periods significant (Table 4.3) The reason why the differences in distances moved are not significant between early and late incubation may be a consequence of the small sample sizes.

Movements of Redshank families

The distance from the nest-site of broods (for each brood the mean distance is used) during each of the three chick-rearing periods (weeks 1, 2 and 2+) are summarised in Tables 4.4 and 4.5 for the northern study-sites and Rubha Ardvule respectively. Results of Mann-Whitney U-tests between different periods of the chick-rearing stage are shown in Table 4.6.

1) General pattern of movements

The results summarized in Tables 4.4 and 4.5 show that Redshank families normally range over a wide area during the chick-rearing period. At both the northern study-sites and Rubha Ardvule the variation in the pattern of movements through the chick-rearing stage is the same: there is a highly significant difference between week 1 and week 2, and between week 1 and week 3+. There is however no difference between week 2 and week 2+ at either site. The principle difference between the first week and subsequent weeks is that the broods are generally closer to the nest-site in the first week.

It must be remembered that this analysis is based on the mean distance observed for each brood during each period; Redshank broods often forage over wide areas in a short space of time, this means that maximum movements from the nest were for most

Table 4.4: Distances moved by Redshank families at the northern study-sites from their nest to chick-rearing areas. The distance categories refer to the mean distance from the nest of all the observations of a given brood during the stage concerned.

DISTANCE FROM NEST-SITE	N U M B E R O F B R O O D S			ROW TOTAL
	S T A G E O F B R O O D 1ST WEEK ¹	2ND WEEK ²	>2ND ³ WEEK ³	
<70m	23 33.8%	16 22.5%	7 11.7%	46 23.1%
70-140m	28 41.2%	18 25.4%	18 30.0%	64 32.2%
141-210m	7 10.3%	13 18.3%	14 23.3%	34 17.1%
211-400m	8 11.8%	15 21.1%	12 20.0%	35 17.6%
>400m	2 2.9%	9 12.7%	9 15.0%	20 10.1%
TOTAL %	68 34.2%	71 35.7%	60 30.2%	199 100.0%

¹ From hatching to 8 days later.

² From 8 days after hatching to 15 days after hatching.

³ From 15 days after hatching to fledging.

Table 4.5: Mean distances moved by Redshank families at Rubha Ardvule from their nest to chick-rearing areas. The distance categories refer to the mean distance from the nest of all the observations of a given brood during the stage concerned.

DISTANCE FROM NEST-SITE	NUMBER OF BROODS			ROW TOTAL
	1ST WEEK ¹	2ND WEEK ²	>2ND WEEK ³	
<70m	20 76.9%	11 47.8%	5 27.8%	36 53.7%
70-140m	5 19.2%	7 30.4%	10 55.6%	22 32.8%
141-210m	0	3 13.0%	0	3 4.5%
211-400m	1 3.8%	2 8.7%	3 16.7%	6 9.0%
TOTAL	26 38.8%	23 34.3%	18 26.9%	67 100.0%

¹ From hatching to 8 days later.
² From 8 days after hatching to 15 days after hatching.
³ From 15 days after hatching to fledging.

Table 4.6: Results of Mann-Whitney U-Tests comparing mean distances moved by broods from nest for successive periods through the chick-rearing stage.

SAMPLE 1	N	SAMPLE 2	N	U-STATISTIC	SIGNIF
NORTHERN STUDY SITES					
Week 1 chicks	68	Week 2 chicks	71	1738	**
Week 2 chicks	71	Week 2+ chicks	60	1956	N.S.
Week 1 chicks	68	Week 2+ chicks	60	1260	***
RUBHA ARDVULE STUDY SITE					
Week 1 chicks	26	Week 2 chicks	23	170	**
Week 2 chicks	23	Week 2+ chicks	18	164	N.S.
week 1 chicks	26	Week 2+ chicks	18	77.5	***

N.S. Not significant

** Significant at 0.01 level

* Significant at 0.05 level

*** Significant at 0.001 level

broods considerably more than the mean distance.

ii) Distances moved at the northern study-sites

During the first week of chick-rearing, 75% of Redshank families at the northern study-sites had a mean distance from the nest of less than 140 m; these families are considered as remaining in the nest site vicinity. The remaining 25% of broods moved away from the nest-site within a few days of hatching. The mean distance that most of these broods moved during the first week was less than 400 m from the nest although two broods moved much greater mean distances, 900 m and 1.3 km respectively.

During week 2 and week 2+ of chick-rearing the mean distance from the nest for 82% of broods was less than 400 m. Most of these were within 210 m. The remaining 18% of broods moved mean distances in excess of 400 m; the majority of these broods moved mean distances of less than 800 m. The greatest mean distance moved by a family from its nest was 1.6 km.

iii) Distances moved at Rubha Ardvule

The geography of Rubha Ardvule probably restricted the movement of Redshank families, the distances moved were generally far shorter than at the northern study-site. During week 1, 77% of broods had mean distances from the nest of less than 70 m and all except one of the remaining broods had mean distances of less than 140 m from the nest. In week 2 and week 2+ 80% of the broods at Rubha Ardvule had a mean distance of less than 140 m and the greatest mean distance was only 360 m.

Discussion of Redshank movements

The lack of defended breeding territories in Redshank (Hale 1956) allows the birds breeding at a site to share the resources of an area. In all stages of the breeding season and for all activities there is a great amount of overlap between neighbouring pairs in the areas used. Areas of favoured feeding habitat were seen to be used by many different individuals, often simultaneously, without any aggressive interactions between the birds. Occasionally some adult Redshank defended small feeding territories in the early part of the breeding season. In all cases these were short stretches of shoreline (seashore strand line at Rubha Ardvule, and muddy loch shore at West Gerinish) where it was clear that the food resources were particularly rich. The only stage in which direct competition for habitat resources was commonly observed was during the chick-rearing period; this is discussed in greater detail below.

Redshank frequently led their chicks from one feeding area to another. This behaviour is probably of general occurrence and has been noted in other Redshank breeding studies (e.g. Hale 1980). As Redshank chicks grow bigger and stronger they become more capable of safely traversing unsuitable feeding habitats to reach new feeding grounds. After the chicks were about one week old many Redshank families either expanded their foraging range or moved to a new area. Usually the chick-rearing area of a family was approximately centred on the nest-site but it was not uncommon for families to undergo journeys of over 400 m, and exceptionally over 1.5 km, to new feeding grounds where they settled. Some broods appeared never to settle in any one place

and led a nomadic existence throughout the chick-rearing period. The size of feeding area typically used by a Redshank brood (excepting nomadic families) was about 4 hectares (*pers. obs.*); often the area was linear, corresponding to a ditch. There was a large amount of overlap in the areas used by adjacent families and it was not uncommon to find that two adjacent broods had swapped places between visits. There is a great variation in the pattern of movements between Redshank broods and it is far from clear which factors determine whether a brood stays in an area or moves to a new one which may involve a hazardous journey over short vegetation or water. Some broods journeyed, for no apparent reason, over unsuitable and hazardous terrain to reach a seemingly similar area to that which they had left behind. On other occasions a new pair would move into an area recently vacated by a previous pair.

By moving them around adults probably enhance the survival chances of their chicks. The wide variation in the observed pattern of movements might be explained by the existence of a large variation between individuals in the threshold level of stimuli that initiates movement behaviour. The proximate factors that initiate movement are unknown but could include food supply, cover availability, disturbance from predators and man, and social interactions with neighbouring pairs (see below).

At any one time all the families at a site were normally well spaced out over the suitable chick rearing habitat, however when two broods got too close vicious fighting often broke out between the adults (both sexes were involved but especially the males). Adults would also aggressively chase away chicks that were not

their own. These quarrels were usually quickly resolved and the two families moved apart. Redshank only defended the area in the immediate vicinity (about 25 m radius) of their chicks, they did not defend a fixed area of ground. The strong competition observed suggests that high quality chick-rearing habitat is at a premium.

Occasionally the competition for chick-rearing habitat between families may be very severe and lead to the deaths of fighting adults. In 1985 two adult male Redshanks were found dead (on separate occasions) on their breeding "territories" at Rubha Ardvule. At the times of their deaths both these birds had chicks of their own and were in places with a particularly high density of broods in a restricted area. Examination of the corpses revealed puncture wounds and bruises which were considered to be the result of prolonged fighting with other chick tending adults.

CHAPTER 4: SECTION II

DAILY MOVEMENTS OF BREEDING DUNLIN

Treatment of the data

The data on Dunlin movements on the breeding grounds were collected from Stilligarry and Drimore Farm study-sites. Preliminary analysis of the data showed that the pattern of movements from the two sites was very similar. Mann-Whitney U-tests showed there were no significant differences between the two sites in the distances moved within each breeding stage, therefore the data from the two sites have been combined.

Movements by adult Dunlin to feeding areas

To investigate the seasonal changes in distances moved to feed the records have been divided into five periods which are defined as follows:

- Pre-laying: To laying of first egg.
- Early incubation: From the laying of the 1st egg to 14 days later
- Late incubation: From 14 days after laying of the 1st egg to hatching
- Chick-rearing: From hatching to the end of brood attendance.
- Post-breeding: From the end of last breeding attempt

The distances travelled from the nest-site to feeding areas by adult Dunlin are summarised for each stage through the breeding season in Table 4.7. The differences between the various stages are tested for significance using the Mann-Whitney U-test (see below Table 4.7).

i) Pre-laying and early incubation stages

There is no significant difference in the distances travelled to feed from the nest-site between the pre-laying and early incubation periods. During these two periods feeding activity was mainly on the breeding territory and its immediate environs; 44% of records are within 70 m of the nest and 64% are within 140 m. The remainder were considered as being away from the breeding territory and they are spread with decreasing frequency to 700 m away from the nest-site (excepting three very early records from the seashore which were just over 1 kilometre away).

ii) Late incubation and chick-rearing stages

There was a significant tendency for the adults to feed further away from the nesting territory during the late incubation and chick-rearing stages than in the two earlier periods (Table 4.8). There is no significant difference in the pattern of distances moved to feed between the late incubation and chick-rearing periods.

During these two periods there is a much smaller proportion of feeding records from the immediate vicinity of the nest; only 24% of records are within 70 m of the nest (cf. 44% in the earlier stages). This difference is highly significant ($\text{Chi}^2 = 9.6$, 1 d.f., $P > 0.01$). Interestingly, the proportion of records between 70 m and 140 m, i.e. near the periphery of the territory, is similar to earlier periods (19% cf. 20%). Therefore, it appears that adult Dunlin were deliberately feeding less close to their nest or chicks during late incubation and chick rearing (however, the intensity of useage per unit area is still greater

within 70m of the nest than further away). This strategy may enhance the survival chances of a bird's nest and chicks either by helping to keep the nest's whereabouts secret from predators or preventing depletion of food supplies for chicks, or both.

The proportion of feeding records between 140 m and 1000 m (37%) from the late incubation and chick-rearing stages is similar to the proportion from the earlier stages (34%), but the proportion over 1 kilometre from the nest (18%) is far higher than in the earlier stages (2%). In most cases these long distance movements are visits to the seashore late in the season (Chapter 3.II). The majority of feeding records during late incubation and chick rearing were clearly from outside the breeding territory (i.e. at least 140 m from the nest); usually, adults chose the closest suitable feeding area to their territory but late in the season the birds at Stilligarry frequently fed on the seashore (Chapter 3.II).

iii) Post-breeding stage

The pattern of feeding movements during the post-breeding stage is significantly different to that of all other stages. By this stage the territory had usually been abandoned and, not surprisingly, there was very little feeding on the nesting territory. The records from this stage are mainly from areas of preferred feeding habitat moderately close (140 to 1000 m) to the nesting territory (31%) and from the seashore (61%). Almost all the records from the seashore were late in the breeding season (Chapter 3.II) and in nearly all cases the birds used the closest area with rich feeding. Birds from both sites favoured the same

stretch of shore for feeding, this was approximately 1.2 km from Stilligarry and 2.2 km from Drimore Farm.

Dunlin brood movements

The records from the chick-rearing stage have been divided into two periods; the first six days (young chicks) and after this period up to fledging (old chicks). Some broods were located more frequently than others. To reduce biases equal weighting is given to each brood by using the mean of the distance from the nest-site for all observations of a brood during each of the two periods. The movement of broods is summarised in Table 4.8. The significance of the differences between the two periods, tested using the Mann-Whitney U-test, is shown below this table.

Old Dunlin chicks (over 6 days old) range significantly further from the nest site than young chicks. The mean distances moved from the nest by broods during the young-chick period show that the broods' activities are concentrated in the immediate vicinity of the nest site; 57% of broods have a mean distance from the nest of under 70 m, and all broods have mean distances of less than 250 m. Later, in the old-chick period, most broods widened the area they used or moved short distances to better habitat. During the old-chick period, 94% of broods remained within a mean distance of less than 250 m from the nest. Only three broods (6%) moved mean distances from the nest of over 250 m the greatest of which was 500 m, in all cases these were broods that hatched late in the season (see below).

Table 4.8: Mean distances moved by Dunlin broods from their nest to chick-rearing areas. The distance categories refer to the mean distance from the nest of all the observations of a given brood during the stage concerned.

MEAN DISTANCE FROM NEST	NUMBER OF BROODS		ROW TOTAL
	Age of brood YOUNG ¹ CHICKS	OLD ² CHICKS	
<70m	26 56.5%	12 26.1%	38 41.3%
70-250m	20 43.5%	31 67.4%	51 55.4%
250-500m	-	3 6.5%	3 3.3%
TOTAL %	46 50.0%	46 50.0%	92 100%

¹ <7 days old
² >6 days old

Result of Mann-Whitney U-test comparing mean distances moved by young and old broods.

SAMPLE 1	N	SAMPLE 2	N	U-STATISTIC	SIGNIF.
Young chicks	46	Old chicks	46	667	***

*** Significant at 0.001 level

Summary and discussion of Dunlin movements

Dunlin defend territories on the breeding grounds (Soikelli 1967, *pers. obs.*). In this study, although there was some overlap between adjacent pairs in the areas utilised, the territories, especially the core of them, were used almost solely by the resident pair. The breeding territories were used for nesting and chick rearing and to a lesser extent for feeding by the adults. Adult Dunlin commonly fed away from their territories, especially during late incubation and chick rearing, and visited communal feeding grounds. These were usually the closest suitable area to the breeding territory; rarely were these feeding areas more than 500 m away. Late in the breeding season, particularly in the post-breeding stage, adult Dunlin often travelled distances of 1-2 km to feed on the seashore.

Dunlin broods were largely reared on the breeding territory, movements of broods of over 250 m from the nest were rare. The size of area used by a Dunlin brood generally increased as the chicks get older. In most cases any movements greater than about 150 m from the nest were well outside the original breeding territory. However, by the time most pairs had chicks other pairs' breeding attempts had failed causing some of them to abandon their territory. The remaining pairs then expanded their territories into these vacated areas. Therefore, the size of area used by a brood depends partly on the density of territory holding pairs present. Some overlap was recorded in the area used by adjacent broods but territorial aggression between adults tending chicks was not seen (cf. Redshank).

CHAPTER 4: SECTION III

DAILY MOVEMENTS OF BREEDING RINGED PLOVER

Treatment of data

To investigate the changes in the pattern of movements of breeding Ringed Plover between different breeding stages the records have been divided up into the following stages:

Early pre-laying: Late March to 20 days before laying.

Late pre-laying: From 20 days before laying to laying.

Incubation: Laying and incubation.

Chick-rearing: From hatching to the end of brood attendance

Post-breeding: From the end of the last breeding attempt

A preliminary comparison between the distances moved during each breeding stage by Ringed Plover at Stilligarry and at Drimore Farm using Mann-Whitney U-tests showed that there was no significant differences between the two sites. The data from these two sites have therefore been combined. The data from Rubha Ardvule are treated separately because of the atypical nature of this site. The sample sizes from Rubha Ardvule are small because for most records the stage of breeding is unknown or the nest site was not found. For the reasons outlined at the start of Chapter 4, all records of feeding and chick-rearing birds are analysed together and all other records are excluded.

The movements of the birds to feed on the seashore are considered separately to the movements within the breeding areas.



Ringed Plover movements at Stilligarry and Drimore Farm

1) Movements on the breeding grounds

The movements of Ringed Plover on the breeding areas at Stilligarry and Drimore Farm are summarised for each stage of the breeding season in Table 4.9; all records from the seashore are excluded from the table. The results of Mann-Whitney U-tests used to determine if the differences in the movements between stages are significant are shown below the table.

There was no significant difference in the range of distances moved by Ringed Plover on the breeding grounds (i.e. not to the seashore) between the incubation and chick-rearing stages. There is also no significant difference between the distances moved from the nest-site by young broods (less than 10 days) and old broods (greater 10 than days). The differences in the movement pattern between the egg and chick stages and the other stages (pre-laying and post-breeding) are however highly significant. The main differences are that during the pre-laying and post-breeding stages the adults foraged over a wider area around the nest-site (i.e up to 200 m from nest-site) and made more trips to forage away from the territory than during the incubation and chick-rearing stages.

Ringed Plover restricted most of their movements to within their breeding territory, especially during incubation and chick-rearing when 80% of records were within 100m of their nest-site. A few adults led their chicks to feeding grounds away from the nest-site. In all these cases the nesting area was on old fallow machair and the chicks were led to habitats that gave better camouflage to the chicks and possibly had better feeding

Table 4.9: Distances moved from the nest-site by Ringed Plover for stages of the breeding season at Stilligarry and Drimore Farm.

DISTANCE FROM NEST	N U M B E R O F R E C O R D S					
	S t a g e ² o f b r e e d i n g					
	EARLY ¹ PRE-LAY	LATE ² PRE-LAY	INCUBTN.	CHICKS	POST-BREED	ROW TOTAL
<100m	32 53.3%	65 73.0%	127 82.5%	149 78.4%	77 64.7%	450 73.5%
100-200m	18 30.0%	12 13.5%	16 10.4%	24 12.6%	26 21.8%	96 15.7%
200-400m	4 6.7%	6 6.7%	10 6.5%	15 7.9%	3 2.5%	38 6.2%
>400m	6 10.0%	6 6.7%	1 .6%	2 1.1%	13 10.9%	28 4.6%
TOTAL	60	89	154	190	119	612
%	12.2%	18.1%	31.2%	31.0%	19.4%	100%

¹ Late March to 20 days before laying

² From 20 days before laying to laying

Results of Mann-Whitney U-tests comparing distances moved in various breeding stages

SAMPLE 1	N	SAMPLE 2	N	U-STATISTIC	SIGNIF.
Early pre-lay	60	Late pre-lay	89	2128	*
Late pre-lay	89	Incubation	154	5456	**
Early pre-lay	60	Incubation	154	2799	***
Young chicks	62	Old chicks	128	3732	N.S.
Incubation	154	Chicks (all)	190	12934	N.S.
Chicks (all)	190	After stage	119	9327	**

N.S. Not significant

** Significant at 0.01 level

* Significant at 0.05 level

*** Significant at 0.001 level

conditions. A few late season broods were moved to the seashore.

In the pre-laying and post-breeding stages approximately 10% of records (excluding seashore records) are from over 400m away from the nest site; in all cases this was considerably outside the territory boundary. The reason why birds should feed away from their territories in these stages is probably connected with finding suitable feeding areas and, in the early part of the breeding season, exploration of alternative breeding areas.

ii) Ringed Plover movements to the seashore

The distances moved to the seashore to feed are summarized in Figure 4.1 At Stilligarry and Drimore Farm none of the Ringed Plover breeding territories included areas of seashore, all visits to the seashore necessitated travelling at least 500 m from the nest site, however, very few nests were more than 1 km from the nearest area of seashore. Ringed Plover rarely fed on the stretch of shore closest to the nest site, instead they flew to the areas with better feeding (Chapter 4). At both sites the same stretch of beach was favoured for feeding, this was approximately 1 km from Stilligarry and 2 km from Drimore Farm. Ringed Plover visiting the seashore before giving up breeding and abandoning their territory always fed no further away than the closest area of seashore with good feeding, this was never more than 2.5 km from the nest site. After abandoning their territory birds also used other more distant beaches for feeding though these were rarely more than 5 km from the breeding territory.

Ringed Plover movements at Rubha Ardvule

The movements of Ringed Plover at Rubha Ardvule are summarised in Table 4.10 for all records except those on the seashore. The movements to feed on the shore are summarised in Figure 4.1.

The general pattern of movements on the breeding grounds at Rubha Ardvule were very similar to those at Stilligarry and Drimore Farm. One difference was that the Rubha Ardvule birds generally remained closer to the core of their territory. This was probably because most of the territories were partly bordered by loch or seashore which restricted movements on the breeding areas. The major difference between Rubha Ardvule and the other sites was in the distance travelled to the seashore to feed. Most seashore feeding was within 400 m of the nest-site; sometimes birds fed on areas of shore adjacent to their territory but in most cases they visited the small beach along the southern edge of the site. After abandoning their territories at the end of the breeding season the majority of Rubha Ardvule Ringed Plovers moved to extensive areas of good seashore feeding habitat nearby (about 900 m north-east and 750 m south-east of the study-site); in the main they stayed here for the non-breeding season.

Summary and discussion of Ringed Plover movements

On their breeding grounds, Ringed Plover pairs occupy distinct territories and these normally contain all the requirements for nesting and chick rearing, as well as most of the adults' feeding requirements. With the exception of visits to the seashore almost all of a Ringed Plover's activity in the breeding season is confined to its territory and immediate

Table 4.10: Distances moved from the nest site by Ringed Plover for stages of the breeding season at Rubha Ardvule.

DISTANCE FROM NEST-SITE	NUMBER OF RECORDS				ROW TOTAL
	Stage ¹ EARLY PRE-LAY	Stage ² LATE PRE-LAY	INCUBTN.	CHICKS	
<100m	10 71.4%	12 85.7%	34 81.0%	5 100.0%	61 81.3%
100-200m	2 14.3%	2 14.3%	7 16.7%	0	11 14.7%
200-400m	0	0			1 1.3%
>400m	2 14.3%		0	0	2 2.7%
TOTAL	18.7%	14 18.7%	42 56.0%	5 6.6%	75 100%

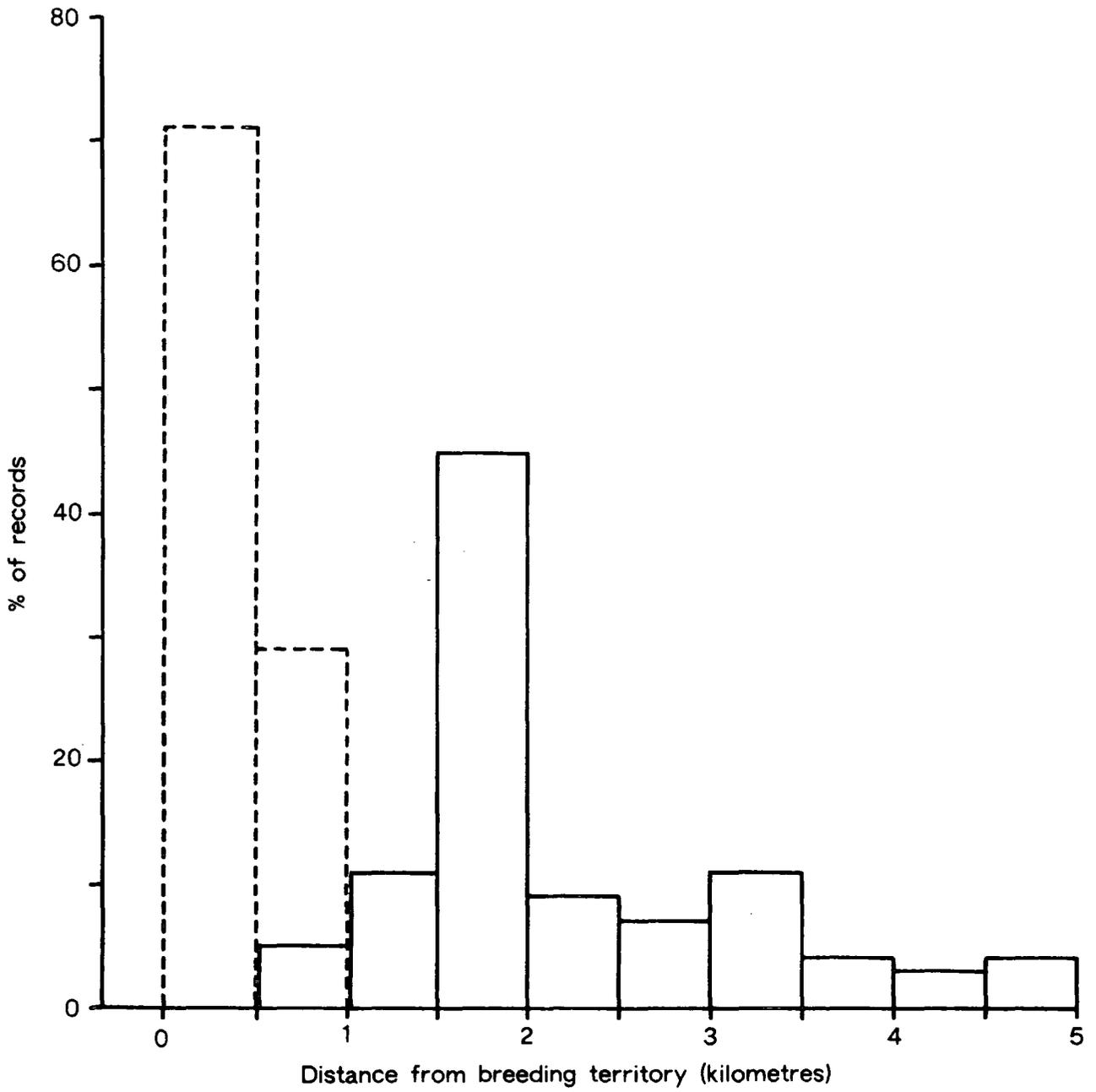
- ¹ Late March to 20 days before laying
² From 20 days before laying to laying

Results of Mann-Whitney U-tests comparing distances moved in various breeding stages

SAMPLE 1		SAMPLE 2	N	U-STATISTIC	SIGNIF.
Early pre-lay	14	Late pre lay	14	71	N.S.
Late pre-lay	14	Incubation	42	272	N.S.
Early pre-lay	14	Incubation	42	175	*
Incubation	42	Chicks (all)	5	86	N.S.

N.S. Not significant ** Significant at 0.01 level
* Significant at 0.05 level *** Significant at 0.001 level

Figure 4.1: Distances travelled by Ringed Plovers from breeding territory to seashore to feed.



 = Rubha Ardvule
n = 89

 = Stilligarry & Drimore Fm.
n = 307

environs; 90% of records were within 200 metres of the nest-site. In this study, chicks were only very occasionally led away from the nest-site to rearing areas outside the territory but this is not surprising because some suitable chick-rearing habitat was available close to most nest-sites. This may not always be the case especially on extensive areas of old fallow. The extent to which pairs in such areas will move their chicks to find better rearing habitat requires further investigation.

Use of a territory was largely confined to the resident pair although there was a certain amount of overlap in the areas utilised by adjacent pairs. Some territory boundaries changed slightly through the season as a result of pairs choosing different nesting areas for their replacement clutches and in response to changes in the habitats. Towards the end of the breeding season, as birds finished attempting to breed, the territories generally broke-up and the remaining breeding birds often expanded their home ranges into unoccupied areas.

The Ringed Plovers' territorial use of their breeding grounds has important implications for their conservation. Clearly, if birds are to benefit, in terms of enhanced breeding success, from having a range of habitat types available in their territory then the patches of habitat need to be of a suitable size and arranged on an appropriate scale.

During the breeding season, the distance moved by Ringed Plover to feed on the seashore was usually the minimum distance to good feeding areas; this ranged from under 100 m to over 2 km from the nest-site. After the breeding season, suitable seashore feeding habitat further from the breeding territory was also

used, though this was rarely more than 5 km away. The majority of Ringed Plover also spent the non-breeding season on beaches within 5 km of their breeding territory (*pers. obs.*).

CHAPTER 5

NEST-SITE CHARACTERISTICS

An important aspect of the breeding habitat requirements of most birds is the nest-site itself. Although birds will use a range of different types of nest-site they usually show preferences for sites with certain characteristics. This is not remarkable because the characteristics of the nest-site can have a marked effect on a bird's fitness. Nests are sought by many predators, either seeking their contents, the attendant adult(s), or both. Because of this birds typically choose nest-sites that minimise the risk of predation e.g. on islands which are often safe from many mammalian predators. Eggs and nidicolous chicks, and to some extent incubating and brooding adults, are confined to the nest for long periods during which they cannot escape from adverse weather. Therefore, birds often choose nest-sites that are in some ways protected from the direct and indirect effects of adverse weather.

In this study, an investigation was made of the characteristics of nest-sites to indicate which are of most importance in nest-site selection. The proximate factors governing nest-site choice by waders in early spring are probably the physical nature of the habitat and the proximity to suitable chick-rearing areas. The physical structure of the habitat around the nest-site can have a marked effect on the survival chances of its contents (Chapter 8). Nests that are well concealed or camouflaged and situated in areas with abundant alternative suitable nest-sites are less likely to be lost to

predators than those that are poorly concealed or situated in small isolated patches of "good" nesting habitat. The most serious danger from adverse weather in the Southern Isles appeared to be the risk of nest flooding after heavy rain.

As will become apparent in the discussions, this approach did not enable a full appraisal of the mechanism of nest-site selection to be made because many characteristics of nest-sites were not independent of each other. Ideally, the process of nest-site selection would be investigated experimentally. This would involve comparing selection in plots where the attributes of potential nest-sites could be manipulated to be independent of each other and in such a way as to provide the birds with simple two-way choices. This approach was not used in this study because it would have involved large scale habitat perturbations which, besides being very expensive to achieve, would not have been allowed on the study-sites because of their legally designated conservation status. (All the study-sites were covered by at least one of the following designations: Site of Special Scientific Interest, National Nature Reserve and Nature Conservation Review site.)

Methods

Each nest-site (defined as the nest and its surrounds up to three metres away) was described at the time of finding. Each description consisted of the habitat type (as defined in Chapter 2) and a nest-site's ratings for various attributes. The attributes were: the height of vegetation, the nature of the ground surface, the tussockiness of the vegetation, the wetness

of the ground, the concealment of the nest and, for Ringed Plover only, the effectiveness of nest camouflage and the presence of surface features next to the nest. The rating method for each of these attributes is detailed in Appendix J.

In most cases, a nest was not described until a few weeks after the time at which birds themselves had selected the site. However, except for a few late nests sited in rapidly growing vegetation, none of a nest-site's characteristics had changed obviously between the dates of selection and later description. Although the nature of the vegetation changes constantly due to growth, senescence and grazing, the magnitude of changes in April and May was too small to seriously affect the broad classification of attribute ratings of a nest-site adopted in this study.

Results

The nest of a Redshank or Dunlin consists of a hollow lined with dried grass positioned in a small tuft or tussock of vegetation or small depression in the ground; typically the nest is well concealed. The Ringed Plover nests in a simple open scrape lined with small items such as pebbles, shell fragments and short straws.

A total of 210 Redshank, 138 Dunlin and 151 Ringed Plover nests were found on the study-sites. The nests of each species were not evenly distributed over the study-sites, they were instead concentrated in areas of preferred nesting habitat (Chapter 6). The number of nests found in each habitat type at each study-site are shown in Appendices G, H, and I for Redshank,

Dunlin and Ringed Plover respectively. The data in these appendices are summarised for groups of similar habitats (habitat categories) using barcharts in Figure 5.1.

The physical attributes of the nest-sites, are summarised in Figures 5.2 to 5.8. The physical attributes are not always independent of each other and, therefore, it is often not always possible to ascertain exactly which factor is of most importance for nest-site selection. However, it is clear that for each species certain types of site predominate whilst others are rarely used.

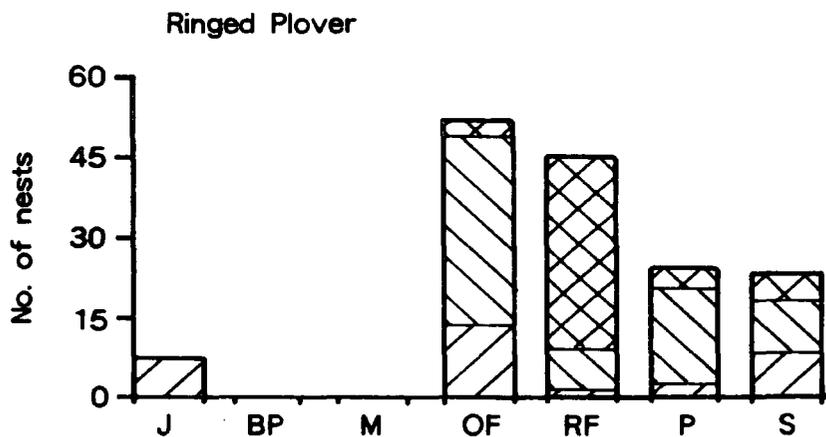
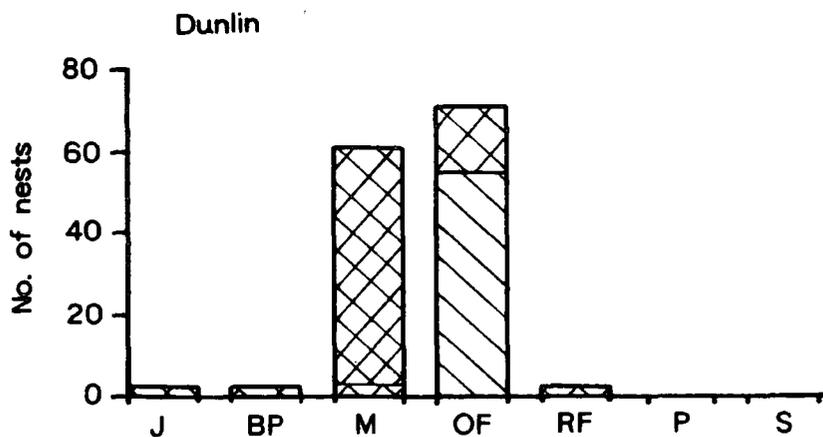
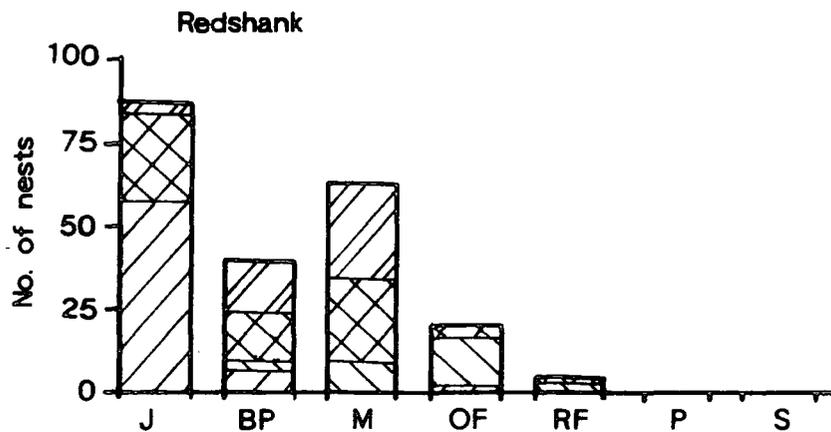
Redshank nest-sites

1) Nesting habitats

Redshank used a wide variety of habitats for nesting, all vegetated habitats except cereal fields, old dry fallow machair, sand dunes and "good" blackland pasture were at times used. However, the most regularly used habitats were those with Soft Rush (*Juncus effusus*) (38% of nests), and all types of marsh (30% of nests). Although old fallow and blackland pasture were used for nesting (27% of nests) they were not used as frequently as expected on the basis of their availability; these were the commonest habitat types. Recent fallow was only rarely used for nesting (1.5% of nests).

The differences between the study-sites in the frequency that each habitat was used for nesting is largely caused by the presence or absence of the habitats. At Stilligarry, where there was very little *Juncus* or marsh habitats, the majority of Redshank nests (56%) were in old damp fallow machair. In

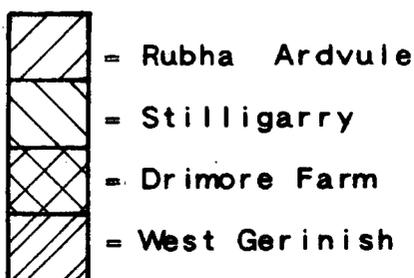
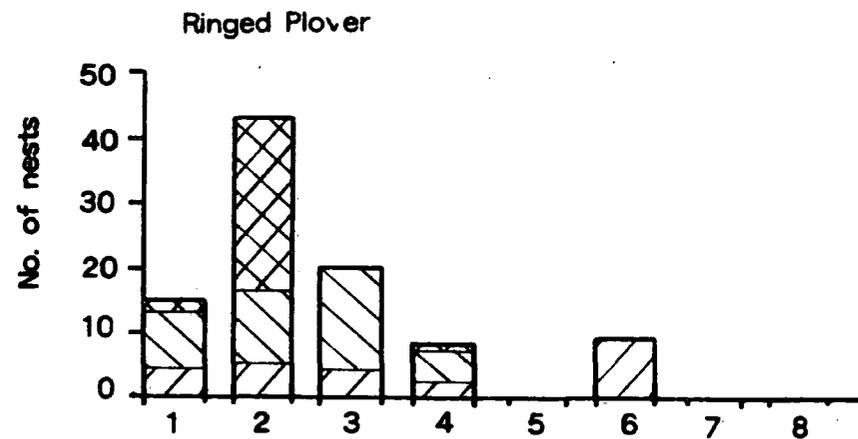
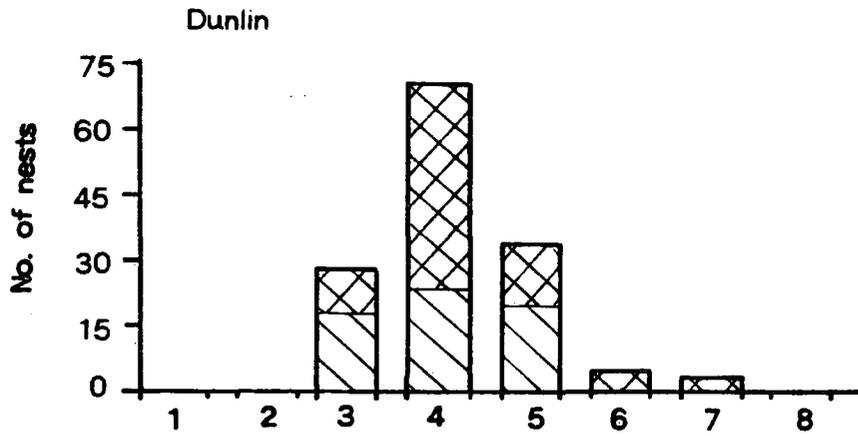
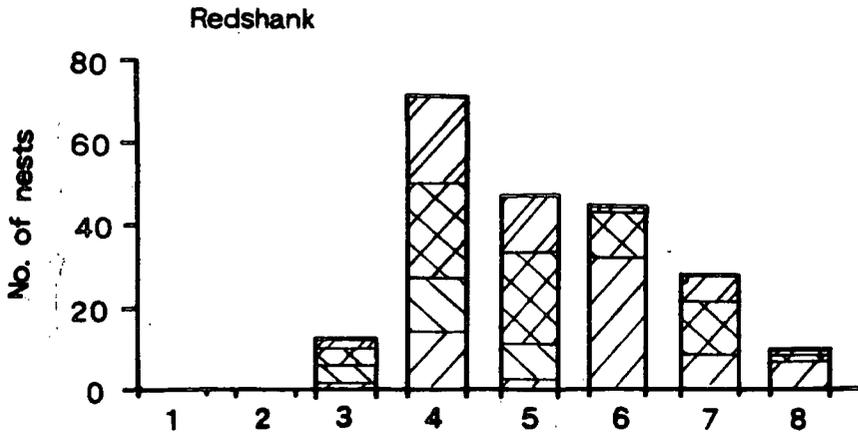
Figure 5.1: Habitats used for nesting by Redshank, Dunlin and Ringed Plover.



= Rubha Ardvule
 = Stilligarry
 = Drimore Farm
 = West Gerinish

J = Juncus & Iris (I, J, K)
 BP = Blackland pasture (W, R)
 M = Marsh (M, N, O)
 OF = Old Fallow (E, B)
 RF = Recent Fallow (F, S)
 P = Plough (P, Q)
 S = Shingle (T, X)

Figure 5.2: Height of vegetation around Redshank, Dunlin, and Ringed Plover nests.



- 1 = Bare ground
- 2 = Bare ground & short vegetation
- 3 = Short veqt. only (<5cm)
- 4 = Short & medium length veqt.
- 5 = Medium veqt. only (>5 & >15cm)
- 6 = Short, medium & tall veqt.
- 7 = Medium and tall veqt.
- 8 = Tall veqt. only (>15cm)

Figure 5.3: Type of ground surface around Redshank, Dunlin, and Ringed Plover nests.

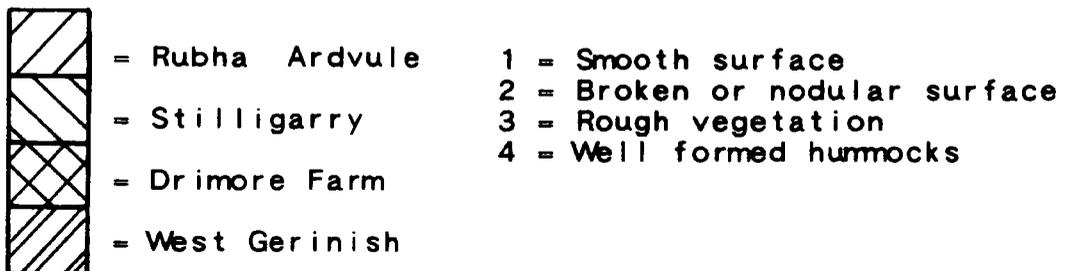
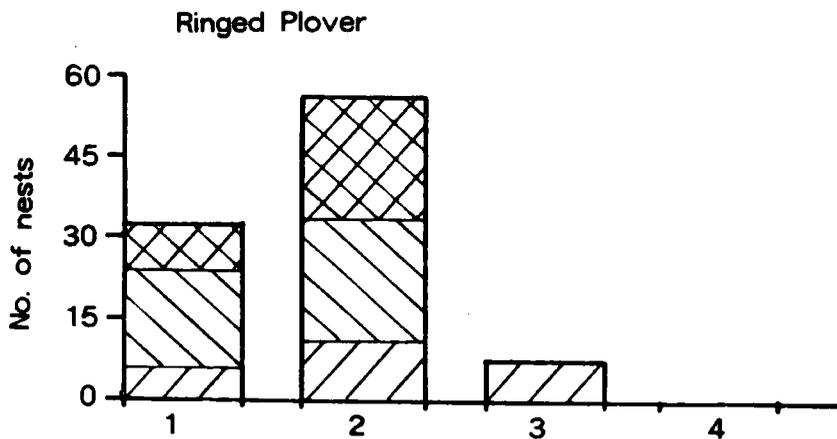
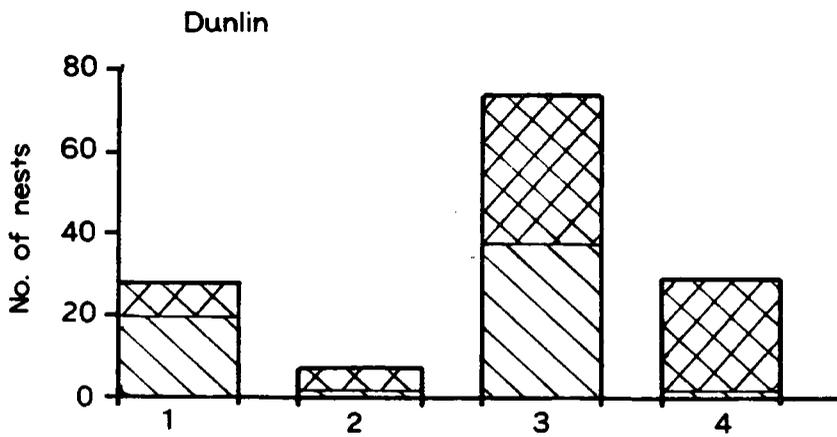
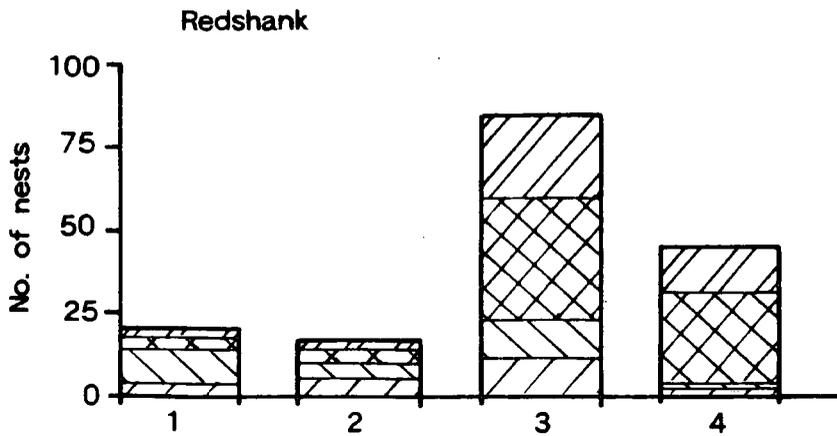


Figure 5.4: Tussockiness of vegetation around Redshank, Dunlin, and Ringed Plover nests.

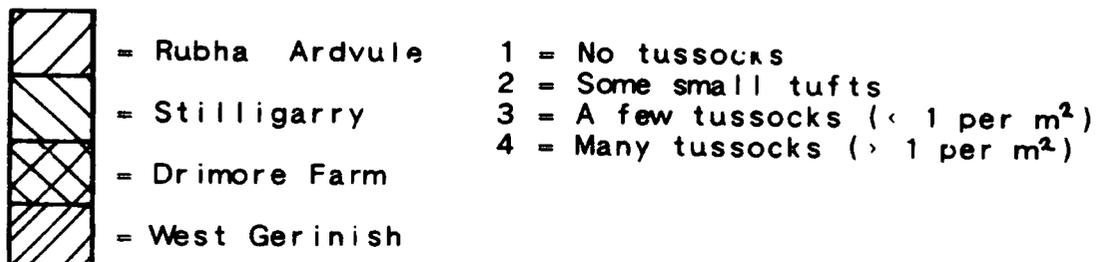
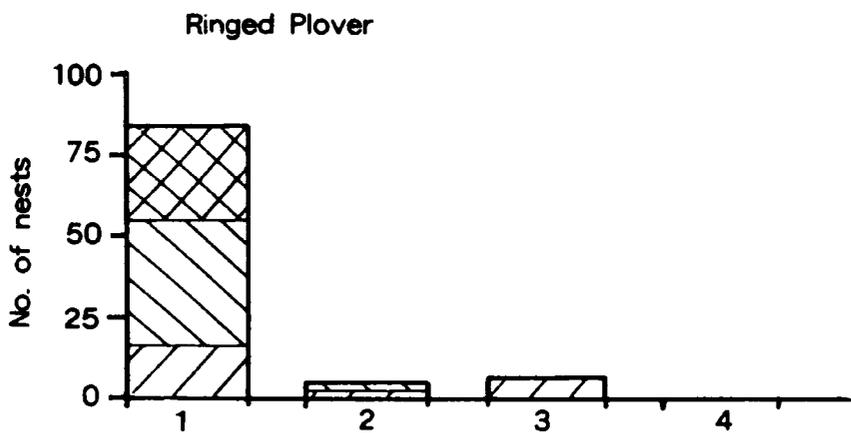
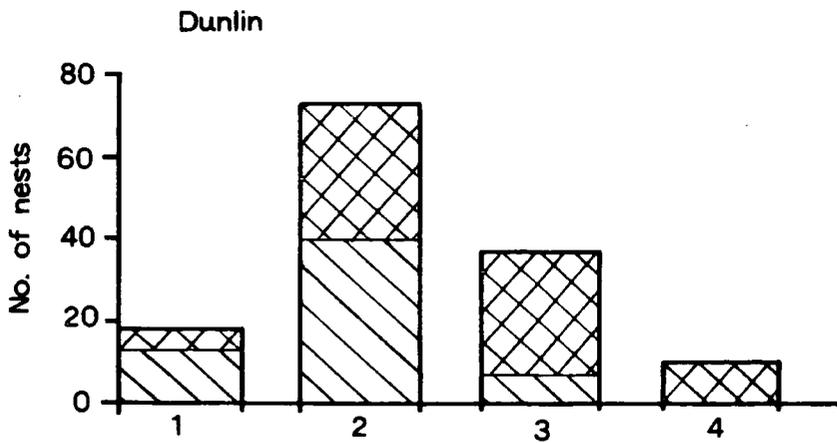
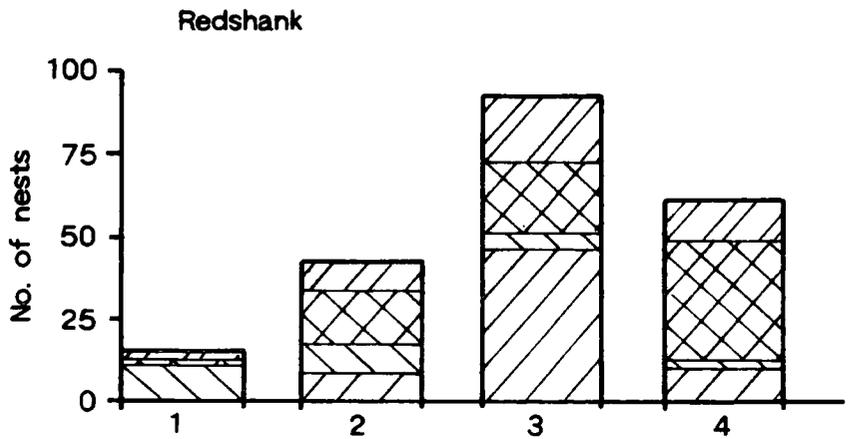
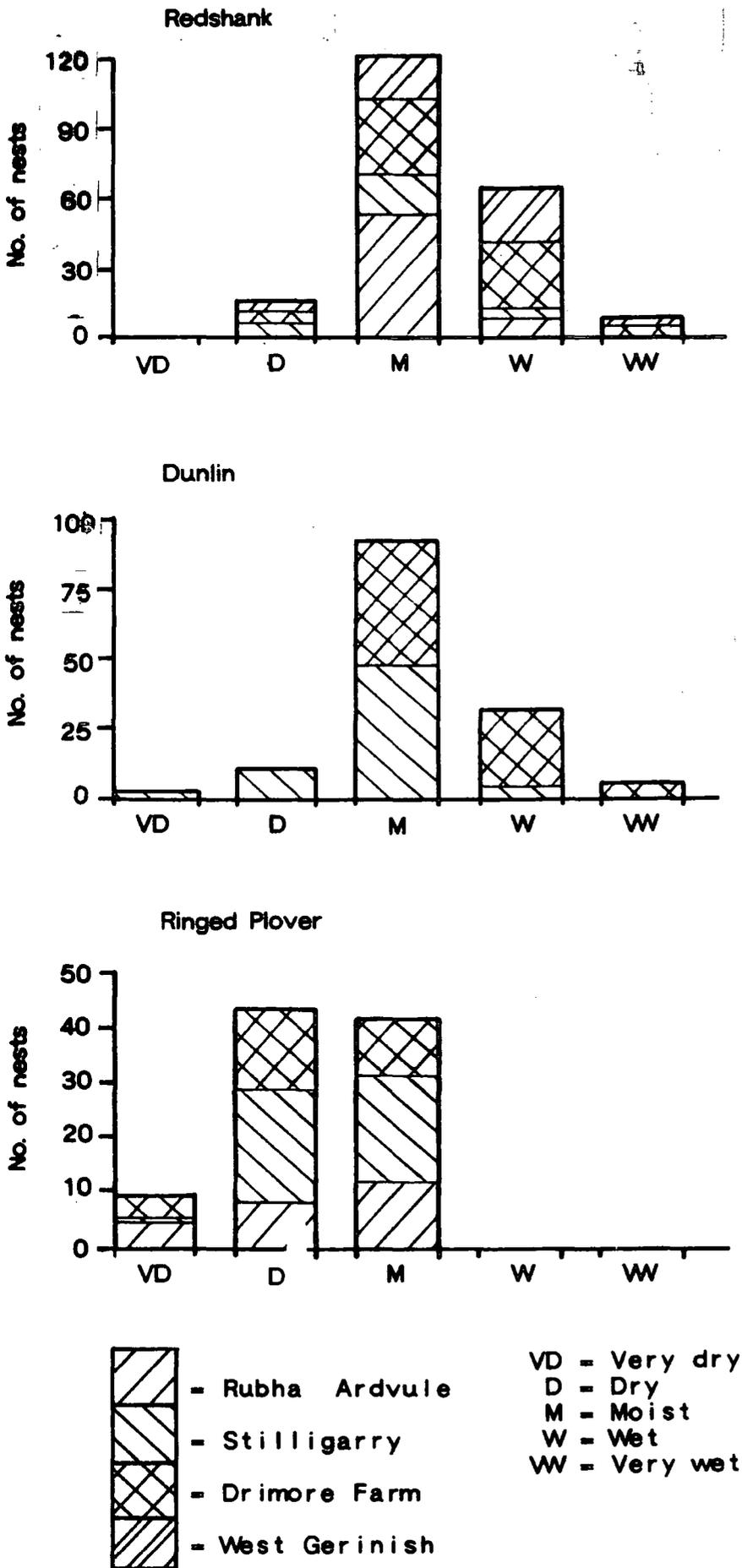
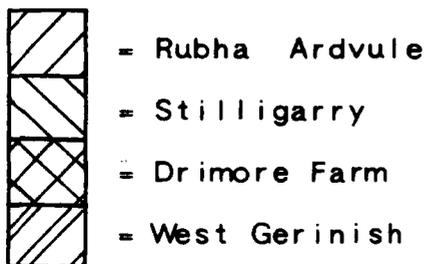
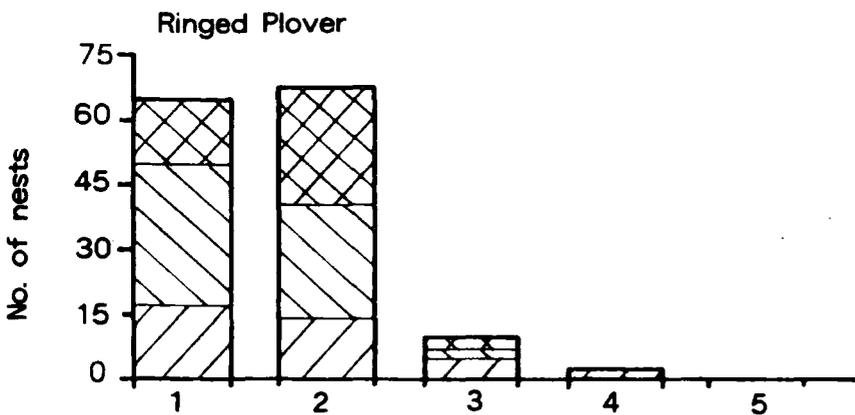
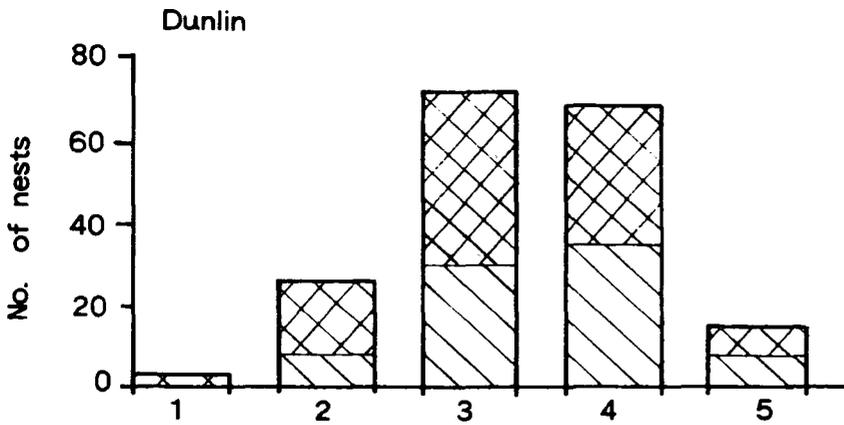
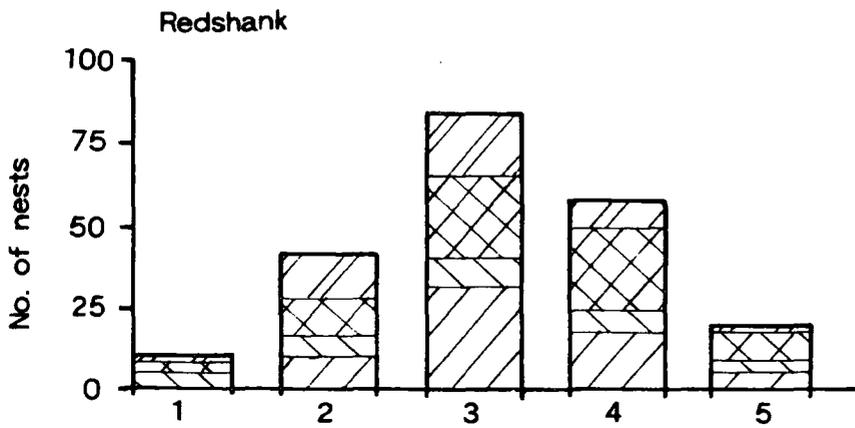


Figure 5.5: Wetness of the ground around Redshank, Dunlin, and Ringed Plover nests.



	= Rubha Ardvule	VD = Very dry
	= Stilligarry	D = Dry
	= Drimore Farm	M = Moist
	= West Gerinish	W = Wet
		WW = Very wet

Figure 5.6: Concealment of Redshank, Dunlin, and Ringed Plover nests.



- 1 = No side or top cover, open
- 2 = A little side cover
- 3 = Good side cover, no top cover
- 4 = Good side cover and some top cover
- 5 = Good top and side cover

Figure 5.7: Presence of features by Ringed Plover nests.

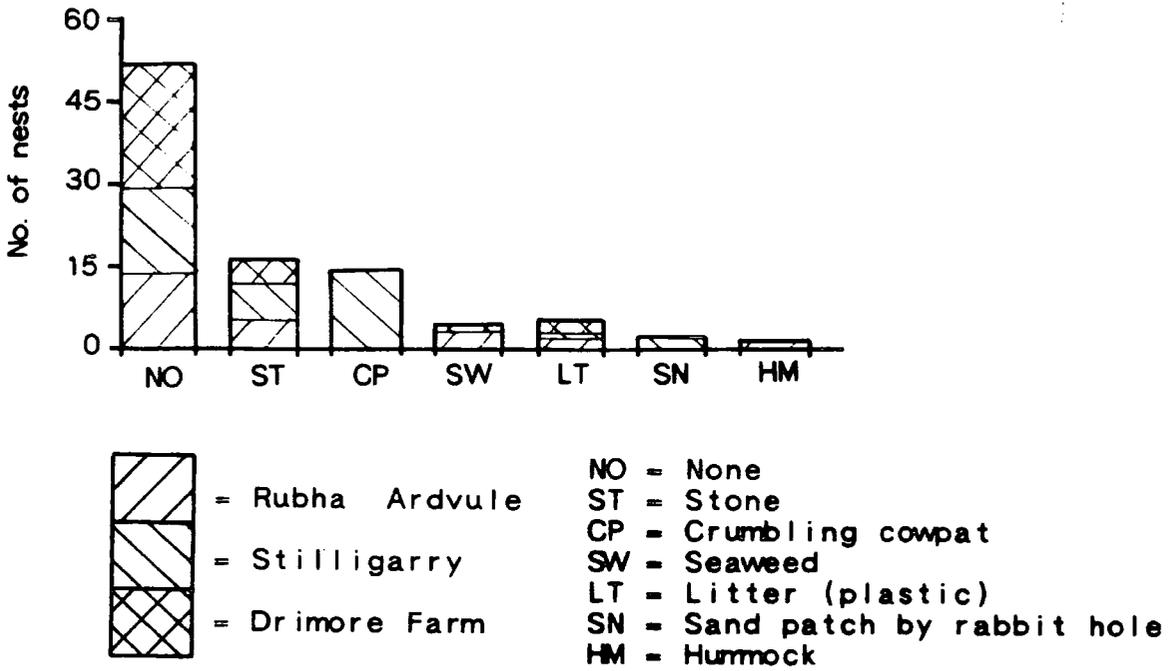
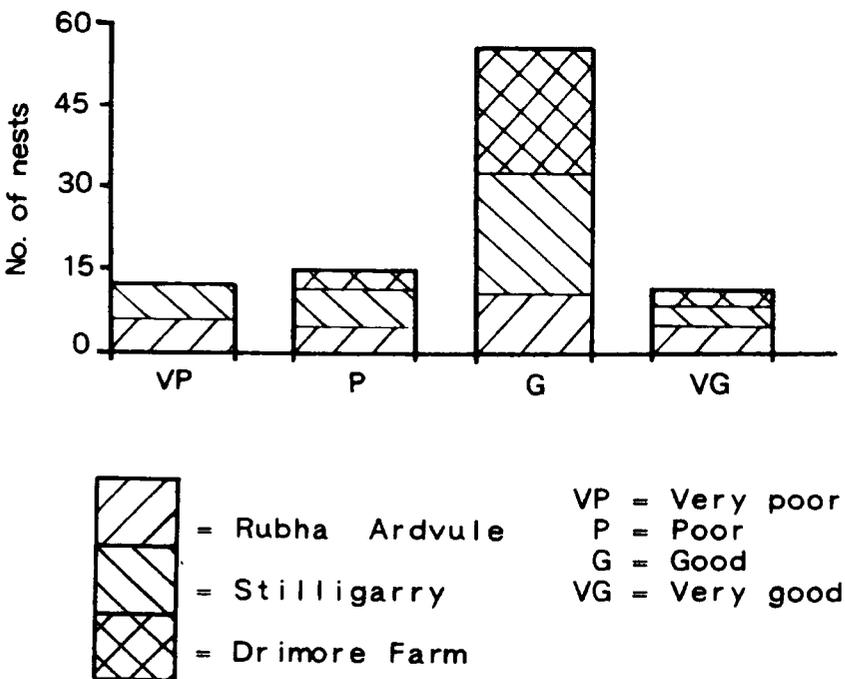


Figure 5.8: Camouflage of Ringed Plover nests.



contrast, at Drimore Farm where there were large amounts of all habitats present, the birds showed a strong preference for marsh and *Juncus* pasture and very few nests (5%) were in old damp fallow machair. This suggests that Redshank preferentially selected certain nesting habitats (those with better cover) when there was a range of nesting habitats available.

ii) Nest-site characteristics

Very few Redshank nests were in areas with solely short sward vegetation presumably because of the difficulty in finding nest-sites with good concealment. Medium length vegetation (5-20 cm. tall), with or without some short or tall vegetation as well, was most preferred for nesting; 90% of nest-sites had some medium length vegetation in their immediate vicinity. Areas composed entirely of tall vegetation (over 20cm) such as hay fields and well grown *Iris* beds were rarely used (4% of nest). Continuous tall vegetation may be avoided for nesting because the incubating bird is unable to see approaching predators (see later discussion).

Most Redshank nest-sites were in areas where the vegetation produces a rough surface texture (61% of nests), or where the ground surface was hummocky (22% of nests). Areas with a smooth even surface and areas where the surface was only slightly broken-up (e.g. poached by livestock) were seldom used for nesting. When such nest-sites were used, the surrounding area rarely had any rough or hummocky ground that the birds could choose from. Redshank clearly preferred to nest in areas with tussocky vegetation as 73 % of nests were in areas that had some

well formed tussocks and areas with no tussocks were rarely used. Very dry areas were not used for nesting by Redshank presumably because they usually had short, even vegetation that provided inadequate cover. Wet marshy areas, despite having suitable cover, were seldom used for nesting, probably because of the risk of flooding and the difficulty of keeping the nest dry. The Redshank nests that were in areas of wet marsh were all sited on a hummock or in a large tussock and were thus protected from flooding and dampness.

Dunlin nest-sites

i) Nesting habitats

Almost all Dunlin nests were on machair and marsh habitats with a closed sward. At Stilligarry, where there was very little marsh habitat available, old damp fallow was by far the most important nesting habitat (77% of nests). Old dry fallow was also used but much less frequently than would have been expected on the basis of the area present (the area of old dry fallow present was only slightly less than that of old damp fallow). This was probably because dry fallow tended to have a shorter sward and was an inferior feeding habitat for chicks (see Chapter 3.II) which is important because Dunlin chicks rarely fed far from their nest (Chapter 4.II). Recent fallow was rarely used by Dunlin for nesting, presumably because of inadequate cover for nest and chicks; the only recorded occurrences were on an area of well vegetated second-year fallow. At Drimore Farm, most Dunlin nests (74%) were on marsh habitat, particularly hummock marsh. Dunlin clearly had a preference for hummock marsh over damp

marsh; the area occupied by hummock marsh is approximately half that occupied by damp marsh yet it was more frequently used for nesting. The nests of Dunlin on hummock marsh were nearly always situated on a hummock, the advantages of this are discussed later. The value of wet marsh as a nesting habitat appears to be about equal to that of damp marsh, the difference in the frequency they were used reflects their availability. Some areas of wet marsh were apparently unsuitable for nesting because the vegetation was too tall or the ground too wet (see below). The Dunlin that nested on old damp fallow at Drimore had no marsh within their territory. In the few territories which contained both marsh and old damp fallow, marsh was invariably chosen for nesting and this suggests that this is the preferred habitat. Dunlin with territories on the machair-blackland transition zone usually nested on marsh habitats but some nested on areas of either rough or damp blackland pasture and also in areas with Soft Rush providing it was not too tall or dense.

ii) Nest-site characteristics

Most Dunlin nests were situated in areas with a mixture of short and medium tall vegetation and very few nests had any tall vegetation (over 20cm) in their immediate vicinity. Areas of continuous short sward were frequently used for nesting, particularly at Stilligarry where many of the territories had no medium length vegetation. The nests in such areas were however usually situated in a small nest-sized depression and were thus moderately well hidden, especially once the vegetation had grown a little. Although Dunlin probably prefer areas with rough

vegetation or hummocks they clearly have no strict requirements as to the surface texture of the nest-site. This is because, being small (cf. Redshank nests), the nest can be effectively hidden in only a small tuft or depression. Few nests were in areas with broken ground but this is not surprising as areas with a closed sward rarely had a broken or nodular surface. Dunlin nested in vegetation of all degrees of tussockiness though areas with small ill-formed tussocks (tufts) were probably the most preferred. Unless there were some small depressions, areas with no dead tussocky vegetation may provide no "good" nest-sites until late in the season when the vegetation has grown sufficiently to give some cover. Areas with a high density of well formed tussocks were of little importance to nesting Dunlin and this may explain why areas of *Juncus* pasture and damp blackland pasture were not important breeding habitats (Chapter 3.II). Nesting Dunlin favoured open situations and appeared to avoid areas that were very tussocky or had tall vegetation. The reason for this may be that the tall vegetation would obscure part of a bird's visual field which would reduce its ability to detect predators. Dunlin nesting on hummocks are slightly raised above the general surface and thus have an enhanced view of their surroundings which may aid early detection of danger. A second advantage in nesting on hummocks is the vastly reduced danger of flooding. Heavy rain in May and June can flood areas of marsh and machair and drown dunlin nests, especially those in surface depressions. In 1985, heavy rain in late May flooded several Dunlin nests causing their desertion, none of these nests were on hummocks. Most Dunlin nests were in areas with damp or wet

ground because these areas tended to have the best nest cover and were preferred for chick rearing (Chapter 3.II).

Ringed Plover nest-sites.

1) Nesting habitats

Ringed Plover nested on all types of machair habitat and gravel tracks. A Ringed Plover's choice of nesting habitat is limited to those habitats present in its territory. Usually Ringed Plover appeared to select the habitat that gave the best camouflage for their eggs. Recent fallow, especially first-year fallow, and newly ploughed land were particularly favoured. Although old damp fallow machair was the most frequently used nesting habitat it was not the most preferred. Old damp fallow was the predominant habitat over much of the machair and many Ringed Plover territories (especially at Stilligarry) had no other habitats available. The nests in territories containing a mixture of old fallow and bare or partly vegetated habitats were invariably located on the latter habitats. Gravel tracks, especially in territories dominated by old fallow were a particularly favoured nesting habitat. At Rubha Ardvule, where most territories have no typical machair habitats, Ringed Plover nested on old grassland, in Iris beds, at the edge of patches of Soft Rush and on shingle beach. Even though some areas of marsh had a short sward, Ringed Plover never nested on marsh habitats.

ii) Nest-site characteristics

Ringed Plover nests were usually in areas with bare ground or short vegetation. Except at Rubha Ardvule, very few nests had

any vegetation greater than 5 cm. high in their vicinity and those that had were late season nests. At Rubha Ardvule, nearly half of the nests had some medium or tall vegetation close to the nest but in all these cases short sward predominated. The preference for short vegetation meant that very few nests were in areas with tussocky vegetation though at Rubha Ardvule, 25% of nest-sites had some well formed tussocks. The range of nest-site used at Rubha Ardvule suggests that Ringed Plover have no strong aversion to nesting in areas with some tussocks and medium/tall vegetation provided that the nesting area is dominated by short vegetation or bare ground.

The effectiveness of a nest's camouflage against detection by predators (mainly gulls) was estimated subjectively from a human point of view. This may not correspond to the true value of camouflage from a point of view of a predator. Although the overall trend in perceived camouflage is likely to be similar, the threshold at which camouflage prevents a nest's detection may vary between predator species. Ringed Plover eggs are pale brownish grey in colour with a few dark flecks and are easily seen against green vegetation. They are less easily seen against machair soil (which is similarly coloured) especially if the surface is somewhat broken (e.g. newly ploughed machair and recent fallow) and they are "difficult" to see against a background of small rounded pebbles (e.g. shingle tracks). It may not only be the camouflage of the eggs that is important, but also the camouflage of the incubating bird. A sitting Ringed Plover with its pale brown mantle and disruptive head markings is generally difficult to see against bare or partly vegetated

habitats, but on short sward is easily spotted. The majority (75%) of Ringed Plover nests on short sward were located adjacent to (within 5 cm) or on a small physical feature such as a dried crumbling cowpat, a small rock, plastic litter or a patch of bare sand by a rabbit-hole. The reason for choosing such sites was probably to aid the camouflage of the nest and sitting bird. If the density of suitable surface features on short sward is low, then nesting next to them could have a deleterious effect on nest survival because predators may learn to associate features (which are easily seen) with nests. The crumbling remains of cowpats were the most common type of surface feature (55% of cases). The reason for this is probably not because they provide the best camouflage but because if present there are usually very many, and thus they may aid camouflage without advertising the nest-site.

iii) Importance of cattle

Most Ringed Plovers nesting on the machair are directly or indirectly dependent on cattle for their nest-sites. The birds nesting on old fallow frequently use cowpats and those nesting on plough and recent fallow are using habitats that exist only because of the need to grow cereals as winter cattle fodder. If the machair was used solely for sheep production, there would almost certainly be a large decrease in ploughing as there would be no absolute necessity to grow winter fodder. Although there would be a corresponding increase in old fallow, its value for nesting would be low because of the absence of cowpats.

It is clear from the information presented above and in

Chapter 3.III that, in general, Ringed Plover habitats are formed as a consequence of cattle rearing. The long term survival of a large breeding population of Ringed Plover in the Southern Isles depends on the availability of suitable habitat. It would seem inevitable that suitable habitat for Ringed Plover will only exist as long as the islands continue to have a traditional, cattle based agricultural system. Whether this is so will be determined by economic factors.

Factors influencing the concealment of nests

i) Winter conditions and grazing pressure

During harsh winters (for example in 1985/86), livestock may eat almost all the standing vegetation and by the time the birds return to nest there can be virtually no dead tussocky vegetation remaining over large tracts of machair and marsh. The availability of adequate nesting cover in a given season was reflected by the concealment ratings of the birds' nests. After a harsh winter Dunlin and Redshank breeding on machair and marshes may not be able to find good quality nesting cover and consequently have poorly concealed nests. In Tables 5.1 and 5.2, (for Redshank and Dunlin respectively) a comparison of the concealment ratings is made between 1986, after a harsh winter, and 1985 and 1987 combined, which both followed benign winters. Only nests started before June are used in this comparison because after that date there was always ample cover from freshly grown vegetation. Chi-squared tests comparing the concealment ratings of the nests after benign and harsh winters show that in both species the concealment of nests was significantly poorer

Table 5.2; Concealment of early season Dunlin nests after harsh and benign winter conditions.

N U M B E R O F N E S T S			
CONCEALMENT RATING	FOLLOWING A HARSH WINTER (1986)	FOLLOWING A BENIGN WINTER (1985 & 87)	ROW TOTAL %
1	1 3.4%	0	1 1.0%
2	9 31.0%	6 8.7%	15 15.3%
3	16 55.2%	26 37.7%	42 42.9%
4	3 10.3%	32 46.4%	35 35.7%
5	0	5 7.2%	5 5.1%
TOTAL %	29 29.6%	69 70.4%	98 100.0%

Chi² = 17.9, 2 d.f., P < 0.0001 SIGNIFICANT

Concealment ratings 1 and 2, and 4 and 5 are combined.

Concealment ratings: 1 = No concealment
5 = Total concealment

Definitions of concealment ratings are given in Appendix J

after a harsh winter (see Tables 5.1 and 5.2). To give large enough sample sizes for the chi-squared tests, concealment ratings 1 and 2, and 4 and 5 were combined.

Nest survival is positively correlated with concealment and therefore, the intensity of winter grazing can clearly influence the birds' breeding success. If winter grazing intensity is too high then the availability of good quality nest-sites is drastically reduced and as a result the birds' breeding success is impaired. Conservation measures for waders requiring dead and tussocky vegetation for nesting must ensure that winter grazing by livestock does not remove too much of the standing vegetation. This could be achieved by controlling stocking levels or by reducing grazing pressure through supplementary winter feeding.

ii) Danger of adult mortality whilst incubating

The probability of a clutch surviving to hatch is positively correlated with a nest's concealment (Chapter 8). However, it appears that Redshank and Dunlin do not always attempt to maximise the concealment of their nests. It was not unusual for there to be many, apparently suitable, potential nest-sites with higher concealment ratings close to a nest. The reasons why this should be so are unclear but there may be some disadvantage to having a very well concealed nest. The disadvantage could be that adults incubating eggs at very well concealed nests have a higher risk of mortality because they can less readily detect approaching predators and are thus more susceptible to being surprised and caught. No known instances of death of incubating birds occurred during this study. However, Soikkeli (1967) found

that Dunlin nesting in Finland were occasionally killed by ground predators whilst incubating. Even if a rare event, the predation of incubating adults could be a strong selective force on nest-site choice. Waders are long-lived birds (Chapter 8) and can expect to breed several times during their life. To optimise their lifetime reproductive output, Redshank and Dunlin may have to compromise between maximising the success of each reproductive attempt and their own survival.

Associations with other species

Ground nesting birds vary in the boldness with which they will defend their nest from predators. Some birds, notably Lapwing (Elliot 1985) and Arctic Tern (*Sterna paradisaea*), and to a lesser extent Oystercatcher, communally mob predators until they leave an area, and in this way enhance the survival of their nests. Other birds particularly the smaller waders such as Dunlin and Ringed Plover, and to a lesser extent Redshank, are much more timid in their reaction to predators. Although they may alarm at, feign injury to, or fly around predators they do not threaten them by "dive-bombing" and consequently they are largely ineffective in driving predators away.

The nesting success of the "timid" species can be significantly enhanced by nesting in the vicinity of "bold" species (Dyrce *et al.* 1981, Goransson *et al.* 1975). In this study, this aspect of nest-site choice was not investigated, however, it was noticed that some nests of Redshank, Dunlin and Ringed Plover were very close (<5 metres) to those of Lapwing and that, in general, those areas with many nesting Lapwing were also

those most favoured by other species. There is no doubt that the presence of bold species can affect both nest-site choice and breeding success of the timid species. The conservation of timid wader species not only requires provision to be made for their habitat requirements but also for those of bold species, especially Lapwing, so that they can benefit from their anti-predator behaviour.

CHAPTER 6

BREEDING DENSITY

The preceding chapters do not enable a full appraisal to be made of the intrinsic value of the major habitat divisions to each species. A measure of this can be obtained by examining the breeding densities achieved in the different habitats. The aim of this chapter is to do this for the birds breeding on the study-sites and to suggest which factors are of most importance in determining breeding density.

Methods

The number of pairs of Redshank, Dunlin and Ringed Plover attempting to breed in the core area of each study-site was estimated, in most cases, each year. The figures were derived by summation of the number of colour-ringed pairs and the number of unmarked pairs present on the study-sites. Typically, approximately 75% of the pairs in an area contained at least one colour-ringed member. The number of unmarked pairs was estimated from the number of nests and broods found belonging to unmarked pairs together with any other unmarked pairs that showed signs of breeding and which were definitely additional (because they were seen simultaneously) to any unmarked pairs already noted. The position of the nesting area of each pair was marked on 1:5000 scale maps of the study-sites divided into major habitat types and from these maps the breeding densities were calculated.

Breeding waders at high densities are difficult to count accurately (Jackson & Percival 1983, Reed *et al.* 1983, 1985),

especially Dunlin and Redshank, because only a proportion of the individuals breeding in an area are usually seen on a single visit. The method described above gives a minimum number of pairs present but may in some cases underestimate the actual population; subjectively however, the degree of underestimation is thought in no case to exceed 10%.

Because the nests of each species were restricted to certain habitats only (Chapter 8), yet the birds themselves often used a far wider range of habitats, an attempt is made to calculate separate values for nesting densities (based on the area of suitable nesting habitats only) and overall breeding densities (based on all habitats used by the birds nesting in an area). The areas of the study-sites covered by loch are excluded from all density calculations.

Results

The number of breeding pairs and the breeding densities at each study-site are shown in Tables 6.1, 6.2 and 6.3 for Redshank, Dunlin and Ringed Plover respectively. For each species there is a great variation in the nesting and overall breeding densities between the major habitat divisions; within each of these habitat divisions however, there is, in general, moderate similarity in density between sites. In all cases the highest nesting densities occurred in areas with abundant good quality nest sites (Chapter 5).

Table 6.1: Number and density of breeding pairs of Redshank on the study-sites.

STUDY-SITE HABITAT	NUMBER OF PAIRS (Area Ha)			MEAN DENSITY PRS/KM ²
	1985	1986	1987	
RUBHA ARDVULE				
Nesting habitats ¹	22 (7.2)	21 (7.2)	20 (7.2)	292
Whole site ²	22 (27.0)	21 (27.0)	20 (27.0)	78
WEST GERINISH				
B-M transit. nest hab. ¹	19 (22.0)	19 (22.0)	21 (22.0)	90
B-M transit. overall	19 (43.0)	19 (43.0)	21 (43.0)	47
STILLIGARRY				
B-M transit. nest hab. ¹	7 (9.8)	6 (9.8)	7 (9.8)	68
B-M transit. overall	7 (17.3)	6 (15.8)	7 (15.8)	41
DRIMORE FARM				
Blackland nest. hab. ¹	/	32 (36.8)	30 (36.8)	84
Blackland overall	/	32 (54.3)	30 (54.3)	57
Machair marsh	/	7 (10.5)	7 (10.5)	67
STILLIGARRY				
Old fallow mach.	3 (40.8)	5 (40.8)	8 (42.8)	13
Recent fallow mach.	1 (4.3)	1 (4.3)	0 (1.3)	20
Plough/cereal	0 (3.3)	0 (4.8)	0 (5.8)	0
Cultiv. mach. overall	4 (48.4)	6 (49.9)	8 (49.9)	12
Dunes	0 (13.0)	0 (13.0)	0 (13.0)	0
DRIMORE FARM				
Old fallow mach.	/	2 (25.3)	3 (25.3)	10
Recent fallow mach.	/	1 (14.3)	0 (7.3)	5
Plough/cereal	/	/	0 (7.0)	0
Re-seeded mach.	/	0 (9.8)	0 (9.8)	0
Cultiv. mach. overall	/	3 (49.3)	3 (49.3)	6
Dunes	/	0 (20.8)	0 (20.8)	0

/ not determined

¹ Includes all habitats used for nesting (Chapter 5).

² Includes all dry-land and littoral habitat, loch excluded.

Table 6.2: Number and density of breeding pairs of Dunlin on the study-sites.

STUDY-SITE HABITAT	NUMBER OF PAIRS (Area Ha)			MEAN
	1985	1986	1987	DENSITY PRS/KM ²
RUBHA ARDVULE				
Nesting habitats ¹	9 (7.2)	9 (7.2)	8 (7.2)	120
Whole site ²	9 (12.8)	9 (12.8)	8 (12.8)	68
WEST GERINISH				
B-M transit. nest habs. ¹	/	22 (22.0)	/	100
B-M transit. overall	/	22 (43.0)	/	51
STILLIGARRY				
B-M transit. nest habs. ¹	4 (13.5)	5 (12.0)	4 (12.0)	35
B-M transit. overall	4 (17.3)	5 (15.8)	4 (15.8)	27
DRIMORE FARM				
Blackland nest. habs. ¹	/	12 (26.8)	15 (26.8)	51
Blackland overall	/	12 (41.0)	15 (41.0)	33
Machair marsh	/	24 (10.5)	23 (10.5)	224
STILLIGARRY				
Old fallow mach.	20 (29.5)	22 (29.5)	30 (42.8)	71
Recent fallow mach.	2 (4.3)	2 (4.3)	0 (1.3)	41
Plough/cereal	0 (3.3)	0 (4.8)	0 (5.8)	0
Cultiv. mach. overall	22 (37.0)	24 (38.5)	30 (49.9)	61
Dunes	0 (11.5)	0 (11.5)	0 (13.0)	0
DRIMORE FARM				
Old fallow mach.	/	21 (25.3)	25 (25.3)	91
Recent fallow mach.	/	3 (14.3)	2 (7.3)	18
Plough/cereal	/	/	0 (7.0)	0
Reseeded mach.	/	0 (9.8)	0 (9.8)	0
Cultiv. mach. overall	/	24 (49.3)	27 (49.3)	52
Dunes	/	0 (20.8)	0 (20.8)	0

/ not determined

¹ Excludes all habitats not used for nesting (Chapter 5).

² All dry land, loch and littoral habitats excluded.

Table 6.3: Number and density of breeding pairs of Ringed Plover on the study-sites.

STUDY-SITE HABITAT	NUMBER OF PAIRS (Area Ha)			MEAN
	1985	1986	1987	DENSITY PRS/KM ²
RUBHA ARDVULE				
Uncultivated land	14 (12.8)	13 (12.8)	13 (12.8)	104
Cultivated machair	3 (4.3)	1 (4.3)	2 (4.3)	47
Whole site ¹	17 (20.0)	14 (20.0)	15 (20.0)	77
STILLIGARRY				
B-M transit. overall	0 (17.3)	0 (15.8)	0 (15.8)	0
DRIMORE FARM				
Blackland overall	/	2* (41.0)	2* (41.0)	5
Machair marsh	/	1# (10.5)	1# (10.5)	10
STILLIGARRY				
Old fallow mach.	18 (29.5)	11 (29.5)	13 (51.5)	38
Recent fallow mach.	7 (4.3)	7 (4.3)	9 (3.8)	188
Plough/cereal	6 (3.3)	9 (4.8)	15 (7.8)	190
Cultiv. mach. overall	31 (37.0)	27 (38.5)	37 (63.0)	69
Dunes	0 (11.5)	0 (11.5)	0 (16.0)	0
DRIMORE FARM				
Old fallow mach.	/	7 (25.3)	6 (25.3)	26
Recent fall. Block 1	/	31 (7.3)	27 (7.3)	400
Recent fall. Block 2	/	6 (7.0)	/	86
Plough/cereal Block2	/	/	5 (7.0)	71
Reseeded machair	/	2 (9.8)	3 (9.8)	26
Cultiv. mach. overall	/	46 (49.3)	41 (49.3)	88
Dunes	/	0 (20.8)	0 (20.8)	0

/ not determined

- ¹ Includes all dry land and beach, loch and rocky shore excluded
 * One pair based on gravel track
 # Pair used gravel track almost exclusively

Determinants of breeding density

1) Theoretical considerations

The breeding density in an area is determined by the number of birds that settle in that area at the start of the season. The high site fidelity (Chapter 7) and survival rates (Chapter 8) of Redshank, Dunlin and Ringed Plover mean that the majority of the birds in an area will have bred there in previous years. Therefore, for most of the population, the decision to breed in an area or move elsewhere is probably based largely on previous knowledge of the area rather than a fresh assessment at the start of each season. This system would be best suited to areas where the habitat remains unchanged from year to year as knowledge of previous conditions can then be used to accurately predict future conditions. In areas where the habitats are liable to change fundamentally between seasons (e.g. cultivated machair) such a system would be less suited and might be expected to result in a lag between the habitat change and any redistribution of the established breeding birds. Birds breeding for the first time in an area will have little or no previous knowledge of the area and must therefore base their decision to settle on an assessment of a site's characteristics or on the presence of established pairs, or both. The above discussion on the theoretical mechanism of settlement is outlined here to demonstrate that the observed breeding density of an area may not always be optimal (in terms of the birds' fitness) for the conditions prevailing at a particular time.

Ultimately the most important factors determining the breeding densities of the birds studied here are thought to be:

- 1) the proportion of the area covered by habitats that are used by that species (Chapters 3).
- 2) the relative quality of these habitats for the species regarding the various aspects of breeding (Chapters 3 & 5). These can be divided into two main aspects, protection from predation and food supplies.

The relative importance of each of these are discussed below.

ii) Availability of nesting habitat.

A species' overall breeding densities on blackland and blackland-machair transition zone areas, which invariably consists of a mosaic of habitats, are probably determined mainly by the proportion of the area covered by suitable nesting and chick-rearing habitats. For example, the density of Dunlin on blackland was much lower than on extensive areas of marsh or machair because only a small proportion of the blackland is covered by habitat types used by Dunlin, i.e. marsh (Chapter 3.II). Ringed Plover bred at very low density in all areas of blackland and marsh habitats and again this was due to a lack of suitable habitat. The few pairs of Ringed Plover that did breed in such areas were normally associated with stretches of shingle track. Redshank occurred at a much lower overall nesting density (approximately six times less) on machair than on marsh or blackland. The reason for this is that large areas of the machair were unsuitable for nesting Redshank either because of a lack of nest cover or remoteness from suitable chick rearing habitats. The Redshank breeding on cultivated machair were concentrated into those parts with better than average nest cover

and which were normally within 200 m of suitable chick rearing habitat. Nevertheless, the density of Redshank on these more suitable areas of machair was considerably lower than on blackland or marsh.

iii) Redshank densities at Rubha Ardvule.

On all three of the blackland and blackland-machair transition zone areas studied the nesting and overall breeding densities of Redshank were similar. This is to be expected, as there was little variation between sites in the ratio of the area of suitable nesting habitat to the area of adult feeding habitat (short pasture). However, at Rubha Ardvule this ratio was much less, and the nesting density (and chick-rearing density) was far greater (approximately three times greater), even though the habitat was similar to that found on blackland and transition areas. At first sight, this result suggests that overall breeding densities of Redshank on blackland would increase if the proportion or quality of adult feeding habitats was increased. This is probably not the case, for the situation at Rubha Ardvule, although clearly demonstrating that Redshank can successfully nest and rear chicks at much higher densities than are usually found on blackland and transition areas, may not be have been optimal in terms of life time reproductive output for the adults involved. Two important costs associated with very high breeding densities were noted at Rubha Ardvule, but not elsewhere. Firstly, in 1985, two adult males (9% of those present) died during the chick-rearing period, probably from wounds incurred whilst fighting with neighbours over

chick-rearing habitat. Secondly, in 1986, egg predation by Hooded Crows (*Corvus corone cornix*) caused very low breeding success; crow predation at all other sites was negligible (despite their presence), presumably because it was not worthwhile for crows to search for nests at low density. (Hooded Crows were not serious egg predators at Rubha Ardvule in 1985 or 1987 because they were destroyed by the local gamekeeper.) Although the blackland and transition areas studied probably had excess suitable Redshank nesting habitat, chick rearing habitat was at a premium, as indicated by the vicious fighting frequently seen between the adults of neighbouring families. Higher breeding densities on blackland and transition areas would almost undoubtedly cause increased competition during the chick rearing stage which may lead to increased mortality of adults and chicks. The situation at Rubha Ardvule indicates that, at least at very high densities, Redshank reproduction and survival may be affected by density dependent processes.

iv) Dunlin and Ringed Plover densities and egg predation.

There is a clear hierarchy of nesting densities in different habitats for Dunlin and Ringed Plover, and this reflects the quality of the habitats to each species. The nesting density of Dunlin on machair marsh was approximately three times that on old fallow, which in turn was much greater than on recent fallow. Ringed Plover showed the opposite trend, with the densities on plough and recent fallow being approximately five times those on old fallow. One of the factors associated with these differences in density is probably predation pressures on eggs and chicks.

The breeding density appears to be related to the level of protection against predators afforded to nests and chicks by cover and camouflage and also by the mobbing behaviour of other breeding birds such as Lapwing. The habitats providing least protection have the lowest breeding densities and vice versa. A bird might be expected to nest where the risk of predation is least. If this is the case, then the predation risk to nests and chicks might be expected to be approximately equal over all densities. A comparison for Ringed Plover and Dunlin nesting at different densities shows that there were no significant differences in nesting success (proportion of pairs hatching chicks) at different densities (Chapter 8, Table 8.3). For Dunlin however, there was a highly significant difference in brood survival rate between high and low density breeding areas (Table 8.4). The suspected reasons for this are discussed in Chapter 8.

Avian predators hunting for wader nests and chicks are opportunistic and do not search for the nests or chicks of one species only (*pers. obs.*). Therefore, it is likely that the settlement pattern and consequent breeding density of a species is not influenced solely by conspecifics but also by other species present. Fretwell (1972) hypothesises that a species' nest survival rate would be dependent on the density of all similar nests, regardless of species, in an area but, as noted by Goransson *et al.* (1975) this hypothesis is over-simple because the presence of some species, notably Lapwing, can enhance the overall nest survival in an area (e.g. Dyrce *et al.* 1981). The relationship between overall breeding wader density and nest

survival is clearly more complex than simple direct density dependence and must take account of inter-specific differences in abundance, relative nest detectability and anti-predator behaviour.

iv) Ringed Plover densities and food resources

A second aspect of habitat quality that may explain differences in density between habitats is food supply for adults and chicks though this was not measured quantitatively during this study. Adult Redshank and Dunlin feed to a large extent away from their nesting area, often at considerable distances, (Chapters 4) and will use a wide range of feeding habitats; it thus seems unlikely that for these species adult food supply plays an important role in determining breeding densities (but see discussion on Redshank above). In contrast to this, Holmes (1970) found that variation in territory size in Dunlin breeding on Alaskan tundra correlated with adult food resources within in the territories. Feeding by adult Ringed Plovers and their chicks, and by Dunlin chicks, is largely confined to the breeding territories; these must therefore contain adequate food supplies. If food was a limiting factor then one would expect territories to be largest (with consequently lower breeding densities) in habitats with the poorest food supply. To investigate this it is necessary to compare the densities in areas having a similar quality of cover and camouflage for nests and chicks. This can be done for Ringed Plover at Drimore Farm in 1986. Here, two adjacent blocks of first-year fallow, each with a similar management history, of similar size (7 Ha) and almost identical

in appearance, held very different breeding densities: 428 pairs km^{-2} compared to 86 pairs km^{-2} . There was however one important difference, namely ground wetness. The high density area had flood pools in spring and early early summer, and the ground remained soft and in parts muddy throughout the season, whereas the low density area was freely draining and dry. As the physical structure of the two areas was very similar it seems likely that the difference may be due to food resources. It is not valid to make further comparisons with the densities of Ringed Plover on first year fallow at Stilligarry, because here the strip layout of the habitats meant that the territories generally comprised of a mixture of cultivated habitats. Areas of very dry cultivated machair at other sites in the Southern Isles (for example Drimsdale machair) are known from extensive surveys (Green 1983a and 1983b, Fuller 1985, Fuller and Percival 1986) to have very low breeding densities of Ringed Plover (a few pairs km^{-2}); again it seems likely that in these cases food resources are limiting the density.

Comparison of densities with those recorded elsewhere

The overall breeding densities of each species for the major habitat divisions found during this study are in all cases slightly higher than those calculated from extensive wader surveys in the Southern Isles (Fuller *et al.* 1986, Pienkowski *et al.* 1986). There are two reasons for this. Firstly, the study-sites used in this study almost certainly had higher densities than average for the whole coastal plain; the extensive surveys covered all areas some of which had low densities. The

blackland areas covered by this study were all adjacent to the machair, and did not extend to the eastern edge of the blackland where wader densities, especially of Dunlin, are generally lower than closer to the machair (Fuller *et al.* 1986). Secondly, the method used in these surveys is known at times to underestimate the actual population (Jackson & Percival 1983). The density of Dunlin on machair marsh (extensive marsh bordering damp machair) at Drimore Farm (224 pairs km⁻²) was only slightly less than that calculated by Etheridge (1982) (300 pairs km⁻²) based on intensive nest searches of similar habitat at nearby Loch Bee.

The breeding densities attained by Redshank, Dunlin and Ringed Plover in the Southern Isles are in general far higher than those typically found elsewhere in north-west Europe. The peak densities found for Ringed Plover during this study and by Etheridge for Dunlin appear to be the highest recorded breeding densities so far recorded for these species. The range of reported densities for each species are discussed by Nethersole-Thompson (1986).

One reason why wader breeding densities in the Southern Isles tend to be considerably higher than on mainland areas might be the absence of many mammalian predators, especially Foxes (*Vulpes vulpes*) and Stoats (*Mustela erminea*). However, this situation is set to change with the recent establishment of Hedgehogs (*Erinaceus europaeus*) on South Uist and the reported early stages of colonisation of the Uists by feral American Mink (*Mustela vison*) from the island of Harris (Cunningham 1987). The threat posed by these two mammals to the wader populations is in urgent need of evaluation.

CHAPTER 7

BREEDING SITE FIDELITY AND NATAL PHILOPATRY

The subject of site fidelity in scolopacid waders has been reviewed by Oring and Lank (1984). Their review shows that there is a great amount of variation in the extent of site fidelity between species. However, in general, individuals of monogamous temperate species, such as those studied here, show a high tendency to breed in the same locality each year and to breed close to their natal area. Beside being of academic interest, a knowledge and understanding of the interspecific and intraspecific differences in site fidelity and the mechanism of settlement of breeding waders are of practical use for evaluating species' conservation needs. For example in determining the extent to which individuals will redistribute to new sites if their original breeding site undergoes major habitat changes, and in quantifying the extent of immigration into, and emigration from, a population.

Although site fidelity and natal philopatry in adult Redshank, Dunlin and Ringed Plover have been the subject of some previous studies the results are in many cases of limited value as generalizations, either because of the lack of opportunity for movements because of habitat limitations (e.g. Soikkeli 1970a) or inadequacies in locating birds that dispersed from the immediate locality (e.g. Grosskopf 1959, Yates 1982). As far as possible, this study aimed to overcome these problems and quantify the extent of movements in all directions and distances for each species.

Methods

The method used to measure site fidelity was based on monitoring the return in a subsequent breeding season of colour-ringed birds from known nesting sites in the case of adults or known natal sites in the case of chicks. Not only the study-sites themselves but also extensive areas of suitable habitat outside their boundaries were searched for returning birds. Full details of the extent of the areas searched outside the study-sites are given in Part 2 of Chapter 8. Briefly, searches for Ringed Plover covered all machair habitats on South Uist and Benbecula, and searches for Redshank and Dunlin covered up to 5 km north and south of the northern study-sites. Except for a few Ringed Plover, the colour-ring sequences used for chicks were site-specific only (i.e. they were not individually unique sequences in contrast to those used for adults) and thus the dispersal distance from the natal site to the breeding site of returning chicks was often only known to within an accuracy of about 1 km. However, if the nest of a returning colour-ringed chick was found, I was often able to catch the bird and then, from the metal ring number, determine its dispersal distance exactly. All distances moved were measured on 1:25,000 scale maps.

Results

The distances moved by the birds were divided into nine categories. The proportions of returning adults and chicks in each category are summarised in Figures 7.1, 7.2 and 7.3 for Redshank, Dunlin and Ringed Plover respectively. The results for

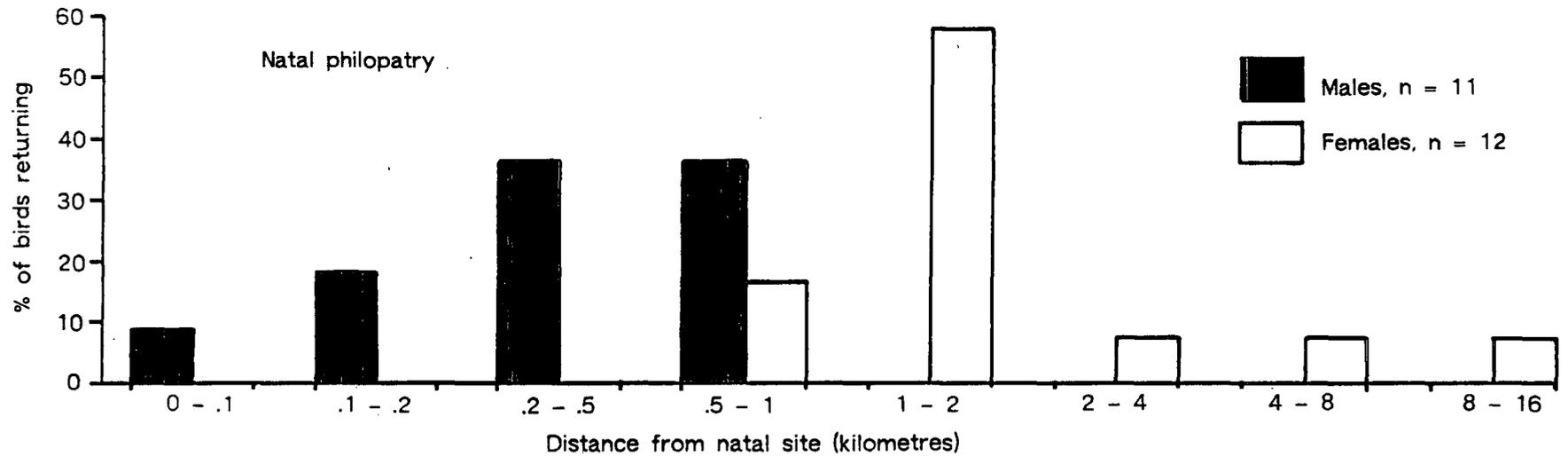
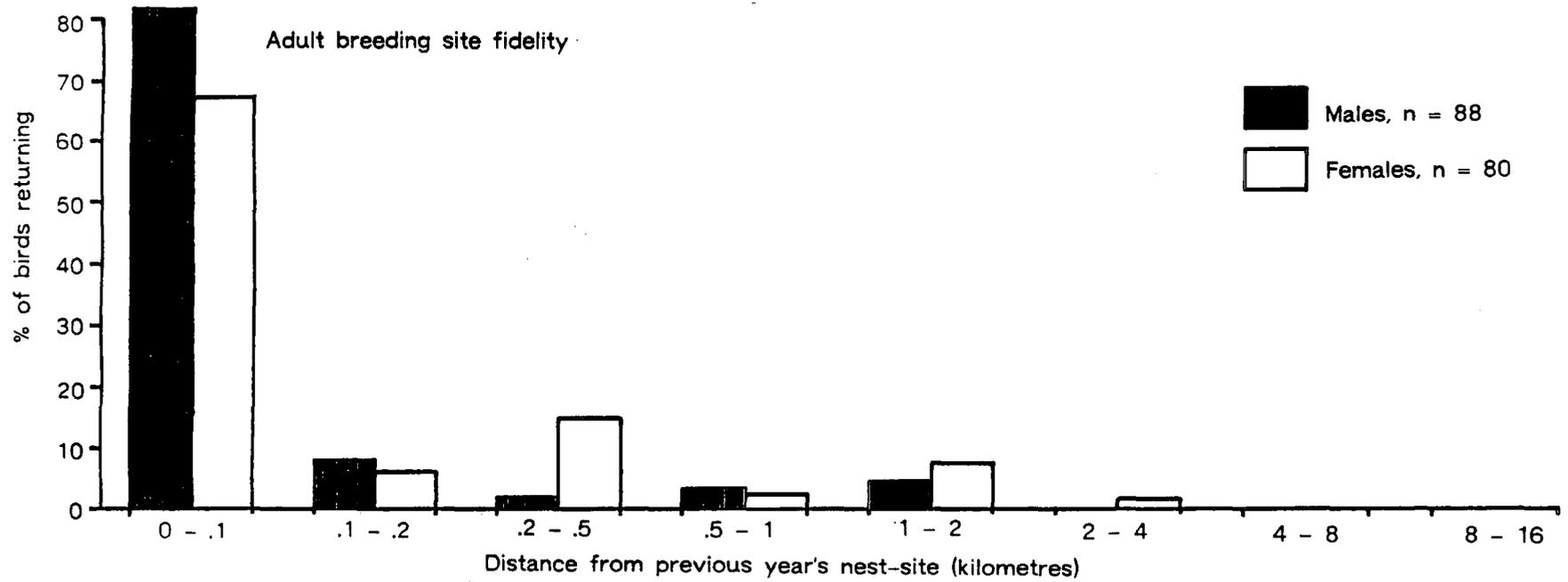


Figure 7.1: Breeding site fidelity and natal philopatry of Redshank, based on return of colour-ringed individuals.

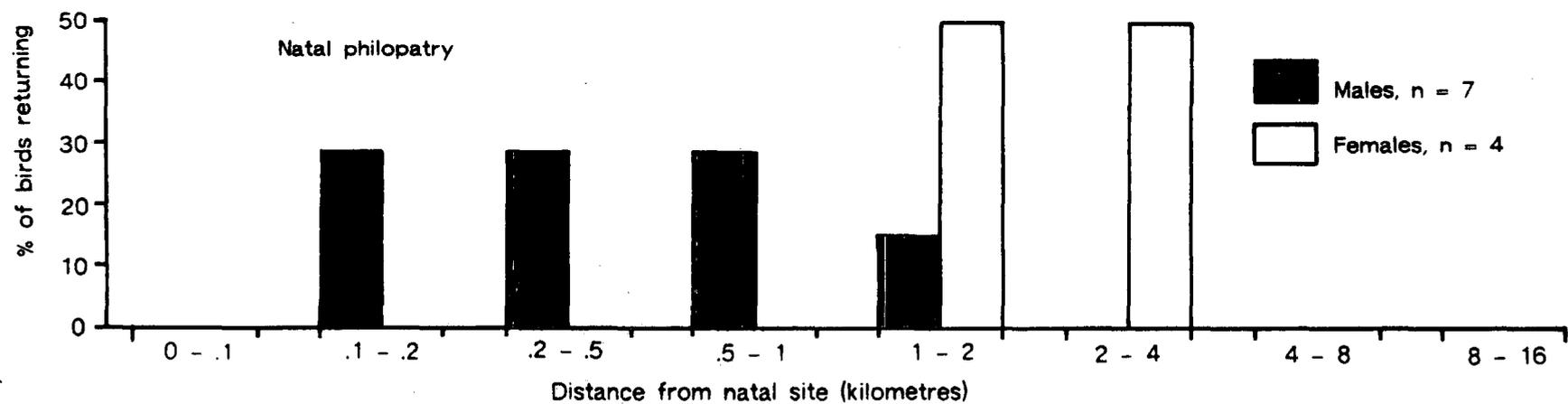
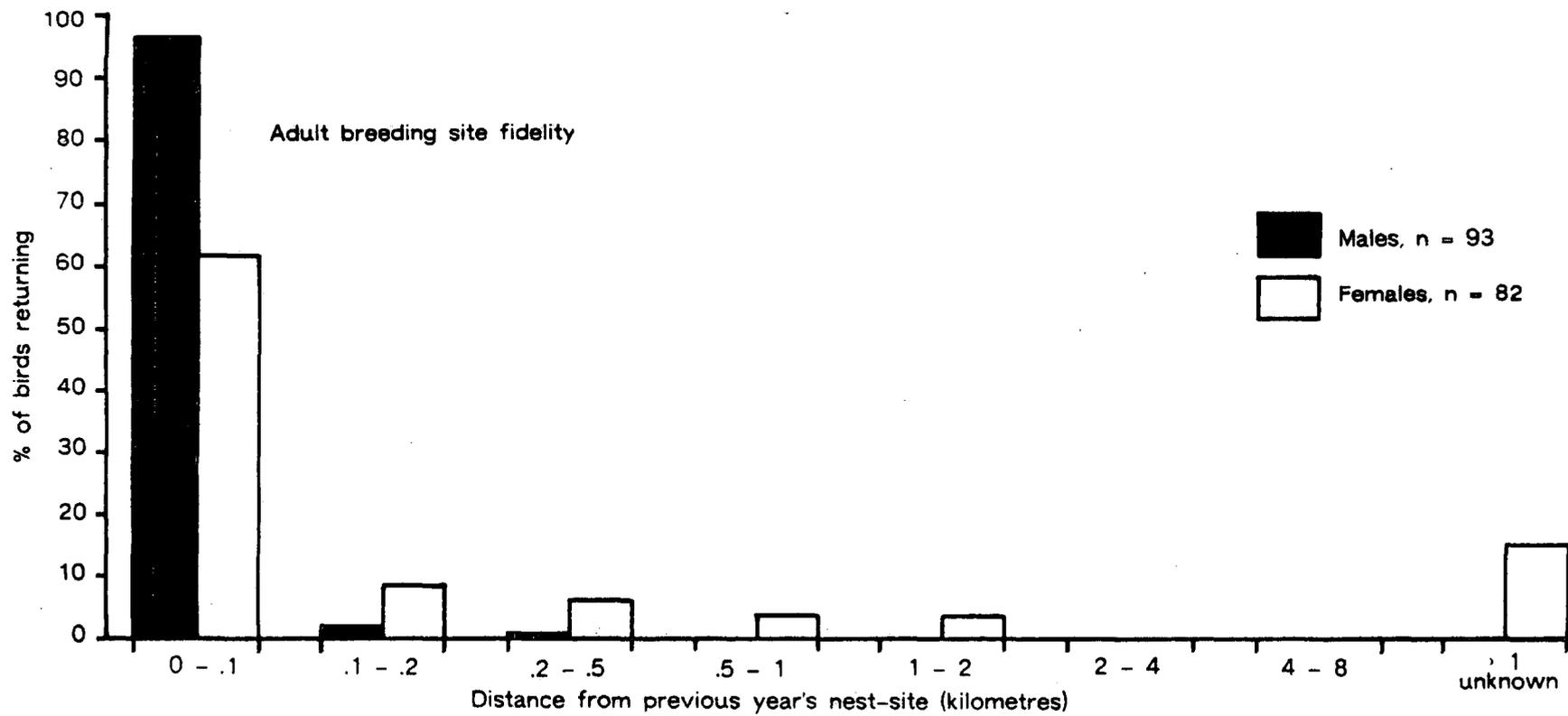


Figure 7.2: Breeding site fidelity and natal philopatry of Dunlin, based on return of colour-ringed individuals.

males and females are shown separately. The breeding sites of a few adult female Dunlin and Ringed Plover, known to have returned because they were seen on the seashore, were not found. In the previous season all of these few individuals had nested within one of the study-sites, and as the study-sites and their immediate environs were very thoroughly searched in the subsequent season it is unlikely that they were overlooked there. Therefore, these birds are considered to have bred at least 1 km away from their previous season's breeding site.

Although the results presented in Figures 7.1 to 7.3 provide a useful summary of the dispersal distances they are in some ways unsatisfactory because they take no account of the area available in each distance category and therefore give no indication of the settlement intensity per unit area. The area included within each concentric zone increases greatly with distance for example the area of the 0.1- 0.2 km zone is 9.43 ha whilst for the 1 - 2 km zone it is 943 ha. However, a correction needs to be made to account for the availability of suitable habitat within each zone. It is not easy to calculate this, but an approximation can be made by assuming that the only suitable habitat in the islands occurs on the coastal plain, which is essentially a straight strip running north-south. Here, this strip is taken as been 2 km wide. Therefore, the available amount of suitable habitat in each of the concentric zone is taken as been only that included by a 2 km wide strip that passes through the centre.

It is very clear that the great majority of established adults settled close to their previous nest-site and in consequence the settlement intensity per unit area follows a

similar pattern for each species i.e. it decreases very rapidly with increasing distance, falling by several orders of magnitude in the first kilometre. The settlement pattern of young birds from their natal site to their site of first breeding is not so clear and in some ways the results in Figures 7.1 to 7.3 give a misleading impression of the process. Therefore, further bar charts have been drawn (Figures 7.4 to 7.6, for Redshank, Dunlin and Ringed Plover respectively) showing the settlement intensity of young birds per unit area for each distance zone from the natal site (this reflects the probability of an individual settling per unit area). To calculate the index of settlement intensity the percentage of birds that settled in a zone has been divided by the area of available habitat in that zone in hectares. The settlement-intensity index values range from greater than 3.0 to less than 0.001, and, so that the smaller values can be seen (without distorting the scale), the x-axis on these figures has been drawn slightly below the zero level of settlement intensity (the y-axis).

Apart from examining the differences between sexes in site fidelity, no attempt is made here to investigate the various factors that may influence a bird's fidelity, for example, habitat changes, previous breeding success, age and partner relationship. Although this will be of interest it is not considered essential to the central themes of this thesis, however, an appreciation of the typical pattern of adult breeding site fidelity and natal philopatry of each species is required for certain calculations in the chapter on population dynamics that follows.

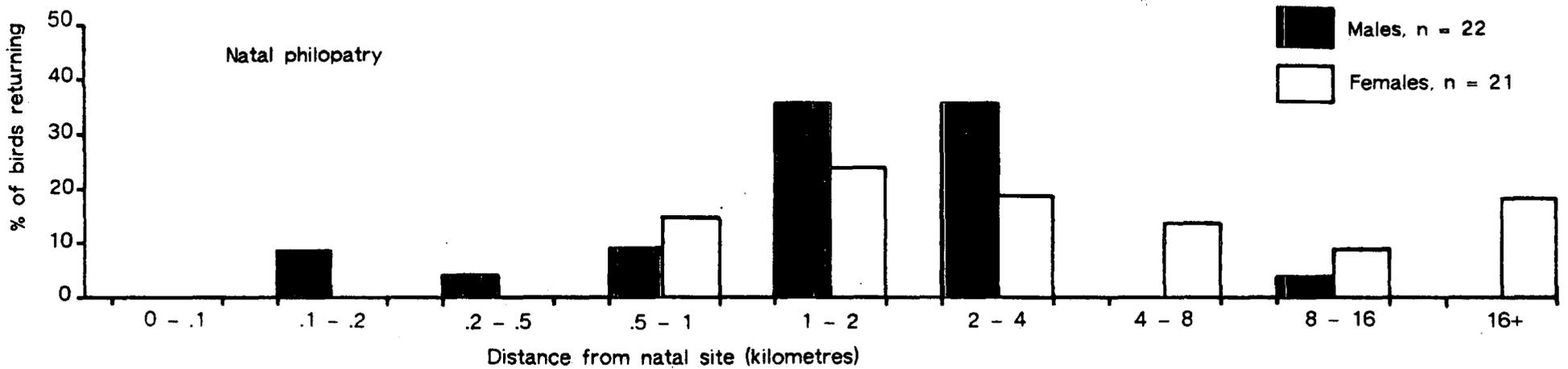
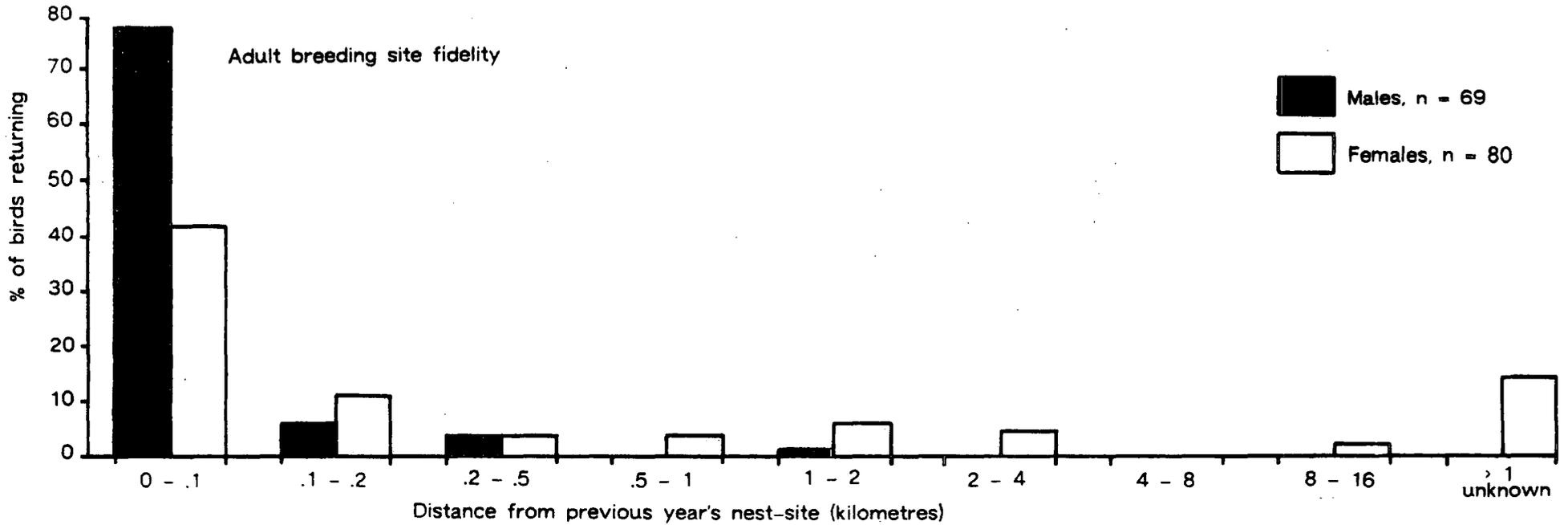


Figure 7.3: Breeding site fidelity and natal philopatry of Ringed Plover, based on return of colour-ringed individuals.

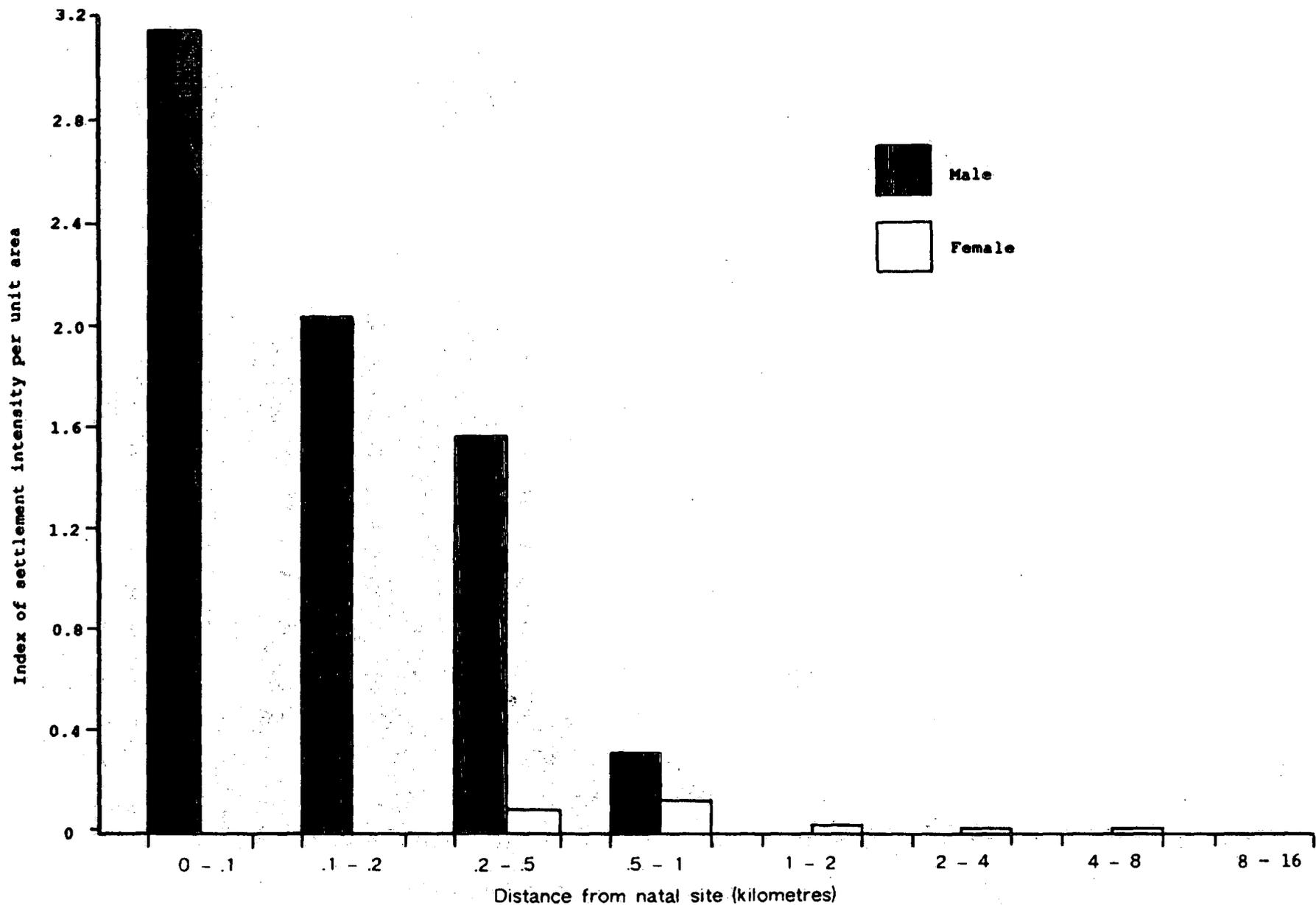


Figure 7.4: Settlement intensity per unit area of young Redshank in various distance zones from their natal site.

The index of settlement intensity is calculated from the percentage birds settling in a zone divided by the area (in hectares) of available habitat in that zone. N.B. the x-axis is drawn slightly below the zero level of settlement intensity.

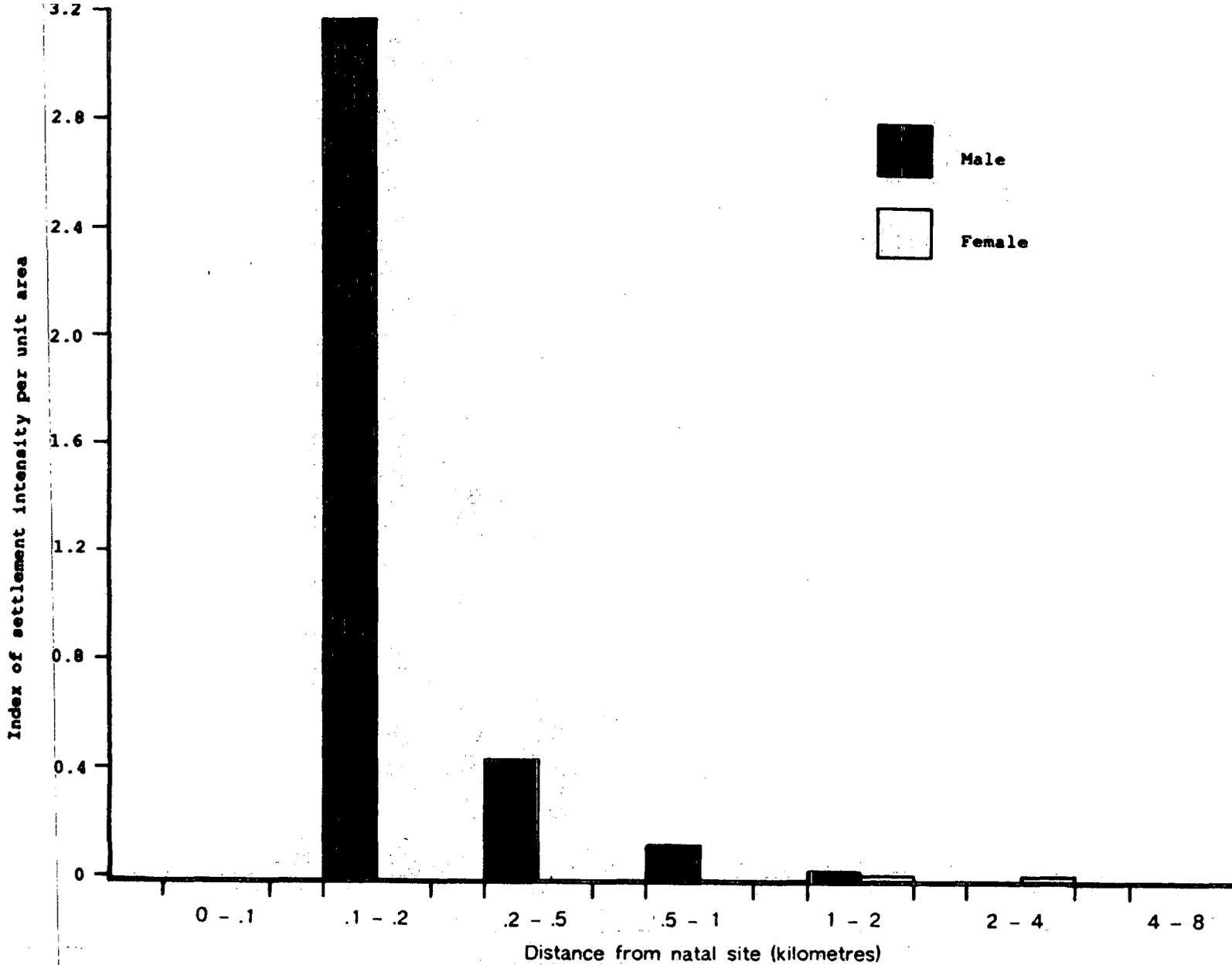


Figure 7.5: Settlement intensity per unit area of young Dunlin in various distance zones from their natal site.

The index of settlement intensity is calculated from the percentage birds settling in a zone divided by the area (in hectares) of available habitat in that zone. N.B. the x-axis is drawn slightly below the zero level of settlement intensity.

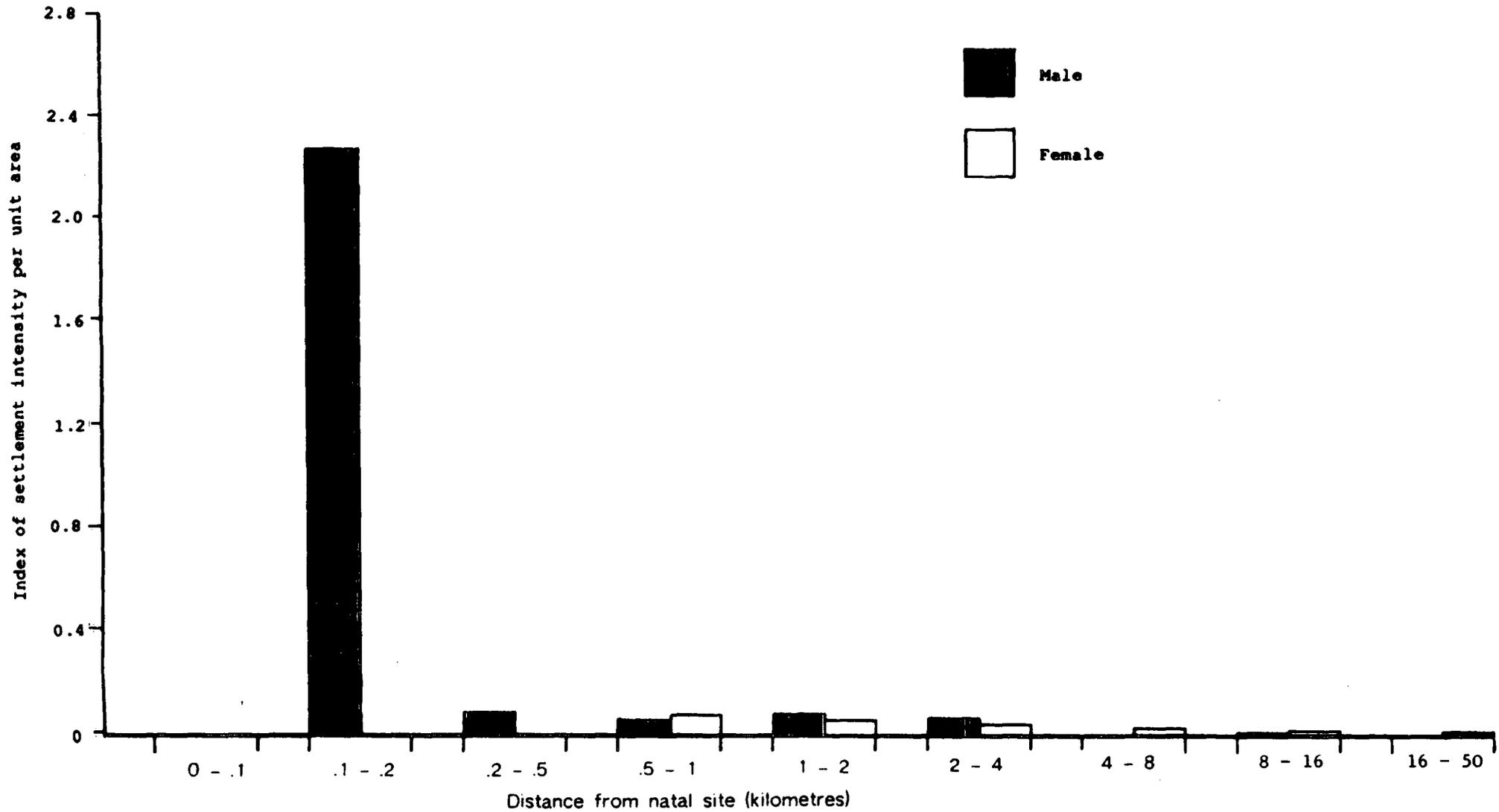


Figure 7.6: Settlement intensity per unit area of young Ringed Plover in various distance zones from their natal site.

The index of settlement intensity is calculated from the percentage birds settling in a zone divided by the area (in hectares) of available habitat in that zone. N.B. the x-axis is drawn slightly below the zero level of settlement intensity.

The results on dispersal and settlement intensity per unit area presented here must be interpreted bearing in mind the limitations of the method, in particular the efficiency of locating the birds. It becomes increasingly difficult to find the birds as dispersal distance increases because the area of habitat that has to be searched tends to increase by the square of the distance moved. This means that the chances of overlooking birds increases disproportionately with distance. For the established adults this is not a serious problem because it is clear that nearly all individuals return to within 4 km of their previous site and this encompasses an area which, although large, could be searched thoroughly and with only a moderate chance of overlooking birds. However, for young birds the dispersal distance to their first-breeding site was frequently over 4 km and for some birds over 10 km. The area that needs to be searched to find all the birds that disperse these relatively long distances is very large (tens of km²). Although, as discussed above, the coastal-strip arrangement of the suitable habitat means that the actual area of habitat available does not necessarily increase by the square of the distance, there is nevertheless a substantial area encompassed by these distances.

Therefore, an inevitable consequence of the method used is a higher chance of overlooking long dispersal movements than short ones. The degree to which this bias has affected the results is unknown. Intuitively, the decline in the number of birds with increasing distance that occurred in both age-groups of all three species is to be expected, (if only because of the disproportionately greater area available), however, the rate of

this decline may be exaggerated by the bias in detection. The importance of the bias can, to some extent, be judged by the differences in the return rates between males and females. In all cases females tended to disperse significantly further and, therefore, if the bias is serious, one would expect less females to have been detected than males (assuming equal survival rates). Infact, with the exception of young Dunlin for which the sample size is only seven birds anyway, there is no tendency for this to be so and this suggests that the bias is small.

Redshank site-fidelity

1) Fidelity by adults to breeding site

The vast majority of adult Redshank (82% of males and 68% of females) still known to be alive returned to within 100 m of their previous year's site. Most of these birds occupied the same nesting area and a few even used the same nest-site as previously. The difference between males and females in the rate of return to within 100m of the previous year's nest-site is, however, significant ($\text{Chi}^2 = 3.9$, 1 d.f., $P < 0.05$, Yates' correction applied)). Of the birds that "moved" more than 100 m, 62% were within 500 m of their previous site. On the basis of the results presented in Chapter 3 on daily movements it is likely that these birds were already familiar with the characteristics of their "new" site and also, perhaps, already "knew" their new neighbours. Adult Redshank often chose a new mate each year even though their previous mate was alive (*pers. obs.*). In these cases the male normally remained at the original breeding "territory" and the female moved a short distance only,

often to an adjacent male's "territory".

Only 10% of the adult Redshank returned to sites over 500 m from their previous site, the greatest movement recorded was 2.5 km. There was a greater tendency to move over 500 m from the previous year's site for females (13%) than males (8%). This difference is not significant ($\text{Chi}^2 = 0.22$, 1 d.f., $P > 0.05$, Yates' correction applied), but the sample size for birds that "moved" is only 16. Most of the adults that "moved" more than 500 m probably had little or no previous experience of their new site. The factors that caused these longer movements are unknown, but in no cases were there any major habitat changes at the original site.

ii) Redshank natal philopatry

The results in Figure 7.1 show that there was a wide range in the dispersal distances of young first-time breeding Redshank from their natal site. The difference between the median distance moved by males and females is highly significant (Mann-Whitney U-test, $U = 7$, 11 males, 12 females, $P < 0.001$). There is in fact very little overlap in the distances moved by males and females. All 11 males returned to within 1 km of their natal site, with a mean distance of ca. 0.5 km. All but 2 of the 12 females moved at least 1 km, the greatest known movement was 12 km and the mean distance moved was ca. 2.7 km.

The results illustrated in Figure 7.4 show that young males had much higher settlement intensities per unit area close to their natal site than did females. The probability of a male settling in a unit area decreases rapidly with increasing

distance from the natal site. Although the settlement intensity of females also appears to diminish with increasing distance it does so less rapidly than with males, showing that the females are less philopatric. The lack of records of females settling within 0.2 km of their natal site is probably a consequence of the comparatively small areas involved rather than deliberate avoidance. In females, the decline in settlement intensity per unit area with increasing distance may be exaggerated by the fact that the likelihood of overlooking birds increased with dispersal distance. However, although settlement intensity may be constant in the first few distance zones it would be expected to decline thereafter, otherwise the chances of locating any returning females would have been very small.

Dunlin site-fidelity

i) Fidelity by adults to breeding site

The vast majority of adult Dunlin (97% of males and 68% of females) returned to their previous territory. All birds that returned to within 100 m are considered here to have re-established their previous territory i.e. they did not "move". The proportion of males that did not change territory was significantly greater than of females ($\text{Chi}^2 = 31$, 1 d.f., $P < 0.001$, Yates' correction applied). Only 3% of males changed territory and all of these resettled within 500 m of their previous year's site. Females that changed territory showed no tendency to settle particularly close (i.e. within 500 m) to their previous breeding site. The breeding locations of 16% of all adult female Dunlin known to have returned were not

discovered and, as discussed above, it is unlikely that any of these birds settled within 1 km of their previous territory. The greatest known dispersal distance of an adult female was 1.7 km. The general pattern of adult site fidelity and dispersal distances presented here for Dunlin is very similar to that found by Soikkeli (1970) for Dunlin in Finland, even though he was studying a much more limited area.

ii) Natal philopatry

The distances from natal site to first breeding site were known for only four female and seven male Dunlin. Such a small sample size may not be representative of the general pattern and any conclusions from these data should be considered tentative. However, the difference between males and females in the number of birds dispersing more than 1 km is significant (Fisher's Exact Test, $P = 0.015$). All except one of the seven males returned to within 1 km of their natal site. The four females all dispersed at least 1 km; the greatest recorded distance was ca. 4 km. One first-year Dunlin, of unknown sex, was seen in suitable breeding habitat on the Isle of Tiree ca. 110 km south of its natal site (R. Broad *pers. comm.*). Unfortunately, it is not known whether this bird attempted to breed there. Soikkeli (1970) reported two instances of female Dunlin in Finland dispersing distances of over 100 km from their natal site to breed. Also, in agreement with this study, Soikkeli found that most Dunlin return to within 5 km of their natal site, however, he was working on a small isolated breeding group which were 100 km distant from the next nearest suitable habitat and therefore any dispersal had to be

either less than 6 km or at least 100 km. Interestingly, Soikkeli, on the basis of 57 young birds (30 males and 27 females), found no significant difference in dispersal distances of the two sexes to their first breeding site.

The pattern of settlement intensity per unit area by young Dunlin (see Figure 7.5) is similar to that of Redshank. However, it should be noted that the sample size is small, especially for females, and therefore, it is inconclusive how settlement intensity changes at distances greater than 2 km.

Ringed Plover site fidelity

1) Fidelity of adults to breeding site

The pattern of adult breeding site fidelity for Ringed Plover illustrated in Figure 7.3 is very similar to that for Dunlin except that a slightly higher proportion of birds "moved". (All birds that did not return to within 100 m of their previous breeding site are considered here to have "moved" and changed territory.) The difference between males and females in the proportion of birds that changed site is highly significant ($\chi^2 = 21, 1 \text{ d.f.}, P < 0.001$, Yates' correction applied). Only one adult male, out of eight that changed territory, moved more than 500 m. As in Dunlin, the breeding sites of some female Ringed Plover known to return were not discovered, but it is unlikely that they were within 1 km of their previous year's site. The known dispersal distances of adult female Ringed Plover were nearly all less than 4 km, however, the two greatest distances recorded were 12 and 16 km respectively.

ii) Natal philopatry

The colour-ringed Ringed Plover chicks that returned to breed settled at a wide range of distances from their natal site. Unlike the findings for Redshank and Dunlin, there was considerable overlap in the distances moved by males and females, however, a Mann-Whitney U-test showed that the median distance moved by males was significantly less than that of females (U-statistic = 150, 22 males, 21 females, $P < 0.05$). The mean distances were ca. 2.2 km for males and ca. 7.8 km for females. The greatest known distance moved was by a female hatched in North Uist and found breeding in South Uist, 42 km south.

The pattern of settlement intensity per unit area of young male Ringed Plover (see Figure 7.6) appears to differ from the other two species. The settlement intensity was very high up to 0.2 km from the natal site but thereafter falls to much lower levels. However, instead of falling off steadily with increasing distance (as is the case for Redshank and Dunlin) it remains approximately constant up to 4 km from the natal site before falling off rapidly. The settlement intensity pattern of young females appears to be similar to Redshank with a gradual decrease with increasing distance.

Discussion

Adult males of all three species were very faithful to their previous breeding sites and most of those that did "move" usually resettled nearby (i.e. within 500 m). Indeed, movements by adult males to unfamiliar areas appears to be a very rare occurrence. This high level of breeding site fidelity indicates that the

advantages to males of remaining in the same place are generally far greater than any disadvantages. The most obvious advantage is familiarity with many aspects of its breeding site, for example, the whereabouts of food resources and cover, predation pressures and the status of conspecifics. Familiarity with the breeding site will generally increase with experience and may consequently increase a bird's lifetime reproductive success. It is clear that many of these advantages depend on a bird being able to use its experience to make predictions about aspects of its environment.

Hinde (1956) suggests that a further advantage of returning to the same area is that a bird may have more "self-confidence" on its "home-ground" which enhances its competitive ability. Maynard Smith and Parker (1976) invoke the idea of an arbitrary asymmetry in resource value to explain such a phenomenon (Barash 1982). This has been shown by Maynard Smith (1978) to be a possible evolutionary stable strategy.

Adult females of all species also showed strong fidelity to breeding areas but less so than males. The advantages of past experience and familiarity would also apply to females. Most of the females that "moved" re-settled close to their previous site, and possibly these birds were settling as close as possible to their previous site by mating with the nearest unpaired male. In Dunlin and Ringed Plover the males defend the nesting territory and a female may be prevented from reoccupying her previous site if the territory holding male there already has a mate. In such a situation a female might be expected to re-settle close-by so that she can reap the benefits of her accrued knowledge of the

area. As the distance from the previous site increases a bird's familiarity with the area will decrease and at some point any advantage the bird may have through familiarity will become negligible. The dispersal distances beyond this point might be expected to be affected only by the availability of suitable unpaired males and breeding habitat as all areas would be equally unfamiliar. Although the sample sizes are small, and the chances of finding birds that dispersed several kilometres were low, there is a suggestion that the dispersal of adult female Ringed Plover, and perhaps also Dunlin, followed this pattern.

Adults that dispersed distances of greater than about 1 km were unlikely to be settling "as close as possible" to their previous site and thus it seems likely that some advantages are gained from dispersal to unfamiliar areas. Reduction of inbreeding is a frequently suggested advantage of dispersing (e.g. Greenwood *et al.* 1978). A second advantage to individuals that disperse to new areas is the opportunity to exploit areas of habitat where their chance of breeding successfully may be higher or risk of mortality lower, or both. This latter suggestion is relevant to the birds' conservation. Species in which individuals respond to breeding habitat quality (either to a decrease in the quality of the present breeding site or increases in habitat quality elsewhere, if they are aware of them) by dispersing are likely to be less vulnerable to spatial and temporal changes in their breeding habitats. On this basis, species that typically live in unstable environments would be expected to show less site-tenacity than species in stable environments. Also, in unstable environments a bird would not be

able to accurately predict aspects of its environment and therefore advantages of familiarity would be lost. The reason why Ringed Plover showed slightly less site-tenacity than Dunlin may be connected with the less stable and therefore less predictable nature of their typical breeding habitats (i.e. cultivated machair vs. marsh).

The sex bias in site-tenacity was much less for Redshank than for the other two species. The explanation for this may lie in the birds' territorial systems. Unlike Dunlin and Ringed Plover, male Redshank do not defend strict nesting territories (Hale 1956) and therefore females are perhaps less likely to be prevented from reoccupying their previous site.

In all three species it was dispersal of young birds that contributed most to the overall dispersion of the population. Greenwood (1980) suggests that, for monogamous species in which males defend breeding territories, there should be greater male natal philopatry. The theoretical reason for this lies in the advantage gained by the young males that are already partly familiar with their breeding area from experience gained as a chick and as a juvenile. Greenwood suggests that young females should gain less advantages from site familiarity than males, and therefore dispersal to reduce the risk of inbreeding should be more frequent in females. For the three species in this study, the potential for gaining familiarity of the breeding areas as a juvenile is small because all three species leave the breeding areas soon after fledging. However, it may be significant that a few recently fledged but independent juvenile Redshank and Ringed Plover were seen up to several kilometres away from their natal

site visiting other suitable breeding areas. In agreement with Greenwood's suggestion, all three species in this study showed significantly greater male philopatry. Interestingly, this result contrasts to previous studies on monogamous waders. The review by Oring and Lank (1985), found no tendency for sexed biased natal philopatry in any monogamous sandpiper species.

Chapter 8

POPULATION DYNAMICS

The long-term survival of a population and its ability to withstand deleterious pressures such as habitat degradation and increased predation, ultimately depends on the balance between reproduction, mortality, immigration and emigration. A closed population that produces more than sufficient potential breeding recruits, i.e. fledglings, to balance adult mortality is likely either to increase, or remain stable due to density dependent mortality acting mainly on the potential breeding recruits. Conversely, if a closed population produces insufficient young to balance adult mortality it will decline.

A wide range of density dependent effects has been shown to operate on the productivity and mortality of birds (e.g. Lack 1966) and it is through these that regulation of most bird populations probably takes place. These effects do not always depend solely on the density of the species under consideration and are therefore rarely of a simple nature (e.g. hole-nesting woodland passerines (Gustafsson 1986)). Therefore, it is not safe to assume that a population's decline (or increase) will always be arrested by simple density dependent processes. The relative importance of density dependent and density independent factors in ultimately determining the size of wader populations has been reviewed by Evans and Pienkowski (1984). It can be concluded from their review that although both types of process have been demonstrated to act on wader populations, it is generally unknown which is the most important. This subject

requires further investigation.

An evaluation of the various aspects of a population's reproduction and mortality, i.e. its population dynamics, can be used to identify the factors that ultimately determine population size. This approach not only identifies the vulnerability of a species to small decreases in reproductive output or adult survival, but also identifies the key stages in the life cycle that determine the size and density of a population. This is essential in the formulation of effective conservation policies as it indicates the stages of a life cycle where conservation effort should be focussed. In this study, the breeding success and survival of Redshank, Dunlin and Ringed Plover were measured to determine the overall well-being of the populations and to identify the periods during the life cycle that are most important in determining population levels.

Part 1. Breeding Performance

Annual breeding success measured in terms of the number of young fledged per breeding adult was calculated by determining the following:

- 1) Mean clutch size.
- 2) Nest survival rate; calculated separately for early and late nests.
- 3) Egg survival rate within successful nests.
- 4) Hatching rate of surviving eggs.
- 5) Brood survival rate.
- 6) Chick survival rate within successful broods.
- 7) Mean number of breeding attempts per pair.

Data for the first three of these were obtained by visiting nests at approximately five-day intervals. For Ringed Plover no attempt was made to find every nest of every colour-ringed pair because of the risk of exacerbating the naturally high level of egg predation by Common and Black-headed Gulls (*Larus canus* and *L. ridibundus*) through the disturbance caused by nest finding and visiting. Consequently the nesting history for most colour-ringed Ringed Plover pairs was incompletely known.

Nesting Success

i) Methods

Nest and egg survival rates were estimated using the method proposed by Mayfield (1961, 1975) which considers survival on a daily basis after the nests are found and therefore accounts for nests that fail before they are found. To obtain the nest/egg survival rate, the daily survival estimator is raised to the power of the nesting period; this equals the mean laying period plus the mean incubation period plus mean number of days the young remain in the nest. The value used here for the mean laying period of each species is based on laying intervals given in Cramp and Simmons (1983), whilst the mean incubation periods and mean lengths of time the chicks remain in the nest are based on data collected in this study. The standard error of Mayfield's daily survival estimator is calculated using the method given by Johnson (1979).

ii) Results

The survival rates of "early" and "late" nests were estimated

separately. The results are summarised in Table 8.1. The definition of early and late nests for each species is given below the table. For Redshank and Dunlin, early nests broadly correspond to initial clutches and late nests to replacement clutches. For Ringed Plover, early nests broadly correspond to both initial and first replacement clutches, and late nests to further replacement clutches.

No attempt is made to calculate separate values for nesting success in different habitats *per se*, instead separate nest survival values are calculated for different degrees of either nest concealment (Redshank and Dunlin) or camouflage (Ringed Plover). The method of scoring nest concealment and camouflage is described in Appendix J. The concealment and camouflage of nests is highly dependent upon habitat type, with nests in a given habitat tending to have a similar degree of concealment or camouflage; this is discussed at length in Chapter 5. The results in Table 8.1 clearly show that early nests and late nests have different survival rates. But nest concealment/camouflage also changes through the season as the vegetation grows (particularly after May). To control for these seasonal effects only early nests are used in the analysis of the effect of camouflage/concealment upon nest survival. The nest survival estimates for nests of different concealment and camouflage ratings are summarised in Table 8.2.

iii) Causes of egg losses

In the vast majority of cases, the cause of nest loss was thought to be gull predation. Common Gulls were by far the most

Table 8.1: Estimated nest survival rates from laying to hatching in 1985, 1986 and 1987 for Redshank, Dunlin and Ringed Plover.

SAMPLE OF NESTS	ESTIMATED SURVIVAL RATE ¹	STANDARD ERROR ²		NO. NESTS	NO. NEST DAYS	NO. NESTS LOST
		-2 S.E.	+2 S.E.			
REDSHANK						
1985 early nests	.609	-.188	+.268	36	424	7
1986 early nests	.401	-.133	+.195	42	674	20
1987 early nests	.579	-.149	+.199	47	716	13
1985 late nests	.547	-.198	+.305	21	350	7
1986 late nests	.282	-.123	+.214	35	457	19
1987 late nests	.462	-.193	+.321	22	316	8
All early nests	.515	-.096	+.117	125	1814	40
All late nests	.400	-.105	+.144	78	1123	34
DUNLIN						
1985 early nests	.665	-.190	+.255	33	412	6
1986 early nests	.691	-.211	+.299	20	303	4
1987 early nests	.794	-.161	+.201	38	484	4
1985 late nests	.545	-.246	+.437	12	185	4
1986 late nests	.310	-.161	+.324	25	242	10
1987 late nests	.326	-.195	+.462	15	152	6
All early nests	.722	-.113	+.134	91	1199	14
All late nests	.376	-.132	+.199	52	579	20
RINGED PLOVER						
1985 early nests	.187	-.088	+.163	42	484	27
1986 early nests	.255	-.118	+.213	31	415	19
1987 early nests	.325	-.127	+.205	38	530	20
1985 late nests	.041	-.036	+.267	10	87	9
1986 late nests	.127	-.086	+.255	18	190	13
1987 late nests	.033	-.030	+.288	8	73	8
All early nests	.251	-.072	+.099	111	1429	66
All late nests	.073	-.045	+.111	36	350	30

¹ based on method given by Mayfield (1961,1975)

² based on method given by Johnson (1979)

Redshank early nests = first egg laid before 5th May

Redshank late nests = first egg laid after 4th May

Redshank mean total nest exposure = 29.6 days

Dunlin early nests = first egg laid before 25th May

Dunlin late nests = first egg laid after 24th May

Dunlin mean total nest exposure = 27.8 days

Ringed Plover early nests = first egg laid before 20th May

Ringed Plover late nests = first egg laid after 19th May

Ringed Plover mean total nest exposure = 29.2 days

Table 8.2: Estimated nest survival rates from laying to hatching for early nests of Redshank and Dunlin with different concealment ratings, and for early nests of Ringed Plover with different camouflage ratings.

CONCEALMENT/ CAMOUFLAGE RATING	ESTIMATED SURVIVAL RATE ¹	STANDARD ERROR ² -2 S.E.	+2 S.E.	NO. NESTS	NO. NEST DAYS	NO. NESTS LOST
REDSHANK						
concealmt. 1	.256	-.191	+.689	7	90	4
" 2	.360	-.170	+.314	24	297	10
" 3	.493	-.135	+.184	57	810	19
" 4	.716	-.169	+.218	32	538	6
" 5	.686	-.361	+.737	5	80	1
DUNLIN						
concealmt. 1	no nests					
" 2	.613	-.263	+.448	12	172	3
" 3	.639	-.171	+.231	38	500	8
" 4	.832	-.157	+.192	35	455	3
" 5	1.00	/	/	6	73	0
RINGED PLOVER						
camouflage 1	.169	-.130	+.509	10	102	6
" 2	.197	-.134	+.398	13	148	8
" 3	.290	-.111	+.175	46	626	26
" 4	.334	-.208	+.526	9	136	5

¹ not calculable

² based on method given by Mayfield (1961,1975)

² based on method given by Johnson (1979)

Redshank early nests = first egg laid before 5th May

Redshank mean total nest exposure = 29.6 days

Dunlin early nests = first egg laid before 25th May

Dunlin mean total nest exposure = 27.8 days

Ringed Plover early nests = first egg laid before 20th May

Ringed Plover mean total nest exposure = 29.2 days

Details of scoring for concealment and camouflage are summarised in Appendix J. (For both, 1 = very poor and 5 = very good)

serious egg thieves followed by Black-headed Gulls. These two species were seen very frequently hunting for wader nests and chicks and many incidences of predation were witnessed. Other avian predators observed taking wader eggs were Hooded Crow, Raven (*Corvus corax*), Hen Harrier (*Circus cyaneus*), Herring Gull (*Larus argentatus*), and Arctic Skua (*Stercorarius parasiticus*). All these species, except for Hooded Crows at Rubha Ardvule in 1986, were observed taking eggs only once. Characteristic signs usually indicate nests lost to mammalian predators (Green 1987), and on this basis two incidences of mammalian predation were identified; both of these were of Redshank nests and were attributed to feral Polecat (*Mustela putorius*) and Common Rat (*Rattus norvegicus*) respectively. Trampling by livestock was not a serious cause of nest failure despite the presence of cattle and sheep over much of each study-site. Only four nests (2 Redshank, 1 Dunlin and 1 Ringed Plover) were lost in this way. Six Ringed Plover nests on plough were destroyed by rolling operations and one Redshank nest was destroyed by a bulldozer clearing ditches. Surprisingly, none of the nests of Ringed Plover on tracks were run over, though this must surely be a common fate of such nests, especially now that the use of wide-wheeled motor-tricycles is commonplace on crofts. Nest failure due to flooding was observed on one occasion only: heavy rain in late May 1985 flooded three Dunlin nests (all on machair marsh) at Drimore Farm; these were subsequently deserted.

iv) Survival of early and late nests

The survival of early nests was significantly greater than late

nests for both Ringed Plover and Dunlin. The trend is the same for Redshank but the difference is not significant. The reason why early nests survived better is that they suffered fewer losses from predation. The higher predation rates of late nests is probably caused by a combination of their higher vulnerability to predation together with more frequent hunting forays by predators.

In the early part of the season all areas with nesting Redshank, Dunlin and Ringed Plover also had many breeding Lapwing and, as discussed in Chapter 5, these are very effective at driving off avian predators through their persistent communal mobbing behaviour (Elliot 1985). The presence of breeding Lapwings undoubtedly affords considerable protection to the nests of other species in their vicinity. Lapwing are early breeders and by early June most have completed breeding and no longer join in communal predator mobbing. The protection gained by other waders from the anti-predator behaviour of Lapwing thus declines from June onwards. The occurrence of hunting gulls over the wader breeding grounds increased through the breeding season (*pers obs.*). This may have been due either to increasing food requirements of the gulls (because they had chicks to feed) or because the gulls found that hunting for wader eggs (and chicks) became increasingly profitable as the season progressed. The latter could be caused by the fall in Lapwing anti-predator behaviour or by the gulls improving their skills of nest (and chick) detection and robbery.

v) Importance of concealment/camouflage for nest survival

The risk of predation was not equal for all nests. Beside the benefits gained from nesting close to Lapwings and Arctic Terns already discussed (Chapter 5), the chances of nest predation also depend on characteristics of the nest-site and the density of nests. The most important aspect of the nest affecting its vulnerability to predation is concealment (for Redshank and Dunlin) or camouflage (for Ringed Plover) of its contents. The results in Table 8.2 show clear-cut trends towards increasing nest survival rates with increasing nest concealment or camouflage. For all three species the estimated survival rate of the best concealed or camouflaged nests was approximately twice that of the least well concealed or camouflaged nests. The standard errors of the estimates in Table 8.2 are generally large due to the small sample sizes. For each species, Kendall's coefficient of rank correlation of estimated nest survival rate with concealment/camouflage rating is as follows:

Redshank	$\tau = 0.7$, $n = 5$, 2-tailed test $P = 0.08$
Dunlin	$\tau = 1.0$, $n = 4$, 2-tailed test $P = 0.08$
Ringed Plover	$\tau = 1.0$, $n = 4$, 2-tailed test $P = 0.08$

For each species, the probability of the observed trend being spurious is small.

The actual benefits of good concealment and camouflage are probably slightly off-set by higher nesting densities in those habitats offering the best potential nest-sites and the implications this has for hunting predators. Predators will tend to hunt where their chances of success are highest which is probably governed by a combination of detectability and density of nests (Chapter 6). The nesting success of Ringed Plover and

Dunlin breeding at high and low density, as indicated by the proportion of colour-ringed pairs known to successfully hatch chicks, is shown in Table 8.3. For both species the nesting success was very similar at high and low density.

vi) Replacement of nests

Following the loss of a first clutch it was usual, in all three of the study species, for a replacement clutch to be laid. Ringed Plover commonly, and Redshank very occasionally, relaid again if the second clutch was also lost. Ringed Plover sometimes laid again after the loss of a brood and were occasionally double brooded. Neither Redshank nor Dunlin were ever observed to be double brooded though Dunlin occasionally laid again after the loss of a brood. The pattern of relaying behaviour observed for each species in this study is in close agreement with that reported by others working on these species (for Redshank by Grosskopf (1963) and Yates (1982), for Dunlin by Soikkeli (1967) and Jonsson (1988), and for Ringed Plover by Pienkowski (1984) and Laven (1940)).

The mean number of breeding attempts per pair per season was estimated by determining the proportion of pairs that attempted to breed again after failure of the first attempt, and also, after failure of the second attempt. Because the number of replacement nests found was an unknown proportion of the total, the replacement rate was estimated indirectly from the number of broods found that had hatched from replacement nests (known or unknown) together with the survival rate of replacement nests. The high detectability of young broods meant that the chances of

Table 8.3: Proportion of colour-ringed pairs that produced broods

YEAR & SITE	NO. C-R PAIRS	NO. OF BROODS	BROODS PER PAIR
REDSHANK			
1985 all sites	56	44	.79
1986 all sites	70	47	.67
1987 all sites	76	62	.82
All years, all sites	202	153	.76
DUNLIN			
1985 all sites	47	39	.83
1986 all sites	56	39	.70
1987 all sites	59	48	.81
All years, all sites	162	126	.78
1986 + 87 low density ¹	82	61	.74
1986 + 87 high density ²	33	26	.79
RINGED PLOVER			
1985 all sites	48	19	.40
1986 all sites	57	27	.47
1987 all sites	50	19	.38
All years, all sites	155	65	.42
1986 + 87 low density ³	11	5	.46
1986 + 87 high density ⁴	36	16	.44

¹Dunlin nesting on fallow machair and blackland at Stilligarry and Drimore Farm (Chapter 6)

²Dunlin nesting on machair marsh at Drimore Farm (Chapter 6)

³Ringed Plover nesting in all habitats at Drimore Farm except damp recent fallow (Chapter 6).

⁴Ringed Plover nesting at Drimore Farm on damp recent fallow (Chapter 6).

overlooking a brood were small. The mean number of breeding attempts by Ringed Plover could only be roughly estimated because of the incompleteness of the nesting histories of most pairs. The estimated replacement rate of lost nests is shown in Tables 8.6, 8.7 and 8.8 for Redshank, Dunlin and Ringed Plover respectively.

The non-replacement of some of the early nests that failed, combined with the low survival rate of replacement nests, meant that the contribution to the annual productivity from late nests was generally small. The estimated proportion of the annual production of each species contributed by late nests is as follows: Redshank 23%, Dunlin 6% and Ringed Plover 5%. Losses of early nests clearly have a disproportionately larger effect on annual production than losses of late nests.

vii) Proportion of pairs successfully nesting

Overall nesting success in terms of the proportion of pairs that successfully hatch chicks (i.e. chicks leave the nest) was determined in two ways. First, indirectly from the estimated nest survival rates together with the estimated mean number of breeding attempts per pair, and second, directly from the proportion of colour-ringed pairs seen with chicks by the end of a season. The observed proportion of colour-ringed pairs successfully hatching chicks is tabulated in Table 8.3. The values from the two methods (based on all three years data) can be compared in Tables 8.6, 8.7 and 8.8 for Redshank, Dunlin and Ringed Plover respectively. The values for Redshank (0.67 and 0.76) and for Ringed plover (0.48 and 0.41) are in moderately close agreement whilst those for Dunlin (0.91 and 0.78) agree

less well. The discrepancies between the values are thought to be caused by inaccuracies in the indirectly calculated value which is based on two estimates; the standard errors of the nest survival estimates in Table 8.1 are quite large even for large samples of nests. The values for overall nesting success determined from the proportion of colour-ringed pairs with chicks are therefore considered to be the most accurate and are chosen for use in calculations of overall productivity.

viii) Comparison of nesting success with other studies

The published figures for nesting success found by other workers are often an over estimate of actual nesting success because they are not corrected (using Mayfield's Method) for nests that were not found before failing. This makes direct comparisons between studies difficult. In north-east England Pienkowski found a mean nest survival rate for Ringed Plovers of 12% (Mayfield's Method used). In contrast to the present study the survival of his nests was lowest in the early part of the season. The reason for this difference may lie in the principal type of egg predators involved; mainly mammalian in Pienkowski's study versus avian in this study. A value of 78% for Dunlin nest survival, similar to this study, was found by Soikkeli (1967) in Finland (Mayfield Method not used, and survival value considered to be slightly too high). In contrast to the findings of the present study and of Soikkeli, Jonsson (1988) found that only 30% of Dunlin nests in south Sweden survived to hatching (Mayfield's Method not used) and it is perhaps not surprising that this population is declining. Both Soikkeli and Jonsson found no

tendency for higher losses in late nests; in both their studies mammals (especially mustelids) and crows, instead of gulls, were the main egg predators. In a study of Redshank breeding on saltmarsh in north-west England (Yates 1982) 41% of nests survived to hatching (Mayfield Method not used) but this was almost certainly artificially low due to very high losses caused by trapping on the nests.

Survival of chicks to fledging

1) Methods

For Redshank and Dunlin it was normally very difficult to see the chicks and practically impossible to readily ascertain the number of chicks in a brood because the chicks normally hid from view in good cover. This meant that brood survival (defined as at least one chick of a brood surviving to fledging) and fledging success for these two species had to be estimated indirectly as described below. Ringed Plover chicks, however, were relatively easily seen, and therefore brood survival was easily determined from direct observation of chicks. However, it was not always possible to accurately count the total number of chicks in Ringed Plover broods, particularly old broods, because the chicks of a brood were often dispersed over a wide area. Therefore, it was not usually possible to be certain of the number of chicks that fledged from surviving broods.

Adult Redshank and Dunlin with chicks normally show characteristic behaviour and give distinctive calls, and therefore the survival of broods belonging to recognisable parents is easily confirmed from the adults' behaviour. For both

Redshank and Dunlin it is normal for only the male parent to stay with the brood up to fledging (Grosskopf 1958 (Redshank); Soikkeli 1967 (Dunlin); *pers. obs.*). Therefore, for these two species, only broods with a colour-ringed father were used in the determination of mean brood survival.

Unless there was evidence to the contrary, all Redshank broods surviving to over 20 days old, Dunlin broods surviving to over 14 days old and Ringed Plover broods surviving to over 18 days old were considered to be "successful", i.e. producing at least one fledged chick. These periods were chosen to be slightly below the fledging period for the species concerned, (25-35 days for Redshank (Grosskopf 1958, 1960), about 18 days for Dunlin (Soikkeli 1967) and about 23 days for Ringed Plover *pers. obs.*) because the interval between successive checks for a brood was about five days and thus the attendant adult(s) of some broods that were successful were not seen in the period 1-4 days before fledging. Misclassification of brood survival because of the early threshold for success is not thought to be serious because most broods that were classified as successful were proven to have survived up to or after fledging, and also brood failure in the latter half of the fledging period was rare. In contrast, it is possible that some Redshank broods were misclassified as "failing" because they moved to areas that were not surveyed. This possible source of error was minimised by searching extensive areas adjacent to the study-sites for missing broods.

The total number of chicks in broods of known age, including those of unmarked adults, was counted whenever possible, (e.g. if

a brood was seen crossing open ground).

ii) Results

The results on brood survival for each species are summarised in Table 8.4.

The counts of the number of chicks in broods of known age, are used to estimate the mean number of chicks fledging from successful broods by plotting mean brood size against brood age. Because of the relatively small sample sizes and because the age of many broods could only be estimated to within a few days' accuracy, brood age has been categorised. Data from all three years for each species is aggregated because there is insufficient data to investigate intra-seasonal and inter-seasonal variation in brood size. The results are shown in Figures 8.1, 8.2 and 8.3 for Redshank, Dunlin and Ringed Plover respectively. The mean brood size at fledging is estimated from the position of the curve at the age of fledging (see above). The estimated mean brood sizes at fledging determined in this way for each species are as follows: Redshank - 2.0 chicks, Dunlin - 2.2 chicks and Ringed Plover - 2.3 chicks. It is possible that for Redshank and Dunlin these figures are slight underestimates because some chicks in old broods may have been overlooked.

The overall chick survival rate of each species was estimated by multiplying together the brood survival rate (Table 8.4) and the estimated reduction in the size of successful broods between hatching and fledging (Figures 8.1 to 8.3). This method makes the assumption that brood survival is independent of initial

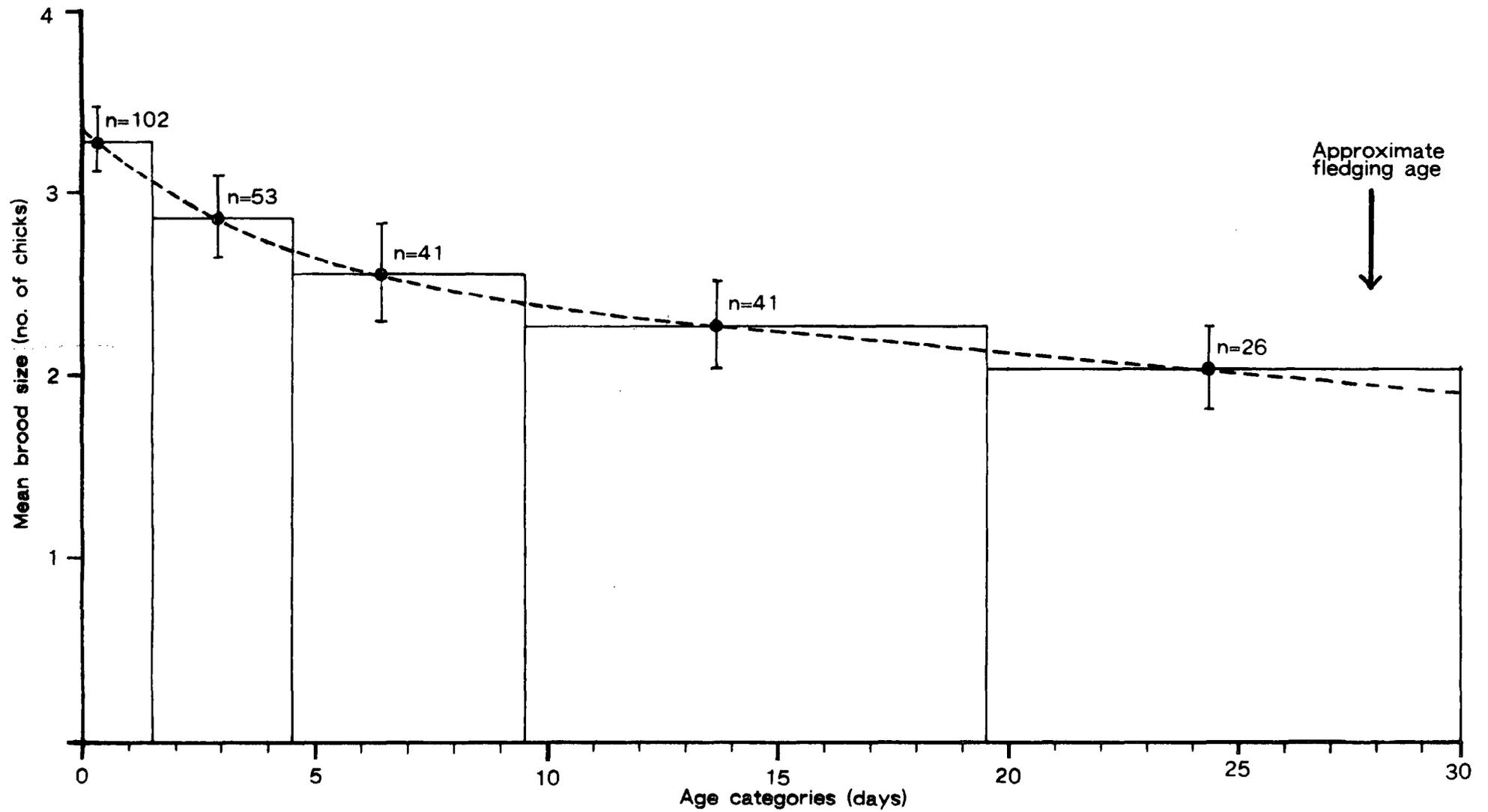


Figure 8.1: Mean size of Redshank broods of different age categories showing $\pm 2SE$

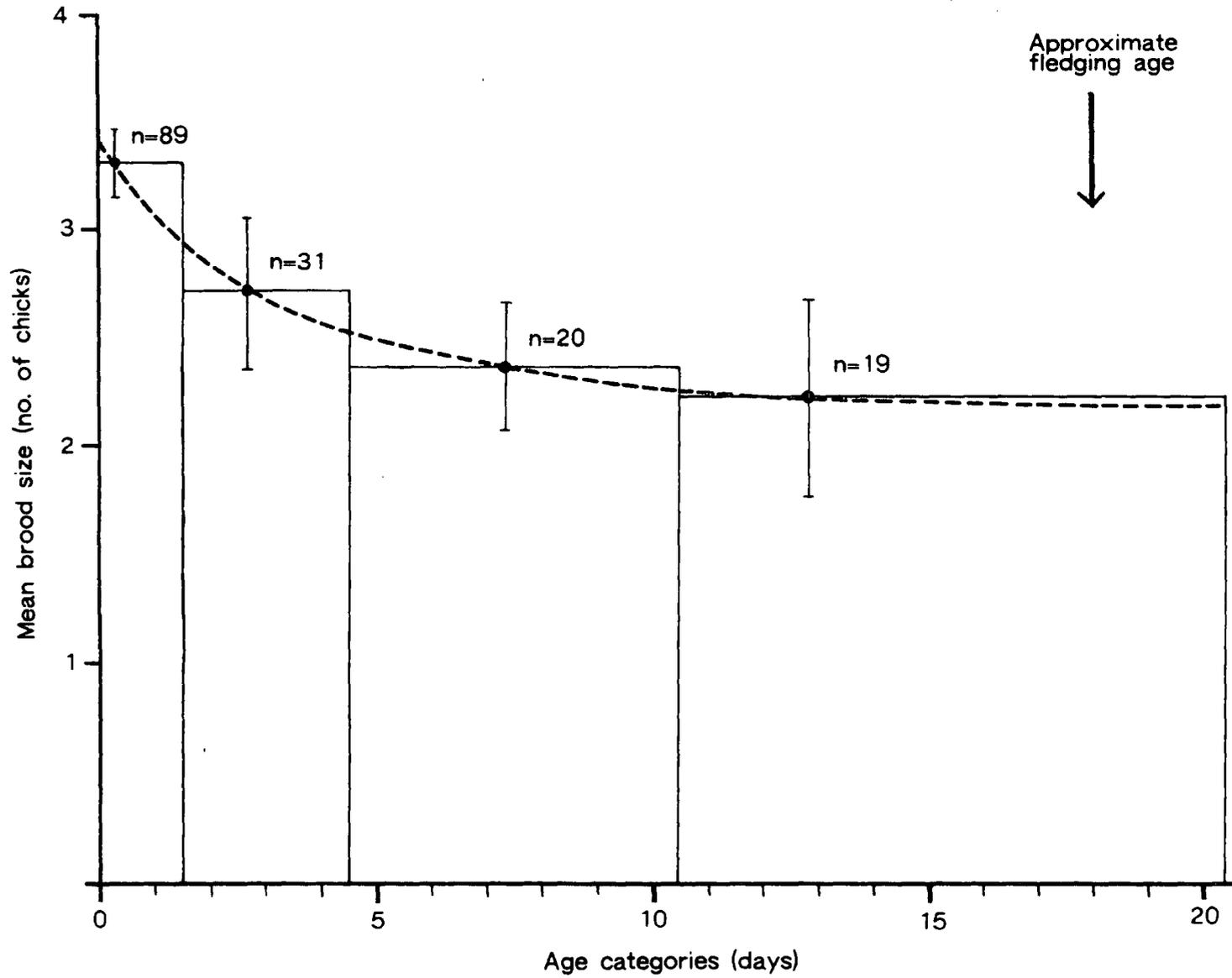


Figure 8.2: Mean size of Dunlin broods of different age categories showing $\pm 2SE$

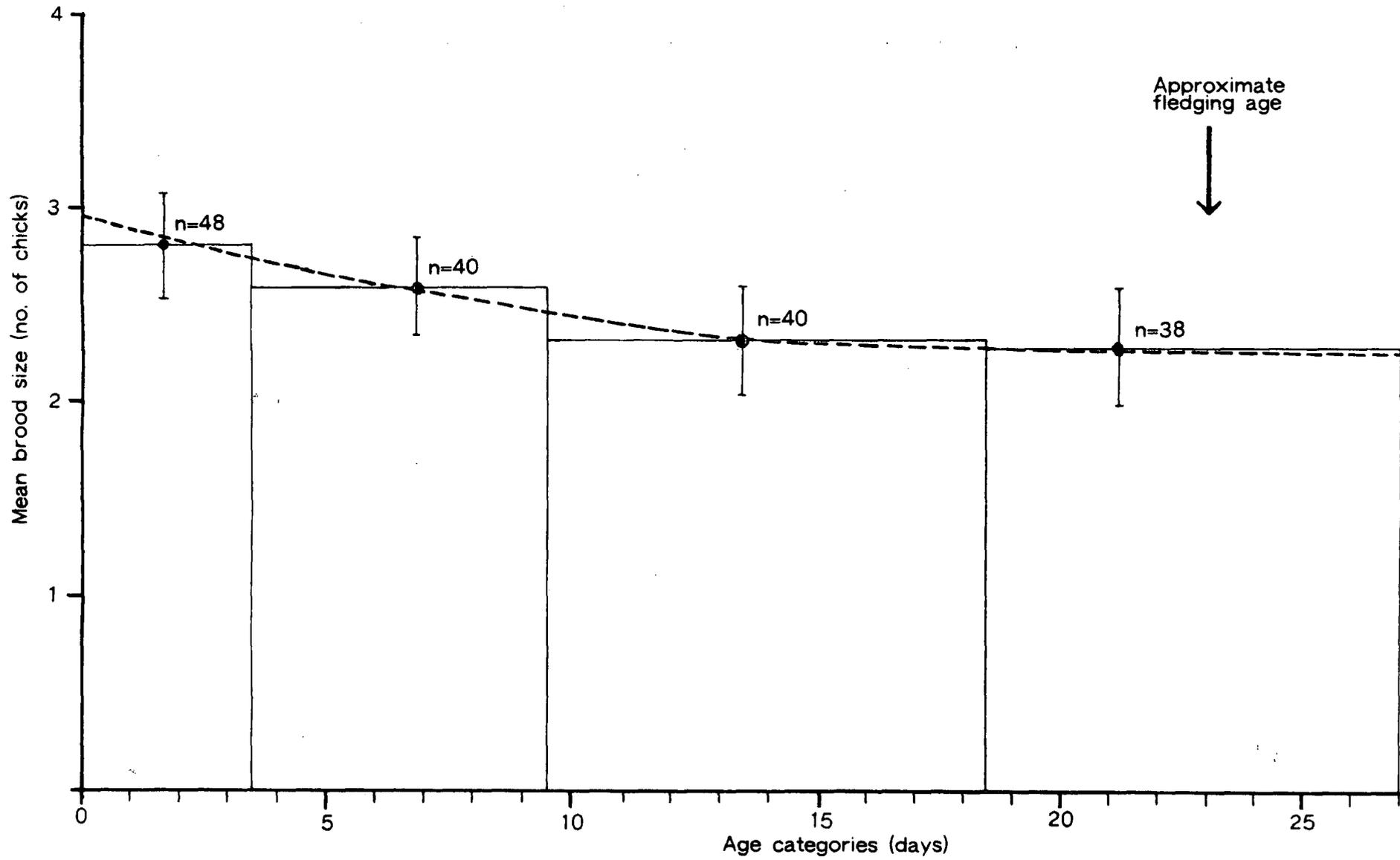


Figure 8.3: Mean size of Ringed Plover broods of different age categories showing ± 2 SE

Table 8.4: Survival of Redshank, Dunlin and Ringed Plover broods.

YEAR & SITE	NO. BROODS	NO. SURVIVING	BROOD ¹ SURVIVAL RATE
REDSHANK			
1985 all sites	39	28	.72
1986 all sites	44	34	.77
1987 all sites	41	26	.63
All years, all sites	124	88	.71
DUNLIN			
1985	NO DATA COLLECTED		
1986 Stilligarry	13	4	.30
1987 Stilligarry	9	4	.44
All years Stilligarry	22	8	.36
1986 Drimore Farm	16	11	.69
1987 Drimore Farm	23	21	.92
All years Drimore Fm.	39	32	.83
RINGED PLOVER			
1985 all sites	19	11	.58
1986 all sites	27	21	.78
1987 all sites	19	14	.74
All years, all sites	65	46	.70

¹ At least one chick surviving to fledge

brood size. Although intuitively this is unlikely, the violation of this assumption is not considered to be a serious source of error because the vast majority of broods initially had either 3 or 4 chicks. The estimated overall chick survival rate up to fledging for each species is summarised in Table 8.5.

iii) Causes of chick mortality

The causes of chick mortality were thought in most cases to be predation. The list of predators known or suspected to take chicks is the same as that for egg predation, with the addition of Buzzard (*Buteo buteo*). This species was witnessed taking a large Redshank chick and many Lapwing chicks. Wet, cold and windy weather may also have been a major cause of mortality, either directly through hypothermia or indirectly through preventing chicks from feeding and leading to their starvation. Although, one small Ringed Plover chick was found dead after heavy rains; the chances of finding dead chicks are very small. Young wader chicks are particularly vulnerable to bad weather because they cannot physiologically thermoregulate (Blix and Steen 1979, Myhre and Steen 1979) and therefore must be brooded regularly to maintain their body temperature. This also makes young chicks more vulnerable to predation, especially in cold weather, because after about 10-20 minutes of remaining crouched motionless in response to a hunting predator, they become too cold and are forced to call out to the parents for brooding. Normally, the adults then approach the chick(s) and commence brooding which reveals their location to the predator (*pers obs.*). Another reason that is thought to make young chicks more

Table 8.5: Overall chick survival estimates derived from brood survival and reduction of brood size between hatching and fledging in surviving broods.

YEAR & SITE	MEAN BROOD SURVIVAL (Table 8.4)	NET OVERALL REDUCTION IN MEAN BROOD SIZE AT FLEDGING (Figures 8.1, 8.2 & 8.3)	ESTIMATED OVERALL CHICK SURVIVAL
REDSHANK			
1985 all sites	.72	x .57	.41
1986 all sites	.77	x .57	.44
1987 all sites	.63	x .57	.36
All years, all sites	.73	x .57	.42
DUNLIN			
1986 Stilligarry	.30	x .67	.20
1987 Stilligarry	.44	x .67	.29
All years, Stillig.	.36	x .67	.24
1986 Drimore Farm	.69	x .67	.46
1987 Drimore Farm	.92	x .67	.62
All years Drimore Fm.	.83	x .67	.56
RINGED PLOVER			
1985 all sites	.58	x .72	.42
1986 all sites	.78	x .72	.56
1987 all sites	.74	x .72	.53
All years, all sites	.72	x .72	.54

susceptible to predation is the tendency of young brood members to stay close together and thus a predator will often find several chicks together; older chicks generally spread out over a wide area. It was apparent when trying to catch chicks to ring that upon the threat of danger (i.e. human disturbance) the brood normally scattered in different directions before crouching. This behaviour has adaptive value by making it more difficult for predators to find all the chicks in a brood.

iv) Differences in chick survival between years and habitats

The small differences in Redshank and Ringed Plover brood survival between years are not significant. The difference between 1987 and 1986 in the survival of Dunlin broods was not quite significant ($\text{Chi}^2 = 3.6$, d.f.= 1, $P > 0.05$, Yates' correction applied), but this is probably a real difference. If so, it was probably caused by the superior cover due to earlier vegetation growth in 1987. Of greater interest is the highly significant difference ($\text{Chi}^2 = 11$, d.f.= 1, $P < 0.01$, Yates' correction applied) between brood survival at Drimore Farm (83%) and Stilligarry (36%). The precise reason for this is not known but probably is connected to habitat considerations. The broods at Stilligarry were nearly all on old, moderately dry fallow machair whilst at Drimore Farm nearly all the broods were on marsh. The fallow machair generally had poorer cover than the marsh which would have made it easier for predators to see chicks. Also, the fallow machair was used on some days by flocks of up to 160 ground-feeding Black-headed and Common Gulls that spent many hours probing for invertebrates during which they

methodically covered large areas of the fallow machair. It would seem inevitable that these feeding gulls encountered wader chicks and eggs which they presumably devoured.

Differences between years, and habitats, in the availability of suitable invertebrate chick-food may also have affected chick survival, but I have no information on this.

Summary of breeding success

The various measures relating to breeding performance are summarised in Tables 8.6, 8.7 and 8.8, for Redshank, Dunlin and Ringed Plover respectively. In these tables an attempt is made to calculate the mean annual productivity per pair from the measures of success for each breeding stage.

Part 2. Survival of Full-grown Birds

Survival of breeding adults

i) Methods

The survival rate of breeding adult birds was calculated from the return rate of marked adults between seasons and their "disappearance" rate within the breeding season. This method assumes that the reason for birds failing to return, or disappearing is their mortality, it is possible however that emigration from the study areas could account for some of the losses. In general, adults of all species were very faithful to their previous breeding sites (Chapter 7). Nearly all known movements were of less than 2 km and because a wide area around the study-sites was thoroughly searched it is thought that very

Table 8.6: Components of Redshank productivity.

Mean clutch size: (n = 190 clutches)	=	3.88
Egg survival rate in successful nests: (9 eggs lost in 6779 egg days)	=	0.964
Hatching rate of surviving eggs: (n = 430 eggs)	=	0.935
Mean no. chicks leaving successful nests:		
	$3.88 \times .964 \times .935 =$	3.5
Survival rate of early nests: (Table 8.1)	=	0.515
Survival rate of late nests: (Table 8.1)	=	0.400
Relaying rate after failure of 1st nest:	=	0.775
Calculated proportion of pairs hatching chicks:		
1st nests (1 x .515)	=	0.515
2nd nests ((1 - .515) x .775 x .400)	=	0.150
Total	=	0.665
Observed proportion of pairs hatching chicks: (Table 8.3)	=	0.757
Brood survival rate: (Table 8.4)	=	0.731
Mean no. of chicks fledged per successful brood: (see Figure 8.1)	=	2.0
No. of chicks fledged per pair:		
	$.757 \times .731 \times 2.0 =$	1.11
No. of chicks fledged per adult:	=	0.56 ca.

Table 8.7: Components of Dunlin productivity.

Mean clutch size: (n = 135 nests)	=	3.83
Egg survival rate in successful nests: (10 eggs lost in 5068 egg days)	=	0.951
Hatching rate of surviving eggs: (n = 405 eggs)	=	0.896
Mean no. chicks leaving successful nests: $3.83 \times .951 \times .896$	=	3.26
Survival rate of early nests: (Table 8.1)	=	0.722
Survival rate of late nests: (Table 8.1)	=	0.376
Relaying rate after failure of 1st nest:	=	0.558
Calculated proportion of pairs hatching chicks: 1st nests (1 x .722)	=	0.722
2nd nests ((1 - .228) x .558 x .376)	=	0.048
Total	=	0.770
Mean brood mortality rate (Table 8.4)	=	0.666
Relaying rate after failure of brood from 1st nest:	=	0.532
Proportion of pairs hatching 2 broods: $.772 \times .333 \times .532$	=	0.136
Calculated mean number of broods hatched per pair: $.770 + .136$	=	0.906
Observed mean number of broods hatched per pair: (Table 8.3)	=	0.777
Brood survival rate: (Table 8.4)	Stilligarry = 0.364 Drimore Farm = 0.825	
Mean no. of chicks fledged per successful brood: (see Figure 8.2)	=	2.2
Mean no. of chicks fledged per pair: $.777 \times (.364 \text{ or } .825) \times 2.2$	Stilligarry = 0.622 Drimore Farm = 1.41	
Mean no. of chicks fledged per adult:	Stilligarry = 0.31 ca. Drimore Farm = 0.71 ca.	

Table 8.8: Components of Ringed Plover productivity.

Mean clutch size (n = 122 clutches)	=	3.57
Egg survival rate in successful nests: (12 eggs lost in 2987 egg days)	=	0.898
Hatching rate of surviving eggs: (n = 156 eggs)	=	0.910
Mean brood size leaving successful nests:		
	$3.57 \times .898 \times .910$	= 2.92
Survival rate of early nests: (Table 8.1)	=	0.251
Survival rate of late nests: (Table 8.1)	=	0.073
Relaying rate after failure of 1st nest:	=	0.9 ca.
Relaying rate after failure of 2nd nest:	=	0.5 ca.
Calculated proportion of pairs hatching chicks:		
1st nests (early) (1 X .251)	=	0.251
2nd nests (early) ((1 -.251) x .251 x .9)	=	0.169
3rd nests (late) (1 - (.251+.169) x .073 x .5)	=	0.021
Total	=	0.441
Brood mortality rate:(Table 8.4)	=	0.29
Relaying rate after failure of brood from 1st nest:	=	0.5 ca.
Proportion of pairs hatching 2 broods:		
	$.251 \times .29 \times .5$	= 0.036
Calculated mean number of broods hatched per pair:		
	$.441 + .036$	= 0.477
Observed mean number of broods hatched per pair: (Table 8.3)	=	0.413
Brood survival rate: (Table 8.4)	=	0.71
Mean brood size at fledging: (Figure 8.3)	=	2.3
Mean no. of chicks fledged per pair:		
	$.413 \times .717 \times 2.3$	= 0.68
Mean no. of chicks fledged per adult:	=	0.34 ca.

few returning birds were overlooked. Female Ringed Plover were the least site faithful and sometimes moved several kilometres; however the survival of "missing" birds was readily ascertained from their presence or absence on the beaches immediately before and after the breeding season. For this reason all suitable beaches on South Uist and Benbecula were regularly checked for Ringed Plover. Colour-ringed female Dunlin were generally seen only a few times each season because of their secrecy and their short stay on the breeding grounds. Therefore, for female Dunlin it was not possible to distinguish with confidence between breeding season and non-breeding season mortality .

ii) Results

The data on adult survival for all three species is summarised in Table 8.9. Within each species the differences in adult survival between years, between males and females, and between birds in their second year of life and those older (not shown in Table 8.9) are in all cases not significant.

iii) Causes of adult mortality

The causes of adult mortality outside the breeding season were unknown. Mortality in the breeding season was mainly through predation by raptors, especially Peregrine Falcons (*Falco peregrinus*), but also Merlins (*Falco columbaris*) and Hen Harriers (*Circus cyaeus*). These three species were seen almost daily hunting over the breeding grounds and the remains of many kills were found. Redshank and Lapwing were the most common wader species taken. In 1986, 11% colour-ringed Redshank (9 out of 81) were almost certainly taken by raptors between their arrival

Table 8.9: Survival of adult Redshank, Dunlin and Ringed Plover.

SPECIES SEX SEASON	NO. ALIVE AT END OF PREVIOUS SEASON	NO. THAT RETURNED AT START OF SEASON	SURVIVAL OUTWITH BREEDING SEASON	NO. ALIVE AT END OF BREEDING SEASON	SURVIVAL DURING BREEDING SEASON	ANNUAL SURVIVAL RATE	1.96 S.E.
REDSHANK							
1986 male	51	40	78.4%	35	87.5%	68.6%	
1986 female	48	41	85.4%	34	82.9%	70.8%	
1986 m & f	99	81	81.8%	69	85.2%	69.7%	
1987 male	63	53	84.1%	47	88.6%	74.6%	
1987 female	61	54	88.5%	53	98.1%	86.8%	
1987 m & f	124	107	86.3%	100	93.5%	80.6%	
86+87 m & f	223	188	84.3%	169	89.9%	75.8%	5.6%
DUNLIN							
1986 male	44	42	95.4%	40	95.2%	90.9%	
1986 female	43	/	/	34	/	79.1%	
1986 m & f	87	/	/	74	/	85.1%	
1987 male	61	49	80.3%	47	95.9%	77.0%	
1987 female	63	/	/	49	/	77.7%	
1987 m & f	124	/	/	96	/	77.4%	
86+87 m & f	211	/	/	170	/	80.6%	5.3%
RINGED PLOVER							
1986 male	37	27	73.0%	26	96.3%	70.3%	
1986 female	45	32	71.1%	30	93.8%	66.7%	
1986 m & f	82	59	72.0%	56	94.9%	68.3%	
1987 male	47	36	76.6%	35	97.2%	74.5%	
1987 female	52	44	84.6%	41	93.2%	78.8%	
1987 m & f	99	80	80.8%	76	95.0%	76.7%	
86+87 m & f	181	139	76.8%	132	95.0%	72.9%	6.5%

/ not determined

back on the breeding grounds in late March or early April and the end of April. If this level of predation at the start of the breeding season is typical then it is likely to be an important ultimate factor controlling the timing of return to the breeding grounds. Other causes of breeding season mortality proven or suspected were: intraspecific fighting (2 male Redshank), collision with vehicle (1 Ringed Plover), leg injuries from sheeps' wool (1 Redshank) and leg injuries caused or exacerbated by the colour-rings (1 Dunlin, 1 Redshank and 1 Ringed Plover).

Leg injuries caused by the colour-rings occurred when grains of sand built up between a ring and the bird's leg. This led to infection and eventually prevented use of the leg which seriously impaired the bird's ability to walk and run. The extent of losses caused by the rings was almost certainly very small, probably less than 1% of birds marked. The birds affected were observed limping for many weeks before their death and thus birds that died in this way were easily identified. Several other individuals, mainly Ringed Plover, were seen with slight limps for short periods, but all these birds recovered from their injuries. The risks of using colour-rings on birds frequenting sandy habitats was apparent before the start of this study (M.J. Wells *pers. comm.*) and to minimise the problem all colour-rings were fitted as loosely as possible.

iv) Comparison with adult survival in other studies

The adult survival rates found in this study are in close agreement with those found by other workers in north-west Europe; these are summarised in Table 8.10.

Table 8.10: Comparison of annual survival rates of adults found in various breeding studies of Redshank, Dunlin and Ringed Plover.

SPECIES	SURVIVAL RATE	STUDY AREA	SOURCE
REDSHANK	76%	Western Isles	This study
	75%	Friesian Islands	Grosskopf (1964)
	78%	N-W England	Yates (1982)
DUNLIN	81%	Western Isles	This study
	73%	Finland	Soikkeli (1967)
	83%	S Sweden	Jonsson (1988)
RINGED PLOVER	73%	Western Isles	This study
	80%	N-E England	Pienkowski (1980)
	59%	Friesian Islands	Laven (1940)
	ca. 73%	Friesian Islands	Bub (1962)

First-year survival

The survival of birds between fledging and the following breeding season (first-year survival) could be estimated only roughly because of the following difficulties:

- 1) The proportion of colour-ringed chicks that successfully fledged is unknown.
- 2) Chicks from a given site dispersed over large areas to breed, (Chapter 7). Although very extensive areas were searched, some birds that returned to breed were almost certainly overlooked.
- 3) Except for a few large Ringed Plover chicks, chicks were given site specific colour-ring sequences (and not unique combinations of colours), and thus there was sometimes difficulty in distinguishing between individuals that returned to breed. The problem of distinguishing individuals was exacerbated by the itinerant behaviour of some first-time breeders, presumably looking for a suitable vacant breeding territory.

In spite of these difficulties, I have used the observed return rates of the marked chicks to estimate the maximum mortality between fledging and first breeding. Although the approach used here makes several assumptions and approximations it does give an indication of the magnitude of mortality for this part of each species' life cycle.

1) Method used to estimate number of ringed chicks fledging

The proportion of the colour-ringed chicks that survive to

fledge can be estimated if the number of chicks in each age class and the survival rate to fledging for chicks of each age class is known. The age of many of the chicks ringed was not known; however it was easily estimated from a growth curve of bill length, derived from recaptures of chicks of known age. Many of the chicks were ringed after they had left the nest and would therefore be expected to have a higher survival rate than the overall chick survival values given in Table 8.5. It is known that daily chick mortality decreases with chick age (see Figures 8.1 to 8.3); the vast majority of losses occurred during the first week after hatching and losses close to fledging were few. Many other studies of breeding waders have also clearly demonstrated that chick mortality rate is inversely related to chick age (e.g. Baines 1988, Pienkowski 1980, Soikkeli 1967). To estimate the number of chicks ringed that survived to fledging, the chicks have been grouped into age categories and approximate survival rates for each category used. The results are shown in Table 8.11.

ii) Method used to monitor return rate of chicks

During 1986, it became clear that one year old birds returning to breed for the first time (i.e. chicks colour-ringed in the first year of this study) were dispersing over considerable areas (Chapter 7), and therefore that very extensive areas of suitable breeding habitat would need to be surveyed if a high proportion of the surviving birds ringed as chicks were to be found. The area that could be searched for returning one year old birds was limited by time and manpower. In 1986 almost all

Table 8.11: Estimates of the number of chicks ringed that survived to fledging, using approximate chick survival rates.

SPECIES & YEAR AGE CLASS	APPROXIMATE CHICK SURVIVAL RATE	NO. OF CHICKS COLOUR-RINGED	ESTIMATED NO. OF CHICKS FLEDGING
REDSHANK 1985			
0- 3 days old	x .5	150	75
4-14 days old	x .75	31	23
14+ days old	x .9	4	4
			Total = 102
REDSHANK 1986			
0- 3 days old	x .5	110	55
4-14 days old	x .75	117	88
14+ days old	x .9	23	21
			Total = 164
DUNLIN 1985			
0- 4 days old	x .5	129	64.5
5-10 days old	x .75	6	4.5
10+ days old	x .9	0	0
			Total = 69
DUNLIN 1986			
0- 4 days old	x .5	100	50
5-10 days old	x .75	17	13
10+ days old	x .9	2	2
			Total = 65
RINGED PLOVER 1985			
0- 4 days old	x .6	41	25
5-14 days old	x .8	9	7
14+ days old	x .9	6	5
			Total = 37
RINGED PLOVER 1986			
0- 4 days old	x .6	72	43
5-14 days old	x .8	62	50
14+ days old	x .9	30	27
			Total = 120

suitable Ringed Plover breeding areas (i.e. cultivated machair) on South Uist were visited at least once in May or June, whereas in 1987, when extra help was available, the area checked for Ringed Plover was extended to Benbecula also. Redshank and Dunlin, especially birds without chicks, were much more likely to be overlooked because of their lower detectability (Reed *et al.* 1985), and consequently thorough searches for these species were more time consuming. Therefore, it was not possible to search all suitable habitat in the Southern Isles. In 1986, only the study-sites and their immediate environs (up to 1 km away) were thoroughly searched for Redshank and Dunlin. The extra help available in 1987 made possible the searching of a much larger area extending approximately 5 km to the north and south of the northern study-sites. The survival of birds ringed as chicks, especially Ringed Plover, was also monitored through checks made of birds on beaches and other feeding areas.

In 1986, a number of Ringed Plover chicks that were very close to fledging were individually colour-ringed, together with a sample of juveniles caught on the beach in August and September.

iii) Results

The number of birds ringed as chicks and found alive in subsequent breeding seasons, together with the minimum estimated survival rate is summarised in Table 8.12.

The survival of the near-fledging Ringed Plover chicks individually marked in 1986, as monitored by their presence on the beaches and breeding grounds, is shown in Table 8.13. The

Table 8.12: Number of birds ringed as chicks returning to breeding grounds in subsequent years.

YEAR OF RINGING AREA	ESTIMATED NO. OF BIRDS FLEDGING (Table 8.11)	TOTAL SEEN ONE YEAR LATER (SEXES)	TOTAL SEEN ONE AND TWO YEARS LATER (SEXES)	MINIMUM SURVIVAL TO ONE YEAR OLD
REDSHANK				
1985 N-sites	65	11 (5M,4F,2?)	13 (5M,4F,4?)	20.0%
1985 elsewhere	37	3 (1F,2?)	4 (1F,3?)	10.8%
1986 N-sites	107	19 (5M,5F,9?)	no data	(17.8%)
1986 elsewhere	57	7 (2M,2F,3?)	no data	(12.3%)
DUNLIN				
1985 N-sites	61	4 (2M,2F)	10 (4M,5F,1?)	16.4%
1985 elsewhere	8	0	0	0%
1986 N-sites	65	5 (3M,1F,1?) ¹	no data	/
1986 elsewhere	0	/	/	/
RINGED PLOVER				
1985 all sites	37	11 (6M,5F)	13 (7M,6F)	35.1%
1986 all sites	120	23 (10M,8F,5?)	no data	(19.2%)

M = male
 F = female
 ? = sex unknown
 / not calculable

¹Includes one Dunlin (sex unknown) seen in suitable breeding habitat on the Isle of Tiree in June.

Table 8.13: First winter survival of individually colour-ringed near-fledgling and juvenile Ringed plovers ringed in 1986.

1) Survival of individually colour-ringed chicks

No. of near-fledglings colour-ringed		= 13
No. seen on beaches in August and September		= 7
Survival from fledging to October 1986	= 7/13	= 54%
No. known to be alive in April 1987		= 3
Survival from October 1986 to May 1987	= 3/7	= 43%
Survival from fledging to May 1987	= 3/13	= 23%

2) Survival of individually colour-ringed juveniles

No. of marked juveniles alive September 1986		= 36
No. known to be alive in April 1987		= 17
Survival from October 1986 to May 1987	= 17/36	= 47%

first-year survival figure for these birds is independent of estimates of pre-fledging survival.

The figures for survival from fledging to one-year old (first-year survival) presented in Tables 8.12 and 8.13 are only considered minimum estimates of the true values because an unknown proportion of surviving birds was overlooked. Birds could be overlooked because they had emigrated to places outside the areas checked or because they were not detected inside the areas checked. Long distance movements to new breeding grounds are particularly difficult to quantify but have been noted. For example, in Soikkeli's Finnish study a female Dunlin moved 280 km (Soikkeli 1970), but this may have been caused by habitat degradation at the natal site. In my study, one Dunlin may have settled in Tiree, about 110km from its natal area, and one female Ringed Plover ringed as a chick in North Uist was found breeding 42km to the south in South Uist (Chapter 7). The data on natal philopatry, presented in Chapter 7, indicates that dispersal frequency within the areas thoroughly checked for returning birds was inversely related to distance from the natal site and this strongly suggests that long distance dispersal is rare. However, as discussed in Chapter 7 the probability of overlooking birds is thought to increase with dispersal distance. If birds are settling at very low densities at long distances away from their natal site (i.e. over 5 km and perhaps as far as 100 km) then the chances of finding them all would be small because of the very extensive areas involved and it is possible that a significant proportion of the birds returning were not detected.

iv) Estimates of first-year survival rate of Redshank

The apparent difference in the return rate of one-year old Redshank between the northern study-sites and elsewhere is almost certainly spurious and merely a reflection of observer effort. The return rate measured for the northern sites, especially for the 1985 cohort, probably approached the actual return rate; the moderately high natal philopatry of Redshank (Chapter 7) and the fact that 85% (11 of 13) of known returning birds of the 1985 cohort were found in the restricted 1986 surveys, suggest that the majority of birds were found. It can be concluded that the actual first-year survival rate in Redshank certainly exceeded 20% but is unlikely to be vastly greater, a realistic estimate is probably ca. 30%. Boyd (1962), using Swedish ringing recoveries, estimates first-year survival in Redshank to be 45% but this figure is probably an overestimate because it was largely based on birds ringed as juveniles.

v) Estimates of first-year survival rate of Dunlin

The combined effects of their low detectability, and the suspected absence of many one-year olds from the breeding grounds, meant that many surviving marked one-year-old Dunlin were overlooked. The minimum survival of 16.4% for the 1985 cohort based on birds seen either in 1986 or 1987, or both, is certainly an underestimate. A correction must be made for first to second year mortality of birds that were not seen in 1986 but were seen for the first time in 1987. Assuming that the survival rate of second-year birds is similar to that of breeding adults, the adjusted minimum first-year survival rate is 18.9%.

Interestingly, there was no apparent bias towards finding more males, yet this might have been expected, as males show greater natal philopatry (Chapter 7) and are more detectable. This suggests that most of the surviving birds were located. Soikkeli (1970) estimated the return rates of marked chicks at one-year old to be 21.6%. This includes pre-fledging mortality and thus the figure for first-year survival must have been considerably higher, probably at least 30%. Martin-Lof (1961, in Boyd 1962) calculated from recoveries of Swedish-ringed juveniles that first-year survival was 38%, whilst Boyd (1962) using Danish ringing recoveries calculates a rate of ca. 25%. These two values are not necessarily comparable to the results in this study because they are mainly based on birds ringed as juveniles and not chicks. Thus they fail to account for some immediate post-fledging mortality. Also, they involve birds of at least two races. It is concluded that the mean first-year survival rate of the Dunlin breeding in the Southern Isles certainly exceeds 20% but is unlikely to be greater than 30%, a realistic estimate is 25%.

vi) Estimates of first-year survival rate of Ringed Plover

The high detectability of Ringed Plover combined with the very extensive areas checked for surviving birds meant that a very high proportion of surviving ringed one-year old birds were located. However, some individuals of this species, especially females, move quite large distances from their natal area (Chapter 7) and although the survival of some birds that bred outside the areas checked was confirmed by their presence on the

beaches, a few were probably overlooked. The slightly higher incidence of returning one-year old males (17) compared to females (14) may be attributable to the greater dispersal distances of females. The difference between the return rate of 1985 chicks and 1986 chicks shown in Table 8.12 is not significant ($\text{Chi}^2 = 1.3$, d.f. = 1, $P > 0.05$, Yates' correction applied). The minimum first-year survival for 1985 and 1986 chicks combined is 23% ($n = 157$), and this agrees very well with the largely independently derived figure from individually colour-ringed near-fledglings in 1986 (Table 8.13). The data presented in Table 8.13 strongly suggests that juvenile Ringed Plover experience high mortality (45%) in the few weeks after fledging; this may be associated with the change from terrestrial to littoral feeding. The estimate of first-winter survival of the sample of juveniles colour-ringed in August and September 1986 (given in Table 8.13) may be slightly too low because of the possibility of some birds being arctic migrants; however, 22 of the 36 juveniles caught were known to be of local origin.

The above evidence suggests that the actual first-year survival rate of Ringed Plover in this study was about 25%. Pienkowski working in north-east England, and using very similar methodology to this study, calculated first-year survival to be 57% (based on 42 colour-ringed fledglings). The difference between the values calculated in the two studies is significant ($\text{Chi}^2 = 15$, d.f. = 1, $P < 0.01$, Yates' correction applied). The data on first-year survival from this study result mainly from 1986 chicks, and these may have survived abnormally poorly (perhaps because of adverse winter conditions). This theory is

supported by the higher survival rate of 1985 chicks (35%) and also by the high survival rate of ten individually colour-ringed near-fledglings which I caught in June 1984 (in a previous study), of which at least 50% survived to one year old. It seems likely that there is considerable annual variation in first-year survival and that the figure of 25% found in this study is lower than the long term mean for the Southern Isles which be at least 35%.

Age of first-breeding

The final component of the species' life cycles that needs to be evaluated in order to make some basic calculations on population dynamics is the age of first-breeding.

1) Methods

Although breeding in the first year of life is easily proven in waders, lack of breeding in the first year is much more difficult to confirm. One can rarely be confident, without very intensive observations, that a one year old bird present on the breeding grounds but apparently not breeding has not attempted to breed but failed early on in the cycle or, in the case of individuals first seen on the breeding grounds in their second year, that they had not attempted to breed elsewhere when one year old. One-year-olds of all three species studied could readily be aged in the hand from their plumage and primary feather wear (Prater, Marchant and Vuorinen 1977). A randomly trapped sample of breeding birds can therefore be used to estimate the proportion of one-year old birds in the breeding population. The birds trapped in the first year of the study

Table 8.14: Proportion of one year old birds in the breeding population as found by random catching on nests in 1985.

SPECIES SEX	NO. OF 1 YEAR OLD BIRDS CAUGHT	NO. OF 2+ YEAR OLD BIRDS CAUGHT	PERCENTAGE OF 1-YEAR-OLDS IN POPULATION
REDSHANK ¹			
Males	5	48	9.4%
Females	14	34	29.2%
DUNLIN			
Males	0	44	0%
Females	1	42	2.3%
RINGED PLOVER ²			
Males	10	24	29.4%
Females	5	25	16.7%

¹Difference between sexes is significant
(Chi² = 5.2, d f = 1, P < 0.05, Yate's correction applied)

²Difference between sexes is not significant
(Chi² = 0.82, d f = 1, P > 0.05, Yate's correction applied)

can be considered as random samples of the breeding populations; the number of birds of each sex and age for each species trapped in 1985 is summarised in Table 8.14. In later years trapping was not random as no trapping was undertaken at nests where both adults were already colour-ringed. The trapped samples were thus biased in favour of one year old birds. The age profile of all the colour-ringed breeding birds after the first year was biased also, this time in favour of older birds.

ii) Age of first-breeding in Redshank

The percentage of one year old female Redshank in the 1985 sample (29%) is similar to the total expected annual recruitment into the breeding population (20-30%, Table 8.9) and this strongly suggests that nearly all females attempt to breed at one year old. The 1985 sample of Redshank contained significantly fewer males. The ratio of one year old males to one year old females caught for all three years is about 1:2 (14 males, 33 females). This suggests that about 50% of males breed for the first time in their first year, the remainder probably breeding for the first time at two years old. The observations on returning colour-ringed chicks tended to confirm these findings and several instances of definite non-breeding males attempting to establish breeding "territories" were recorded. Grosskopf (1959) found that most Redshank breeding on the Friesian Islands in Germany did not breed until two years old.

iii) Age of first-breeding in Dunlin

During this study only two one-year old Dunlin (both females)

were trapped on the nest out of a total of 79 males and 80 females. The observed pattern of return of birds marked as chicks suggests that about 50% of one year old birds may not visit the breeding grounds; there is evidence to suggest that they remain on their wintering grounds in west Africa (Pienkowski and Dick 1975). None of the marked birds that were seen on the breeding grounds in their first summer were proven to breed and most did not arrive until the middle of the season. It can be concluded that most Dunlin breed for the first time when they are at least two years old. Soikkeli (1967), working in Finland, estimated that about one third of Dunlin bred for the first time at one year old, and the majority of the remainder at two years old. The higher frequency of breeding by one-year-olds in Soikkeli's study may have been associated with the fact that the population was declining.

v) Age of first-breeding in Ringed Plover

The difference between the proportion of one-year old male and one-year old female Ringed Plover in the 1985 trapping sample is not significant. The ratio of males to females for all one year old birds caught in the study is almost 1:1 (16 males to 14 females) and this is further evidence that the age of first breeding is similar in males and females. One-year old birds comprise 23% of the 1985 sample, which is similar to the expected annual recruitment into the breeding population (23-32%, Table 8.9). Observations on returning ringed one-year-olds suggested that most attempted to breed; however, two females were noted on the seashore throughout the breeding season and were almost

certainly non-breeders. It can be concluded that the vast majority of Ringed Plover first bred in their first year. Pienkowski (1980) found that about 70% of Ringed Plover breeding in north-east England first attempted to breed at one year old and the rest at two years old.

iv) Proportions of one-year-olds attempting to breed

The calculations in the next part of this chapter require a figure for the proportion of one-year-olds that attempt to breed. All one-year-olds that do not breed are assumed to breed as two-year-olds (if still alive). Based on the information presented above the approximate percentage of one-year-olds

attempting to breed are as follows:	Redshank males	50%
	Redshank females	100%
	Dunlin	0%
	Ringed Plover	100%

No evidence was obtained in this study to suggest that established breeding birds ever chose to opt out of breeding in some years.

Part 3. Population Trends

Recruitment rate and its implications for populations

The estimates of productivity and survival in Parts 1 and 2 of this chapter are now brought together in an attempt to show whether or not the populations are producing sufficient breeding recruits (young surviving to breeding age) to balance breeding adult mortality. Assuming that emigration and immigration are negligible, the annual production of breeding recruits per breeding adult per year required to maintain a stable population,

Table 8.15: Estimated annual recruitment rate into breeding population compared with estimated annual mortality of breeding adults for Redshank, Dunlin and Ringed Plover.

SPECIES	COMPONENT OF POPULATION DYNAMICS EQUATION ¹						ADULT MORTALITY RATE
	A	B	C	D	E	X	
REDSHANK							
males	.56	c .3	.72	.5	.5	.14	.28
females	.56	c .3	.80	1	0	.17	.20
both sexes	.56	c .3	.76	.75	.25	.16	.24
DUNLIN							
both sexes Stilligarry	.40	c .25	.81	0	1	.08	.19
both sexes Drimore Farm	.91	c .25	.81	0	1	.18	.19
RINGED PLOVER							
both sexes	.34	.25+	.73	1	0	.09	.27

$$^1X = A \times B \times (D + (E \times C))$$

Where:

- X = Estimated annual recruitment into breeding population, (no. of chicks surviving to breed per adult per year).
- A = Number of chicks fledged per adult per year
- B = First-year survival rate
- C = Adult survival rate
- D = Proportion of birds first-breeding at one year old
- E = Proportion of one-year-olds that defer breeding (i.e. they breed at two years old if still alive)

Dunlin at Stilligarry and Drimore Farm because of the markedly different productivity between the two sites.

The estimated recruitment rates (see Table 8.15) are in all cases lower than the corresponding estimates of the adult mortality rate. It remains to be seen whether the imbalance between productivity and adult mortality for each species suggested by the results from this study is genuine or due, at least in part, to the limitations of the methods. The possibility of overlooking returning birds means that the estimates of adult and first-year survival are in all cases minimum estimates and this will tend to create an imbalance. Therefore, if in reality productivity was sufficient to balance adult mortality, but only by a small margin, it is, perhaps, to be expected that a study like this would show a small imbalance, particularly for the less detectable species such as Redshank and Dunlin. Even when the productivity rates are arbitrarily increased by 1.5 times (this should more than compensate for any underestimation) the recruitment rate of Ringed Plover and Dunlin breeding at Stilligarry remains insufficient to balance adult mortality and only just sufficient for Redshank. Although the imbalance found for Redshank and Dunlin could be largely spurious, that for Ringed Plover, which are more detectable, would appear to be too large to be accounted for in this way. Dunlin at Drimore Farm were almost certainly producing enough first-time breeders to balance adult mortality. It should also be noted that an error in the estimate of adult survival has a disproportionately larger effect upon the population equation than an error in the estimate of productivity; with a 33%

first-year survival rate, a 1% error in adult survival has approximately the same effect as a 3% error in productivity. The estimates of adult survival (Table 8.9) have 95% confidence limits of about 5% . If adult survival was 5% higher than estimated, the imbalance for Redshank and Dunlin becomes small but for Ringed Plover it remains large.

The observed differences in the population dynamics of male and female Redshank suggest that there may be an excess of females in the adult population, but no direct evidence was found to support this theory.

Although every attempt was made to minimise it, some disturbance of the birds by me was inevitable and it is possible that this adversely affected their breeding success, in particular through increased egg predation. It was not possible to evaluate this objectively, however, as most predation occurred in my absence it was clear that any extra predation caused directly as a result of my disturbance was very small. Also, visits to areas outside the study-sites (i.e. where there was less disturbance) had no appearance of greater breeding success than that inside the study-sites.

Population changes

If the populations are not stable the changes in the number of adults should be detectable in annual population estimates. Two independent assessments of population changes are available: firstly, the estimates made of the total number of pairs breeding on the study-sites (Chapter 6) and secondly, the results from extensive transect-surveys undertaken at eight large sites (each

of about 4 km²) in the Southern Isles annually between 1983 and 1987, by the Nature Conservancy Council and the Wader Study Group (Green 1983a and 1983b, Reed and Fuller 1983, Fuller 1985, Fuller and Percival 1986, and S.M. Percival *pers. comm.*). The value of comparing the results from the intensively worked sites with those from extensive surveys is that the latter are able to give a general view of population trends and are able to detect any gross distribution changes.

The study-site population estimates for each year are summarised in Table 8.16; the figures in this table exclude all pairs breeding in the study-site extensions. The number of Dunlin and Redshank breeding on the study-sites remained almost constant during the three years of this study and there was no evidence of an overall decline in these species. The numbers of Ringed Plovers declined at all sites during the study, and overall the decrease amounted to about 10% per year. The results from the extensive transect-surveys must be interpreted cautiously, particularly for Redshank and Dunlin, because the detectability of breeding waders varies according to their stage of breeding, and with weather and time of day (Jackson and Percival 1983, Reed *et al.* 1985 and Reed, Williams and Webb 1983). The surveys found that Redshank and Dunlin decreased by c. 17% between 1985 and 1987. Although these apparent decreases may possibly be within the error limits of the method (these are unknown), they probably do reflect small population decline. The transect-survey results for Ringed Plover show a decrease of 24% between 1985 and 1987. The high detectability of Ringed Plover means that this figure is almost certainly a reliable assessment

of this species' population changes in the Southern Isles

Table 8.16: Estimated number of pairs of Redshank, Dunlin and Ringed Plover breeding each year on the study-sites (pairs breeding in the study-site extensions are excluded).

SITE	NUMBER OF PAIRS		
	1985	1986	1987
REDSHANK			
Rubha Ardvule	22	21	20
Stilligarry	11	12	15
Drimore Farm	/	35	33
West Gerinish	19	19	21
DUNLIN			
Rubha Ardvule	9	9	8
Stilligarry	26	29	25
Drimore Farm	/	60	65
RINGED PLOVER			
Rubha Ardvule	17	14	15
Stilligarry	31	27	24
Drimore Farm	/	49	44

/ = no estimate made

Conclusions

The productivity and survival estimates for each species together with the annual population assessments lead to the following conclusions about the wader populations during the study-years:

- i) Ringed Plover were producing insufficient young to balance mortality and as a consequence the population was declining by at least 10% per year. The very low number of potential breeding recruits was mainly caused by poor nesting success and, in some years at least, poor first-year survival.
- ii) Redshank and Dunlin (for which the results are less reliable) were producing overall either slightly insufficient or just enough young to balance adult mortality. Evidence from extensive surveys suggests that the populations were in slight decline.
- iii) The productivity of Dunlin pairs nesting on fallow machair was less than half that of pairs nesting on marsh. The Dunlin breeding on fallow machair are probably not self-sustaining. The low productivity of Dunlin on fallow machair was caused by poor chick survival.

The decline in Ringed Plover numbers and, if genuine, in Redshank and Dunlin numbers too, must reflect a recent change in either adult survival or productivity. Raptor predation of adults can undoubtedly be a major component of mortality. Results presented earlier in this chapter on breeding season predation of Redshank and by Whitfield (1985) show that, at least at a local level, raptor predation can be very important. It is

conceivable that there has been an general increase in raptor predation brought about by the recovery in the last ten years of certain raptor populations such as Peregrine Falcon and Sparrowhawk (*Accipiter nisus*) following their acute population crashes caused by environmental pollutants. However, this explanation is largely unsatisfactory because the wader showing the greatest decrease i.e. Ringed Plover, remains in the Hebrides all year and this was an area where raptors were not seriously affected by pollutants (Cooke *et al* 1982). Also, this explanation leads to the suggestion that the wader populations in the islands would have been smaller previous to the 1960's, (i.e. prior to the effects of pollutants on raptors) but local opinion suggests that, if anything, populations were then higher than at present. It seems more likely that the change has been in productivity. This may have been induced by either greater numbers of gulls or small habitat changes that mean greater predation of eggs and chicks (i.e. less cover and camouflage). Black-headed Gulls, at least, appear to be presently increasing on South Uist (Pers. obs.) and there have been widespread changes in crofting activity.

CHAPTER 9

GENERAL DISCUSSION

This final chapter discusses the conservation of the populations of Redshank, Dunlin and Ringed Plover breeding in the Southern Isles in light of the information presented in earlier chapters and the results of other studies. The chapter starts with a brief review of the factors that may determine the overall size of the populations, this is important to indicate where and when conservation measures should be concentrated. The chapter goes on to discuss the two types of conservation measures considered to be of most importance namely maintenance of suitable habitat and ensuring adequate productivity.

1) Determination of overall population size

Conservation measures on the breeding grounds intended to maintain or increase the size of a wader population will be worthwhile only if it is the amount of suitable breeding habitat that limits the size of the population. If there is an excess of breeding habitat, the loss or degradation of a portion may be of no long term consequence to the overall size of a species' population.

The ultimate factors determining the size of wader populations are not fully understood (Evans and Pienkowski 1984). If some form of density dependence controls overall population size, then either the breeding habitat or the non-breeding habitat, or both, would, in some years, be expected to be at carrying capacity. If area of suitable breeding habitat is not

limiting then it can be hypothesised that the breeding areas should be capable of supporting more breeding pairs and that there should be little or no competition for area-dependent resources on the breeding grounds. There is however much evidence to suggest that at least for some wader populations this is not the case.

Males of all the species looked at in this study defended some form of territory at some stage(s) during their breeding cycle and this strongly suggests that there was competition for some area-dependent resource such as food or cover. The inter-habitat differences in nesting density found in this study for Redshank and Dunlin were thought to be largely related to cover and camouflage for nests and chicks, and not food. The fact that Dunlin largely fed outside their breeding territories supports the idea that food was not the resource being defended by Dunlin. In contrast, Holmes (1970) found that for Dunlin in Alaska the size of breeding territories was negatively correlated with the food resources of the territory. The variation in Ringed Plover nesting density found in this study could not be explained solely by availability of camouflage for nesting; food resources were thought to be important also.

If breeding habitat was limiting the population size, then it can also be hypothesised that some sexually mature adults would either be unsuccessful in finding a breeding territory or would attempt to breed in places that were unsuitable. No evidence was found in this study, or in most other intensive breeding studies, of non-breeding pools of sexually mature adults though such a phenomena was found in Oystercatchers by Harris (1970) in Wales,

and has been suggested to occur in Alaskan Dunlin, at least for males, by Holmes (1970). Non-breeding birds, thought to include sexually mature adults, have also been noticed in arctic populations in years of late snow melt even though some adjacent breeding habitat was available (Green *et al* 1977). The extent to which more individuals can be absorbed into the breeding areas before reducing overall productivity to a level too low to balance mortality is unknown. Although annual variation in breeding density (i.e. territory size) has been shown by Soikkeli (1967, 1970) in Dunlin, and in Pectoral Sandpipers (*Calidris melanotos*) by Holmes (1966a), it is not known whether this affected the mean productivity per pair (i.e. whether productivity was density dependent). In practice, territorial behaviour may force some birds into less favourable breeding habitat where their productivity is below that of birds in the preferred breeding habitat (by definition). The possibility that some birds in this study bred in areas that were unsuitable, i.e. where mean productivity over many years was insufficient to balance mortality, cannot be conclusively shown because the study was too short term. However, Dunlin, and perhaps Ringed Plover, breeding on old fallow machair, probably did not produce enough young to balance adult mortality.

The recent declines of many wader populations breeding in England and Wales and attributed to breeding habitat degradation (Smith 1983, Baines 1988) have not been paralleled by any noted increases elsewhere brought about by a redistribution of individuals, or led to increased densities in the remaining non-degraded habitat. This suggests that all suitable breeding

habitat was occupied and that it was not capable of absorbing more birds. Although adult breeding site-fidelity and natal philopatry will effect the rate of changes in distribution and density they should not, in the long-term, determine the distribution and density in stable environments; the inclusive fitness of any individuals successfully colonising vacant areas of suitable breeding habitat or becoming successfully incorporated in to partly utilised habitat, would be very high. It is a popularly held view (e.g. Evans & Pienkowski 1984) that for many wader species extensive areas of suitable breeding habitat remain unoccupied or only occupied at low densities far below their carrying capacity. For some species this may be true, for example Knot (*Calidris canutus*) breed at extremely low density (compared to most other waders) on arctic tundra (Cramp and Simmons 1983), and Oystercatchers breeding on temperate pastureland have colonised many areas of Britain this century (Buxton 1962, Sharrock 1976). For some species however, the theory that extensive areas of unoccupied breeding habitat exist is probably incorrect. Although unoccupied habitat may appear suitable for breeding and, in some cases, have been used in the past, predation pressure may now be too high for adequate long term productivity and survival of any birds settling there. The reduction of predators by gamekeepers has been shown by Potts (1986) to have marked effects on the breeding density of Grey Partridge (*Perdix perdix*). The decline on moorland in parts of England and Wales of Golden Plovers (*Pluvialis apricaria*) that has occurred this century (Sharrock 1976) may be due to the lack of predator control by gamekeepers. Indeed, the southern limits

of the breeding range of some species such as Ringed Plover is probably determined by predation (Pienkowski 1984a).

Mortality of adults on the breeding grounds, if brought about by predation or competition, as found for Redshank in this study, may be density dependent. If "good" breeding habitat was superabundant one would expect breeding pairs to occur at densities that are sufficiently low to ensure that any density dependent adult mortality was negligible. The evidence obtained in this study for Redshank shows that this is not the case and that there is a very high risk of mortality on the breeding grounds. A high adult mortality rate in the breeding season was also noted by Soikkeli (1967) who found that breeding Dunlin were frequently taken by raptors and mustelids. Other ground nesting birds are known to be particularly vulnerable to predation whilst nesting, for example Grey Partridge (Potts 1986). The vacation of the breeding habitat at the earliest opportunity for the non-breeding habitat, noted for Dunlin and Redshank during this study, may be driven by the high mortality risk associated with remaining on the breeding grounds. Alternatively it may be driven by a need to arrive back on the non-breeding grounds or migration staging posts early to establish a good site. If this is the case then the birds would be expected to defend territories on the non-breeding grounds (see below).

Competition in the non-breeding habitat for food or space has been found to occur in Redshank and Oystercatchers (Goss-Custard 1977, 1980) but unless some birds are actually prevented from obtaining enough food its effect on mortality will be negligible (Evans and Pienkowski 1984). Territoriality in the non-breeding

habitat is unusual in waders but has been found for some individuals of in Grey Plover (*Pluvialis squatarola*) by Townshend (1982a, 1984), Curlew by Boere and Smit (1983), Redshank by Goss-Custard (1980) and Ringed Plover (in the Outer Hebrides) by Wells and Ferns (*pers. comm.*). In such cases, it is possible that this produces some density dependent mortality. Mortality on the non-breeding habitat is often extremely low (Evans and Pienkowski 1984) which would, perhaps, not be expected if there was strong competition for resources leading to mortality. In general, it is thought that most of the mortality acting on waders on the non-breeding habitat, especially in temperate latitudes, is density independent and results mainly from adverse weather (Evans and Pienkowski 1984). Extreme winter weather is known occasionally to cause high mortality of such coastal species as Redshank and Dunlin wintering in eastern Britain (Pilcher 1964), and inland species such as Lapwing (Vespalainen 1968), but some individuals of a few species, such as Grey Plover, avoid the effects of bad weather by moving to more benign areas (Townshend 1982b). That they are able to do this is evidence that not all areas of non-breeding habitat are at or close to their carrying capacity.

Recent increases in the numbers of Grey Plover wintering on British estuaries and accompanied by an extension of their winter distribution suggest that the total amount of wintering habitat for this species is not limiting, however, the preferred wintering estuaries may be at carrying capacity (Moser 1988). Unfortunately, it is not known whether the population increase has resulted from increased breeding density, or the occupation

of new breeding areas, or both. In contrast to this, there is evidence that the recent decline in the numbers of Dunlin (of the *alpina* race) wintering on British estuaries is attributable to the loss of mud flats due to colonisation by Chord Grass (*Spartina anglica*) (Goss-Custard and Moser 1988). This result suggests that the availability of wintering habitat may be limiting the population size. However, in the absence of detailed information for the period concerned on mortality, breeding performance and changes to breeding habitats, conclusions drawn from this evidence can only be tentative.

The evidence presented above suggests that many wader populations breeding in temperate latitudes, and in particular those investigated in this study, are limited by the area of suitable breeding habitat. Although both density dependent and density independent processes almost certainly act on productivity and mortality, ultimately it is probably density dependent regulation of mortality of eggs and chicks that determines population size of the species considered in this study. This is not the case for all species; Lapwing productivity has been shown to be greater at higher breeding densities because of the greater effectiveness of antipredator behaviour (Elliot 1985, Baines 1988). Alerstam and Hogstedt (1982) looked for common aspects in the biology of birds which could be considered to have either excess breeding habitat or excess non-breeding habitat. They concluded that there should be strong competition for area-dependent resources in species where breeding habitat was limited and that this would be likely to result in a deferred age of first breeding, small clutch size and

poor reproductive success. These species would also be expected to return to breeding areas early as there would be competition for territories, and to leave again as soon as breeding was completed. Conversely species with excess breeding habitat would be expected to breed at an early age, have large clutches, remain on the breeding grounds to moult and to have a late autumn migration. The populations of Redshank, Dunlin and Ringed Plover in the Southern Isles generally show all the life cycle features predicted by the theory put forward by Alerstam and Hogstedt. The "late" arrival of Dunlin on the breeding grounds, compared to the other two species, could be considered contradictory to the theory but the Dunlins' long migration may impose constraints on an earlier return. If Alerstam and Hogstedt's theory is generally applicable then it is clear that the wader populations considered in this study are limited by the area of breeding habitat. This being so any conservation measures aimed at these populations ought to be concentrated on the breeding grounds.

Conservation measures for the breeding waders in the Southern Isles should aim to maintain extensive areas of suitable breeding habitat and to ensure that the productivity of the birds is adequate. These two aspects are discussed separately.

ii) Habitat conservation

Birds are very selective in their use of breeding habitats. The mechanism of how they achieve this selection is not known exactly but in general they are thought to respond to proximate factors that enable them to identify areas where successful breeding can take place (Hilden 1965). Clearly, the existing

habitats on the coastal plain of the Southern Isles and their arrangement provide extensive suitable areas for each of the three wader species studied. The conservation of these breeding populations depends on these areas remaining suitable.

With regard to the bird's existing habitats, the major conservation threat in the Southern Isles is from changes in agricultural practice. Direct habitat loss by for example building developments or afforestation do not currently appear to be a significant threat. Two categories of agricultural change are currently taking place and are likely to continue. These are agricultural neglect and agricultural intensification. Both of these processes can potentially result in significant changes to the suitability of an area for breeding by a species. Briefly, the most important consequences of neglect are the cessation of cereal cultivation on the machair (usually accompanied by a switch from cattle to sheep rearing), inappropriate grazing intensities and choking-up of ditch systems. All aspects of agricultural intensification have some affect on the habitats, probably the most important are: increase in size of crop fields, drainage of wet ground, reseeding of natural grasslands, high applications of fertilizer to promote rapid spring growth, apportionment and fencing of common grazing, shift from hay to silage production and the use of pesticides. Not all the changes noted above are necessarily deleterious to birds and often a change that reduces the suitability of an area to one species will increase the suitability for another. The waders in the Southern Isles are largely dependent on agricultural management of the land to maintain its suitability for breeding. The sheer

extensiveness of the breeding grounds means that it is not possible to safeguard their ornithological interest purely through conventional, carefully managed nature reserves. Therefore, over the majority of the breeding grounds, agriculture, and not managed nature reserve, is likely to remain as the primary land use objective. It is unrealistic to expect the current, and in many ways already out-dated, agricultural practices in the Southern Isles to continue unchanged; changes are inevitable. The challenge of conserving breeding wader habitat in the Southern Isles is largely one of knowing the extent of land management changes that can take place without jeopardising the long-term ornithological value of an area. The first step towards this is a clear understanding of the habitat requirements of each species.

The information presented in Chapters 3, 4 and 5 deals with habitat use by each species for each activity. Although this information was collected with the intention of being useful to the birds conservation, it is beyond the scope of this thesis to produce detailed "recipes" of the habitat requirements of each species or to produce detailed habitat management guidelines. However, it is considered useful to discuss the results in general terms and their implications for the birds' conservation. In particular the importance of habitat heterogeneity is discussed, a factor that appears to have received little attention in previous breeding wader studies.

In general, each species had distinct habitat preferences for a given activity during the breeding season. Also, any given activity such as feeding, nesting, chick-rearing etc. was not

confined to a single habitat type. Without using an experimental approach involving habitat manipulation, the minimum habitat requirements for successful breeding by a species are impossible to define rigidly. However, it is clear that the requirements for successful breeding can be met by several different habitat assemblages. For example, Redshank used ditches very frequently for feeding and chick-rearing but also bred successfully where ditches were absent (i.e. at Rubha Ardvule). No single habitat type appeared essential to any species, i.e. none was used by every individual of a species (excepting the seashore after the breeding season). The information in Chapters 3 and 5 shows which habitats were used for each activity by a species, and to some extent which were preferred. From this it is possible to make some inference of a species' minimal breeding habitat requirements viz. the presence of a sufficient quantity of suitable habitat for each essential activity. It was apparent that in many cases the value of a habitat for a given activity to a species was approximately matched by that of another habitat of similar characteristics, an "equivalent" habitat. To meet the minimum habitat requirements it is probably necessary for only one of the equivalent habitat types to be represented. For example loch-edges, pool-edges, ditches and rock pools were all used for feeding by Redshank in approximate proportion to their availability; none of these habitats is an absolute requirement for breeding but the presence of one of these water's-edge feeding habitats probably is.

The concept of a species' minimal breeding habitat requirements, although useful in determining qualitatively the

suitability of an area for breeding of a species, does not in any way indicate the "optimal" habitat requirements, i.e. those that will support the greatest breeding density. A conservation policy for waders in the Southern Isles should not be aimed purely at maintaining breeding populations of each species over wide areas but also at maintaining (or enhancing) the densities within these areas. Although the "optimal" habitat requirements of each species cannot be determined from this study, a common-sense-approach, as outlined below, indicates some of the important considerations in identifying "optimal" habitat conditions for a species.

Whether or not an area is used for breeding by a species will depend on whether that area meets the species' minimum habitat requirements. But the actual number of individuals that breed there will depend on the quality of the habitats (including predation pressures). Although the habitat requirements of a species for a given activity may be met by any of several "equivalent" habitat types, the quality of these may not always be equal. Areas comprising high quality habitats will generally support higher breeding densities than areas with low quality habitats. However, the absolute and relative quality of "equivalent" habitats is unlikely to be constant because the resources they contain that are of ultimate importance to the birds, e.g. food and cover, are constantly changing. Therefore, the preferred habitat for a given activity by a species may change with prevailing conditions and seasonally. Some habitats are particularly prone to unpredictable changes in quality (i.e. resource availability), for example the drying out of marshes and

the amount of nesting cover at the start of the season. Other habitat changes are more predictable, such as vegetation growth. Predictable and unpredictable environmental changes, such as weather conditions, will effect the value of a habitat to a species in different ways; a change that may make one habitat less attractive may enhance the quality of another. For example, heavy rains may make some habitats, such as "dry" pasture more attractive for feeding yet cause others to become unavailable through flooding. Birds breeding in areas where there is a good choice of habitat types for a given activity will have an advantage over those where the choice is poor because they are less likely to suffer from resource shortages. Therefore, the value of an area as a breeding habitat will depend not only on the quality of the constituent habitats but also the degree of habitat choice available.

To summarise, habitat heterogeneity is important for breeding waders for two reasons. Firstly, so that there is a suitable habitat for each essential breeding activity, i.e. to meet the species' minimum habitat requirements. Secondly, to give individuals a choice of habitats for each activity and thus enabling them to select the "best" habitat at any given time and safeguard against unpredictable resource shortage in any one habitat.

From the above discussion, it can be hypothesised that the "optimal" long-term habitat assemblage for a species will be comprised of wide range of habitats all of which are, at least potentially, of high value to the species and that between them provide a choice of several habitats for each essential

activity.

The importance of habitat heterogeneity to a species will depend on two considerations. Firstly, the predictability and stability of the preferred habitats and, secondly, the extent to which the habitat requirements of the essential activities can be met by the same habitats. In this study, Ringed Plover had relatively simple habitat requirements viz. short sward or bare ground for feeding adults and chicks and areas with suitable camouflage for nesting. Recent fallow habitat provides all these requirements, it is also relatively stable and predictable, it is unlikely to be totally flooded and remains similar in character throughout the season. Clearly under such circumstances the needs for, and the benefits of, habitat heterogeneity are low. Conversely, Ringed Plover breeding on plough find themselves in a very unstable habitat that changes from bare soil to tall cereals in a few weeks, and although it is suitable for all activities early in the season it is not suitable for any later on. In this situation habitat heterogeneity is essential. Redshank and Dunlin had more complex habitat requirements, typically they used different habitats for each activity, and also some of the habitats they use, such as marsh and water's-edge habitats, change unpredictably due to water table fluctuations. Therefore, their requirements for heterogeneity are very high.

Having discussed the requirement for habitat heterogeneity, the next consideration to address is the appropriate spatial scale of the heterogeneity. The implications of the spatial aspects of habitat use by each species, based on the information in Chapter 4, for the appropriate scale of habitat heterogeneity

are now discussed. The optimal spacing of habitat blocks largely depends on the distances that individuals will travel between habitats and the extent to which neighbouring individuals can share the resources of an area. There appear to be two extremes at each end of a continuum. At one extreme are birds that will travel long distances and use areas communally; Redshank lie close to this extreme. At the other extreme are birds that confine all their activities to a small area (i.e. the breeding territory) in which they and their mate, have exclusive use; Ringed Plover lie close to this extreme. Dunlin would appear to lie about midway along the continuum. Clearly, if species like Ringed Plover are to gain the full benefit of a heterogenous habitat mosaic, the fragments of the mosaic must be small enough to ensure that the heterogeneity exists within individual territories (typically in the order of 1 Ha). Species like Redshank will benefit from heterogeneity even if the habitat mosaic is arranged on a comparatively large scale, perhaps with distances as great as 1 km from one habitat to another. However, the best mosaic is probably one arranged at as small a scale as possible because there will always be costs associated with travelling, these costs are probably particularly high for chicks. The very high density of breeding Redshank at Rubha Ardvule was probably largely a result of a wide variety of habitats arranged on a small scale to form an intricate mosaic.

iii) Conservation measures for increasing productivity

If the observed productivity and survival rates found in this study continue for several years, and there is no appreciable

immigration from other breeding grounds, it is likely that the Ringed Plover population will decline rapidly, and that the Redshank and Dunlin populations will also decline but more slowly. Waders have a low fecundity and therefore, even under favourable conditions, the doubling time of a population is likely to be several years. Therefore any recovery in numbers after a major population decline would take many years.

Any conservation measures implemented should aim to increase the birds' productivity rather than attempt to enhance adult survival (which is likely to be difficult as much of the mortality takes place away from the breeding grounds, or unacceptable as it may require raptor control on the breeding grounds). The main factor found to limit productivity was predation of eggs and chicks by avian predators. The predation rate of eggs and chicks was lowest in those habitats that provided the best concealment and camouflage. Controlled management of the breeding areas to ensure the provision of adequate areas of rough vegetation, broken ground, shingle and bare earth could be used to reduce the losses of eggs and chicks to predators. Cultivation of the machair is essential for providing such habitats for Ringed Plover and it is therefore of paramount importance that this is continued and actively encouraged. Predation could also be decreased by controlling the numbers of predators; Hooded Crow control already takes place on South Uist by local gamekeepers. By far the most important predator of eggs and chicks is the Common Gull and any control programme ought to be mainly directed at this species. There is evidence, from recognisable individuals, that some Common Gulls

are specialising in hunting for wader eggs and chicks (*pers. obs.*). If a gull control programme was deemed necessary this aspect of the gulls' behaviour would first require investigation, as it may be possible to substantially reduce predation by controlling only a few individuals.

The protection against predators gained by other waders from nesting in association with Lapwing is probably of great importance for their productivity. Any measures that increase Lapwing numbers may indirectly benefit other wader species. One measure that would increase Lapwing productivity (and that of Ringed Plover) is to encourage crofters not to roll the ploughed fields as this is a frequent cause of egg loss (*pers. obs.*). If rolling is necessary it should be undertaken as early as possible to minimise losses and maximise probability of clutch replacement. The proportion of egg losses in this study attributable to livestock trampling were negligible but other studies (e.g. Bientema and Muskens 1987, Green 1986, Mason and Macdonald 1976) have shown that at high stocking rates there is a high risk of nest trampling. An increase in the stocking density over the present typical levels in the Southern Isles would add further to egg losses and decrease productivity. Higher stocking levels would also effect the structure of the vegetation, in particular tussock growth would be less likely to develop (O'Connor and Shrubbs 1986) and this could result in poorer cover for Redshank and Dunlin nests and chicks. Losses of eggs and chicks to mammalian predators were thought to be of negligible importance in this study but this may not be the case in certain parts of South Uist where Hedgehogs are now abundant (W.A.K.

Neill *pers. comm.*). The impending widespread colonisation of the Southern Isles by feral American Mink (Cunningham 1987) is likely to pose a further predation pressure in the future. The possible threat that these two recent additions to the islands' fauna pose to the ground nesting birds is in urgent need of evaluation. If their control is necessary it will be much more easily achieved before they become well established.

SUMMARY

- 1) The coastal plain of the Southern Isles supports large numbers of six species of breeding waders. It has been estimated that these include approximately 25% of all Dunlin and Ringed Plover, and 8% of all Redshank, that breed in the British Isles.
- 2) The waders in the Southern Isles breed predominantly on agricultural land and, therefore, their breeding habitats are influenced by farming activities.
- 3) This study aimed to quantify aspects of habitat use and population dynamics of Redshank, Dunlin and Ringed Plover breeding in the Southern Isles with a view to indentifying the conservation requirements of these birds and the causes of variation in breeding density.
- 4) Adult Redshank mainly fed in two distinct habitat groups: water's-edge habitat, such as ditches, loch-edges and, at some sites, rocky seashore, and short sward habitats such as good quality blackland pasture and old fallow machair. Use of the water's-edge habitats was significantly greater during the pre-laying stage than during the incubation stage (54% vs. 31%).
- 7) Redshank chicks were reared in habitats that provided good cover and that were usually marshy. The most important chick-rearing habitats were ditches, wet marsh, *Juncus* pasture and, late in the season, cereal crops.
- 8) Adult Redshank did not defend a breeding territory and

individuals' home ranges overlapped greatly. Adult Redshank typically fed within 500 m of the nest-site although the area within 100 m of the nest-site appeared to be deliberately avoided during the second half of the incubation stage. During chick-rearing the adults (provided they had not left the breeding area altogether) rarely strayed more than 50 m from their brood. Redshank families used a large area around their nest-site, most broods used areas up to at least 400 m from the nest at times. Some Redshank families appeared to lead a nomadic existence, frequently moving on to new feeding areas. Some broods moved as far as 2 km from the nest site.

9) Adult male Dunlin and Ringed Plover defended a breeding territory which was used for nesting and chick-rearing and feeding. In both species use of a breeding territory was mainly confined to the occupying pair though there was some overlap in the areas used by adjacent pairs.

10) From their arrival in late April, adult Dunlin fed almost exclusively up to mid-June on areas with a short sward such as damp marsh and fallow machair. From mid-June they made increasing use of certain areas of sandy seashore and wrack for feeding and by the end of the breeding season (mid-July) the seashore was the most important feeding habitat.

11) Adult Dunlin fed partly within their territory and also at communal feeding areas. These latter were, in the case of grassland feeding habitats typically within 500 m of the nest-site whilst the seashore habitats used late in the season were more distant, typically about 2 km away.

12) Dunlin chicks were reared almost exclusively on marsh habitats and old damp fallow machair. The areas used were usually within the immediate vicinity of the nest-site, i.e. within the breeding territory. Rarely did the chicks use areas further than 200 m from the nest-site.

13) Ringed Plover territories were nearly all on the areas of machair that are used for cultivation, especially those parts recently ploughed or lain fallow. Except for seashore feeding, adult Ringed Plover fed almost entirely within their breeding territory. These territories were also used for nesting, and chick-rearing. Except for use of the seashore, adult Ringed Plover during the main part of the breeding season seldom used areas more than 200m from their nest-site, i.e. outside their territories.

14) Use of the seashore by adult Ringed Plover for feeding was frequent during April (ca. 30% of records). Between April and mid-June the seashore was seldom used (ca. 2% of records), but after this there was a rapid increase and by mid-July ca. 80% of feeding was on the seashore. On the breeding areas, bare plough and recent fallow machair became increasingly important feeding habitats as the breeding season progressed, with a corresponding decrease in the use of old fallow machair (closed sward). This shift was probably associated with vegetation growth, the habitats with taller vegetation being less suitable for feeding and vice versa.

15) The preferred chick-rearing habitats of Ringed Plover were

those with only a partly vegetated surface such as plough and recent fallow.

16) Redshank typically nested in areas with moderarely tall vegetation (at least 5-15 cm tall in parts), especially where there were well-formed tussocks. Pastures with Soft Rush (*Juncus effusus*) and marshes were the most important Redshank nesting habitats.

17) Dunlin typically chose areas with short to medium length vegetation (i.e. less than 15 cm tall) with tufts (rather than well formed tussocks) or small hummocks for nesting. Marsh habitats, particularly hummock marsh, and old fallow machair were the only important Dunlin nesting habitats.

18) Ringed Plover nested in habitats with bare ground or short vegetation (less than 5 cm). The only important nesting habitats were plough, recent fallow, old fallow and shingle tracks.

19) Dunlin and Redshank nests were typically situated in a tussock/tuft or in a surface depression and were thus generally well concealed. Following the relatively harsh winter of 1986 there was less suitable nesting cover and the concealment of Dunlin and Redshank nests was significantly poorer than in seasons following benign winters (1985 and 1987). As Dunlin and Redshank do not always select nest-sites that give maximum concealment of the nests contents, it is suggested that adults with very well concealed nests may be more susceptible to predation whilst incubating.

20) Ringed Plover appeared to chose nest-sites that enhanced the camouflage of the eggs and, perhaps of the sitting bird also. Pairs that nested on old fallow (i.e. a short sward), the habitat generally having the poorest camouflaging effect, usually nested adjacent to or on some surface feature such as a stone or a dried-up cowpat. The benefit of this aspect of nest-site selection is not known for certain but is probably an increase in nest camouflage.

21) The Ringed Plovers in the Southern Isles are to a very large extent dependent on traditional cattle rearing practices to create and maintain suitable breeding habitat. Without cattle there would be no requirement to grow cereals for winter fodder and thus it can be predicted that cultivation of the machair would largely cease. Extensive machair sheep pasture would probably be an unsuitable breeding habitat for Ringed Plover, especially since old cowpats would be absent to provide suitable nest-sites. The future survival of a large population of Ringed Plover in the Southern Isles is dependent on the continuance of traditional-type cattle rearing.

22) The breeding density of each species showed marked differences between major habitat categories. The factors that determined breeding densities were thought to be the proportion of an area comprising suitable habitat and the quality of these habitats, particularly with respect to predation pressures.

23) Redshank overall breeding densities ranged from 78 to 41 pairs/km² on areas of blackland and marsh, whereas on areas of

machair used for cultivation the densities ranged from 6 to 12 pairs/km². The densities of nests in suitable nesting habitat (i.e. the nesting density) ranged between 68 to 90 pairs/km² on blackland-transition areas but at the Rubha Ardvule (an atypical site with very limited areas of nesting cover) the nesting density was 292 pairs/km².

24) The highest breeding density of Dunlin was on machair marsh with 224 pairs/km². The breeding densities on other habitats were generally far lower. On areas of machair used for cultivation overall Dunlin densities ranged from 52 to 71 pairs/km², however, the nests were concentrated on old fallow, where nesting densities were up to 91 pairs/km². The overall density of Dunlin nests on blackland and transition areas varied from 33 to 68 pairs/km² and appeared to be mainly determined by the proportion of suitable breeding habitat.

25) The overall breeding density of Ringed Plover on cultivated machair ranged from 69 to 88 pairs/km², however, the nesting densities within each component habitat were very different. On old fallow and reseeded machair nesting densities ranged from 26 to 38 pairs/km² whereas on plough and recent fallow densities ranged from 71 to 400 pairs/km². The very large variation within within the latter habitats appeared to be largely attributable to ground wetness, the areas with the driest soils having the lowest densities. The disadvantage of very dry soils may have been poor food resources.

26) In general, the breeding densities of Dunlin, Ringed Plover

and Redshank in the Southern Isles are far greater than found in mainland areas in north-west Europe. The absence of many mammalian predators such as Foxes, Stoats and Weasels may partly explain this. (Although some mammalian predators, including introduced Polecat Ferrets, do occur in the Southern Isles they appeared to be of negligible importance as predators of waders.)

27) Established adults of all three species studied normally bred in the same area as in the previous season, or close by. Adult males were significantly more site faithful than females. Males rarely nested further than 100 m from their previous year's site, those that moved further (17% of Redshank, 4% of Dunlin and 21% of Ringed Plover) usually settled within 500 m and thus were probably already largely familiar with their new site. Adult female Redshank were only slightly less site faithful than males and those that moved usually settled within 500 m. Female Dunlin and Ringed Plover were far less site faithful to their previous years' nest site than males (only about 50% returned to within 100 m) and often resettled several kilometres away (up to 16 km) where they would be unlikely to have any previous familiarity.

28) In each of the three species studied young males bred significantly closer to their natal site than young females. The distance from the natal site to the breeding site for Dunlin and Redshank was usually less than 1 km for males and for females typically between 1 and 10 km. Young Ringed Plover generally moved greater distances than the other two species, often over 10 km, the greatest known movement was 42 km by a female.

30) The survival rate of clutches laid early in the season

(mainly first clutches) was generally far greater than those laid later (mainly relays). The estimated survival rate of clutches (based on the Mayfield Method) for first early and then late clutches of each species was as follows: Redshank 52% and 40%, Dunlin 72% and 38%, and Ringed Plover 25% and 7%. The poorer survival of late nests may have been caused by a decline in communal anti-predator behaviour of neighbouring breeding Lapwing.

31) The amount of concealment of Redshank and Dunlin nests and the effectiveness of camouflage of Ringed Plover nests was positively correlated to nest survival.

32) By far the most important cause of nest failure was avian predation, especially by Common Gulls.

33) The estimated mean number of chicks fledged per breeding adult each year was 0.56 for Redshank and 0.34 for Ringed Plover. For Dunlin there was a large difference in this value between the two sites at which it was determined; at Drimore Farm (breeding territories mainly on marsh) the figure was 0.71 whilst at Stilligarry (territories mainly on old fallow) it was only 0.31.

34) The annual survival rate of adults of each species based on the return rate of colour-ringed birds were as follows: Redshank 76%, Dunlin 81% and Ringed Plover 73%.

35) Raptor predation during the breeding season was an important component of adult annual mortality, Redshank in particular suffered heavy mortality in April. This high risk of predation

may be an important factor controlling the time birds spend on the breeding grounds.

36) The survival rate of fledglings to the age of first breeding could be estimated only approximately. These survival rates for each species were as follows: Redshank 20%, Dunlin 16% and Ringed Plover 23%. These values are minimum survival rates, there is good reason to suppose that the actual survival rates were higher, perhaps by up to half as much again.

37) The vast majority of Ringed Plover and female Redshank and approximately 50% of male Redshank bred for the first time at one year old. The remaining male Redshank and almost all Dunlin deferred breeding and in most cases probably bred for the first time at two years old.

38) Allowing for suspected underestimation of the first year survival values, the annual recruitment rate into the breeding population was probably sufficient to balance adult mortality for both Redshank and Dunlin; however, for Ringed Plover it was undoubtedly insufficient. Productivity of Dunlin breeding on old fallow areas may be insufficient to balance adult mortality and these areas may partly rely on Dunlin reared in marsh habitats for recruitment.

39) Intensive and extensive population surveys showed that the numbers of Ringed Plover were declining by about 10% per year whereas those of Redshank or Dunlin were stable or, perhaps, declining slowly.

40) The ultimate factors limiting the size of wader populations are discussed. It is concluded that for the three species studied there is strong evidence to indicate that the extent of suitable breeding habitat limits population size.

41) Conservation measures aimed at maintaining large breeding populations of Redshank, Dunlin and Ringed Plover in the Southern Isles are discussed. The two principle conservation aims should be to maintain the suitability of extensive areas for breeding by appropriate management and to enhance the birds productivity through reducing predation. The latter could be achieved by habitat management that promotes good cover/camouflage for nests and chicks and through control of predators especially Common Gulls.

42) The threat posed to the breeding wader populations in the Southern Isles by Hedgehogs and feral American Mink is in urgent need of evaluation.

REFERENCES

- ALERSTAM, T. & HOGSTEDT, G. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. *Ornis Scand.* 13, 25-37
- BAINES, D., 1988a. The effects of improvement of upland, marginal grasslands on breeding waders (Charadriiformes). *Biol. Cons.* 45, 221-236.
- BAINES, D., 1988b. The effects of improvement of upland, marginal grasslands on breeding waders (Charadriiformes) and invertebrates. Unpubl. Ph.D. thesis, Univ of Durham.
- BARASH, D.P., 1982. *Sociobiology and Behaviour*. Second Edition. Elsevier. New York.
- BEINTEMA, A.J. & MUSKENS, G.K.D.M. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. *J. Appl. Ecol.* 24, 743-758.
- BLIX, A.S., & STEEN J.B. 1979. Thermoregulation in new born polar homeotherms. *Physiol. Review.* 59, 285-304.
- BOERE, G.C., & SMIT, C.J. 1983. *The ecology of the Wadden Sea* Vol II. (Wolff W.J. ed.). Balkema, Rotterdam. pp.6/179-189.
- BOYD, H. 1962. Mortality and fertility of European Charadrii. *Ibis* 104, 368-387.
- BUXTON, E.J.M. 1962. The inland breeding of the Oystercatcher in

- Great Britain, 1958-59. *Bird Study* 8, 194-209.
- CADBURY, C.J. & HOUSDEN, S. 1982. Outer Hebrides - Treat to Breeding Waders. *Wader Study Group Bull.* 35, 5.
- CAIRD, J.B., 1979. Land use in the Uists since 1800. *Proc. Roy. Soc. Edinb.* 77B, 505-526.
- CHANDLER, D.F. & WALKER, A.J. 1985. Habitat use by breeding Redshanks on South Uist. *Wader study Group Bull.* 45, 25-28.
- COOKE, A.S., BELL, A.A. & HAAS, M.B. 1982. Predatory birds, pesticides and pollution. *Natural Environment Research Council.*
- CRAMP, S. & SIMMONS, K.E.L., 1983. *Handbook of the birds of Europe, the Middle East and North Africa. Vol III.* Oxford Univ. Press, Oxford.
- CUNNINGHAM, P. 1987. Mink in the Outer Hebrides. *Scottish Bird News* 8, 4.
- DICKINSON, G. & RANDALL, R.E. 1979. An interpretation of machair vegetation. *Proc. Roy. Soc. Edinb.* 77B, 267-278.
- DWERNYCHUK, L.W. & BOAG, D.A. 1972. How vegetative cover protects duck nests from egg-eating birds. *J. Wildl. Mgmt.* 36, 955-961.
- DYRCZ, A., WITKOWSKI, J. & OKULEWICZ, J. 1981. Nesting of "timid" waders in the vicinity of "bold" ones as an anti-predator adaption. *Ibis* 123, 542-545.

- ELLIOT, R.D. 1985. The exclusion of avian predators from aggregations of nesting Lapwings (*Vanellus vanellus*). *Anim. Behav.* 33, 308-314.
- ETHERIDGE, B. 1982. Distribution of Dunlin *Calidris alpina* nests on an area of South Uist machair. *Bird Study* 29, 239-243
- EVANS, P.R. & PIENKOWSKI, M.W. 1984. Population dynamics of shorebirds. In: *Behaviour of Marine Animals*, Vol. 5. (Burger, J. & Olla, B.L. eds.), pp. 83-123. Plenum Press, New York.
- FULLER, R.J., 1978. Breeding populations of Ringed Plover and Dunlins in the Uists and Benbecula, Outer Hebrides. *Bird Study* 25, 97-102.
- FULLER, R.J., REED, T.M., BUXTON, A., WILLIAMS, T.D. & PIENKOWSKI, M.W. 1986. Populations of breeding waders Charadrii and their habitats on the crofting lands of the Outer Hebrides, Scotland. *Biol. Cons.* 37, 333-361.
- FULLER, R.J. 1985. Studies on breeding waders in the Southern Isles of the Outer Hebrides, 1985. Unpublished Nature Conservancy Council report. (CSD Report 606)
- FULLER, R.J. & PERCIVAL, S. M. 1986. Surveys on breeding waders in the Southern Isles of the Outer Hebrides, 1986. Unpublished Nature Conservancy Council report. (CSD Report 690)
- FRETWELL, S. 1972. *Populations in a seasonal environment.* Princeton University Press.

- GLENTWORTH, R. 1979. Observations on the soils of the Outer Hebrides. Proc. Roy. Soc. Edinb. 77B, 123-137.
- GORANSSON, G., KARLSSON, J., NILSSON, S.G. & ULFSTRAND, S. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26, 117-120.
- GOSS-CUSTARD, J.D. 1977. The ecology of the Wash. III. Density-related behaviour and the possible effects of a loss of feeding grounds on wading birds (Charadrii). J. Appl. Ecol. 14, 721-739.
- GOSS-CUSTARD, J.D. 1980. Competition for food and interference among waders. Ardea 68, 31-52.
- GRANT, J.W. 1979. Cereals and grass production in Lewis and the Uists. Proc. Roy. Soc. Edinb. 77B, 527-533.
- GREEN, G.H., 1983a. WSG Survey to determine the number and distribution of waders breeding on the western seaboard of the Outer Hebrides, Scotland. Wader Study Group Bull. 38, 6-7.
- GREEN, G.H., 1983b. Wader Study Group and Nature Conservancy Council survey of waders breeding on the Hebridean machair and adjacent land. Wader Study Group Bull. 39, 5-8.
- GREEN, R.E. 1986. The management of lowland wet grasslands for breeding waders. Unpubl. RSPB report.
- GREEN, R.E, HAWELL, J. & JOHNSON, T.H. 1987. Identification of

- predators of wader eggs from egg remains. *Bird Study* 34, 87-91.
- GREEN, G.H., GREENWOOD, J.J.D., LLOYD, C.S., 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. *J. Zool.* 183, 311-328.
- GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28, 1140-1162.
- GREENWOOD, P.J., HARVEY, P.H. & PERRINS, C.M. 1978. In breeding and dispersal Great Tit. *Nature (London)* 271, 52-54.
- GROSSKOPF, G. 1958. Zur Biologie des Rotschenkels (*Tringa t. totanus* L) I. *J. Ornithol.* 99, 1-17.
- GROSSKOPF, G. 1959. Zur Biologie des Rotschenkels (*Tringa t. totanus* L) II. *J. Ornithol.* 100, 210-236.
- GROSSKOPF, G. 1963. Weitere beitrage zur biologie des rotschenkels. *Vogelwelt* 84, 65-83.
- GROSSKOPF, G. 1964. Sterblichkeit und Durchschnittsalter einiger Kustenvogel. *J. Ornithol.* 105, 427-449.
- HALE, W.G. 1956. The lack of territory in the Redshank *Tringa totanus*. *Ibis* 98, 398-400.
- HALE, W.G. 1980. *Waders*. Collins, London.
- HARRIS, M.P. 1970. Territory limiting the size of the breeding population of the Oystercatcher (*Haematopus ostralegus*): A removal experiment. *J. Anim. Ecol.* 39, 707-713.

- HILL, M.O., BUNCE, R.G.H. & SHAW, M.W. 1975. Indicator species analysis, a divisive polythetic method of classification and its application to a survey of native pinewoods in Scotland. *J. Ani. Ecol.* 63, 597-613.
- HILL, M.O. 1979. TWINSpan - a Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University. Ithaca. New York.
- HILL, M.O. & GAUCH, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, 42, 47-58.
- HINDE, R.A., 1956. The biological significance of territories in birds. *Ibis* 98, 340-369.
- HOLMES, R.T. 1966a. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. *Condor* 68, 3-46.
- HOLMES, R.T. 1966b. Feeding Ecology of the Red-backed Sandpiper (*Calidris alpina*) in arctic Alaska. *Ecology* 47, 32-45
- HOLMES, R.T. 1970. Differences on population density, territoriality, and food supply of Dunlin on Arctic and subarctic tundra. In: *Animal Populations in Relation to Their Food Resources*. (A. Watson, ed.) pp. 303-319, Blackwell, Oxford.
- JACKSON, D.B. & PERCIVAL, S.M. 1983. The breeding waders of the Hebridean machair: a validation check of the census method. *Wader Study Group Bull.* 39, 20-24.

- JOHNSON, D.H. 1979. Estimating nest success: the Mayfield Method and an alternative. *Auk* 96, 651-661.
- JONSSON, P.E. 1988. The ecology of the Southern Dunlin *Calidris alpina schinzii*. Lund University, Sweden.
- LACK, D. 1966. *Population Studies of Birds*. Clarendon Press, Oxford.
- LAVEN, H. 1940. Beitrage zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.) *J. Ornithol.* 88, 183-287.
- MARTIN-LOF, P. 1961. Mortality rate calculations on ringed birds with special reference to Dunlin *Calidris alpina*. *Ark. Zool.* 13, 483-491.
- MASON, C.F. & MACDONALD, S.M. 1976. Aspects of the breeding biology of the Snipe. *Bird Study* 23, 33-38.
- MAYFIELD, H.F. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73, 255-261.
- MAYFIELD, H.F. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87, 456-466.
- MAYNARD SMITH, J. 1978. The evolution of behaviour. *Sci. Amer.* 239, 176-192.
- MAYNARD SMITH, J. & PARKER, G. 1976. The logic of asymmetric contests. *Anim. Behav.* 24, 159-175
- MYHRE, K. & STEEN, J.B. 1979. Body temperature and aspects of behavioural thermoregulation in some neonate subarctic

birds. *Ornis Scand.* 10, 1-9.

NETHERSOLE-THOMPSON D, 1986. *Waders: their breeding, haunts and watchers.* Poyser, Berkhamstead.

O'CONNOR, R.J. & SHRUBB, M. 1986. *Farming and Birds.* Cambridge University Press, Cambridge.

ORING, L.W. & LANK, D.B. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. In: *Behaviour of Marine Animals, Vol. 5.* (Burger, J. & Olla, B.L. eds.), pp. 125-147. Plenum Press, New York.

PIENKOWSKI, M.W., 1980. Aspects of the ecology and behaviour of Ringed and Grey Plovers *Charadrius hiaticula* and *Pluvialis squatarola*. Unpubl. Ph.D. thesis, Univ. of Durham.

PIENKOWSKI, M.W., 1984a. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: Nest predation as a possible factor limiting distribution and timing of breeding. *J. Zool.* 202, 83-114.

PIENKOWSKI, M.W., 1984b. Behaviour of young Ringed Plovers *Charadrius hiaticula* and its relationship to growth and survival to reproductive age. *Ibis* 126, 133-155.

PIENKOWSKI, M.W. & DICK, W.J.A. 1975. The migration and wintering of Dunlin *Calidris alpina* in north-west Africa. *Ornis Scand.* 6, 151-167.

PIENKOWSKI, M.W., FULLER, R.J., JACKSON, D.B. & PERCIVAL, S.M. 1986. Breeding waders of blackland, moorland and

agriculturally improved moorland in the Uists and Benbecula.
Scot. Birds 14, 9-16.

PIERSMA, T., 1986. Breeding Waders in Europe: A review of
population size estimates and a bibliography of information
sources. Wader Study Group Bull. 48, Supplement.

PILCHER, R.E.M, 1964. Effects of cold weather of 1962/63 on
birds of the north coast of the Wash. Wildfowl Trust Annu.
Rep. 15, 23-26.

PRATER, A.J., MARCHANT, J.H. & VOURIEN, J. 1977. Guide to the
identification and ageing of holarctic waders. B.T.O. Guide
No.7, Tring, England.

REED, T.M., BARRET, C., BARRET, J., HAYHOW, S. & MINSHULL, B.
1985. Diurnal variability in the detection of waders on
their breeding grounds. Bird Study 32, 71-74

REED, T.M. & FULLER, R.J. 1983. Methods used to assess
populations of breeding waders on machair in the Outer
Hebrides. Wader Study Group Bull. 39, 14-16.

REED, T.M., WILLIAMS, T.D. & WEBB, A. 1983. The Wader Study
Group survey of Hebridean waders: Was the timing right?
Wader Study Group Bull. 39, 17-19.

RITCHIE, R. 1967. The machair of South Uist. Scott. Geogr. Mag.
83, 161-173.

RITCHIE, R. 1979. Machair development and chronology in the
Uists and adjacent islands. Proc. Roy. Soc. Edinb. 77B,

107-122.

- SHARROCK, J.T.R. 1976. The Atlas of Breeding Birds in Britain and Ireland. BTO/IWC, Tring.
- SMITH, K.W., 1983. The status and distribution of waders breeding on wet lowland grasslands in England and Wales. Bird Study 30, 177-92.
- SOIKKELI, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4, 158-198.
- SOIKKELI, M. 1970 a. Dispersal of Dunlin *Calidris alpina* in relation to sites of birth and breeding. Ornis Fenn. 47, 1-9.
- SOIKKELI, M. 1970 b. Mortality and reproductive rates in a Finnish population of Dunlin *Calidris alpina*. Ornis Fenn. 47, 149-158.
- SMITH, K.W. 1983, The status and distribution of waders breeding on wet, lowland grasslands in England and Wales. Bird Study. 30, 177-192.
- SMITH, D.I. & FETTES, D.J. 1979. The geological framework of the Outer Hebrides. Proc. Roy. Soc. Edinb. 77B, 75-83.
- STROUD, D.A., REED, T.M., PIENKOWSKI, M.W. & LINDSAY, R.A. 1987. Birds, Bogs and Forestry: The peatlands of Caithness and Sutherland. Nature Conservancy Council, Peterborough.
- TOWNSHEND, D.J. 1982a. The use of intertidal habitats by

shorebird populations with special reference to Grey Plover
(*Pluvialis squatarola*) and Curlew (*Numenius arquata*).

Unpubl. Ph.D. thesis, Univ. of Durham.

TOWNSHEND, D.J. 1982b. The Lazarus syndrome in Grey Plover.

Wader Study Group Bull. 34, 11-12.

TOWNSHEND, D.J., DUGAN, P.J. & PIENKOWSKI, M.W., 1984. The
unsociable plover - use of intertidal areas by Grey Plovers.

In: Coastal Waders and Wildfowl in Winter. (Evans, P.R.,

Goss-Custard, J.D. & Hale, W.G. eds.) pp. 140-159.

Cambridge University Press

WALKER, A.J. & CHANDLER, D.F. 1985. Family group movements by

Redshank on South Uist. Wader Study Group Bull. 45, 29-31.

WHITFIELD, D.P. 1985. Raptor predation on wintering waders in

southeast Scotland. Ibis 127, 544-558.

WILLIAMS, G., 1959. Seasonal and diurnal activity of Carabidae,
with particular reference to *Nebria*, *Notophilus* and *Feronia*.

J. Anim. Ecol. 31, 309-330

WILSON, J.R. 1978. Agricultural influences on waders nesting on

the South Uist machair. Bird Study 25, 198-206.

YATES, B.J. 1982. A population biology of breeding Redshanks

Tringa totanus. Unpub. Ph.D. thesis. Liverpool Poly.

Appendix A: Habitat classification.

Vegetation classification

The technique used to classify the vegetation quadrat-data (see page 13, Chapter 2) was TWINSpan (Two Way Indicator Species Analysis). This is a divisive hierarchical method well suited to classifying heterogeneous habitat assemblages. The theory and details of TWINSpan are described by Hill (1975 and 1979).

TWINSpan is a computer programme that operates by dividing the initial data set into two groups of quadrats (division level 1). These two groups are themselves divided in two (division level 2) and so on. TWINSpan continues in this way dividing the data into ever smaller groups. The process of division needs to be interrupted as otherwise groups will be split which in reality constitute a single vegetation type. The decision of when to stop further divisions is largely arbitrary, here it has been based on stopping the division at levels that gave recognisable stand-types which appeared ecologically distinct. The divisions leading to each of the 14 stand-types recognised in this analysis are shown in Figure A.1.

One of the advantages of TWINSpan is that it can be used to produce a key, based on the scoring of the so called "indicator species", showing the basis of the classification at each level of division. Such a key can then be used in the field to identify areas of vegetation as one of the predetermined stand-types defined by the classification of the original data set. The classification key showing the basis of the present analysis is given in Table A.1.

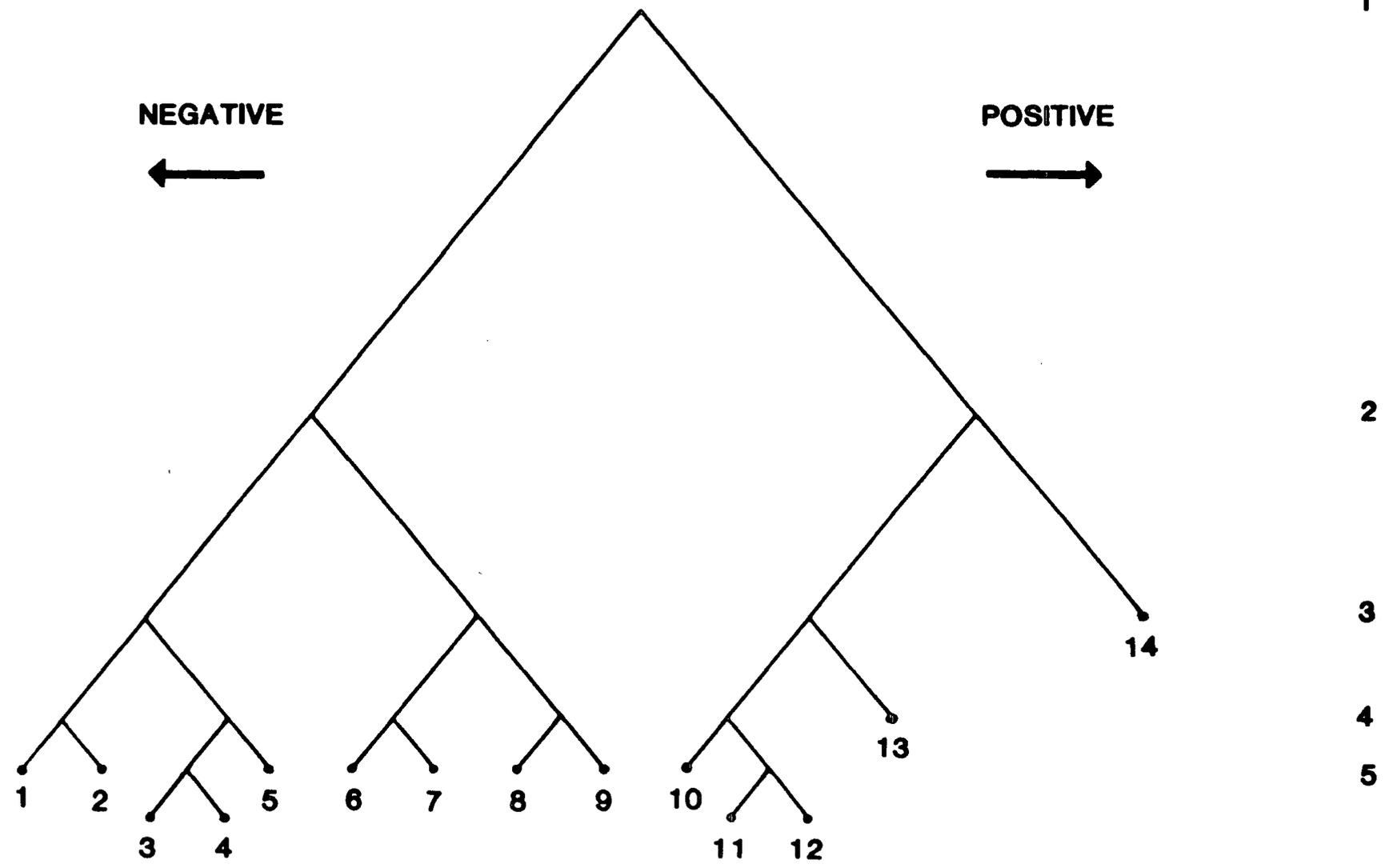


Figure A.1: Dendrogram of TWINSpan classification of vegetation data collected from 281 quadrat samples taken on the breeding-wader study-sites on South Uist. The division of the data set into 14 vegetation stand types is shown.

A summary of the floristic details of each of the 14 stand-types is given in Table A.2. This is a constancy table that shows the regularity with which each species occurs in each stand-type. It should be noted that the constancy value does not indicate dominance, a species can have a high constancy value yet typically form a very small component of the vegetation. An attempt is made to indicate the most important species in each stand-type by indicating in bold type those species that, when present, form a major component of the vegetation.

One of the drawbacks of TWINSpan is that it does not give any indication of the magnitude of differences between the various groups. An ordination of the data set using DECORANA (Detrended Correspondance Analysis) can indicate the magnitude of the similarities between groups and aid the identification of the underlying trends in the data in relation to environmental factors. DECORANA is an ordination technique developed by Hill and Gauch (1980) for vegetation data. It has certain mathematical advantages over other ordination techniques. The ordination can be carried out on either the individual quadrats or the individual species. The ordination plots of species are particularly useful because, when considered in conjunction with the known ecological requirements of the species, they can be used to indicate the predominant environmental gradients that correspond to each ordination axis.

The ordination of the quadrat samples is shown in Figure A.2 for Axis 1 vs. Axis 2, and in Figure A.3 for Axis 1 vs. Axis 3. In these figures the area that includes the cluster of quadrat points corresponding to each stand-type is drawn in and labelled

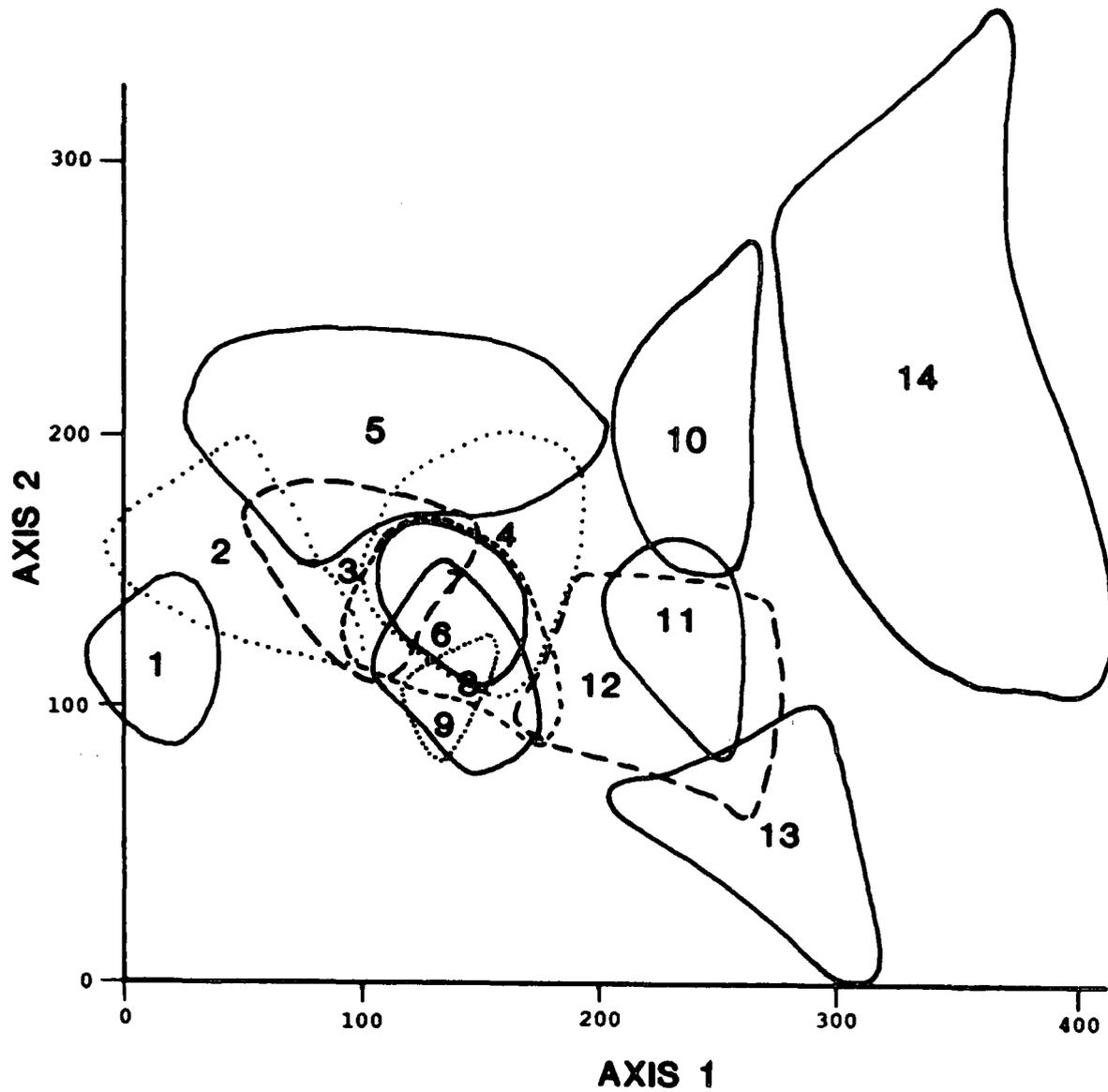


Figure A.2: DECORANA ordination plot (Axis 1 vs. Axis 2) of data from 281 vegetation quadrats sampled on the breeding-wader study-sites on South Uist.
 The areas labelled 1-14 show the areas covered by the cluster of quadrat points corresponding to each of the 14 stand types identified by the TWINSpan analysis.

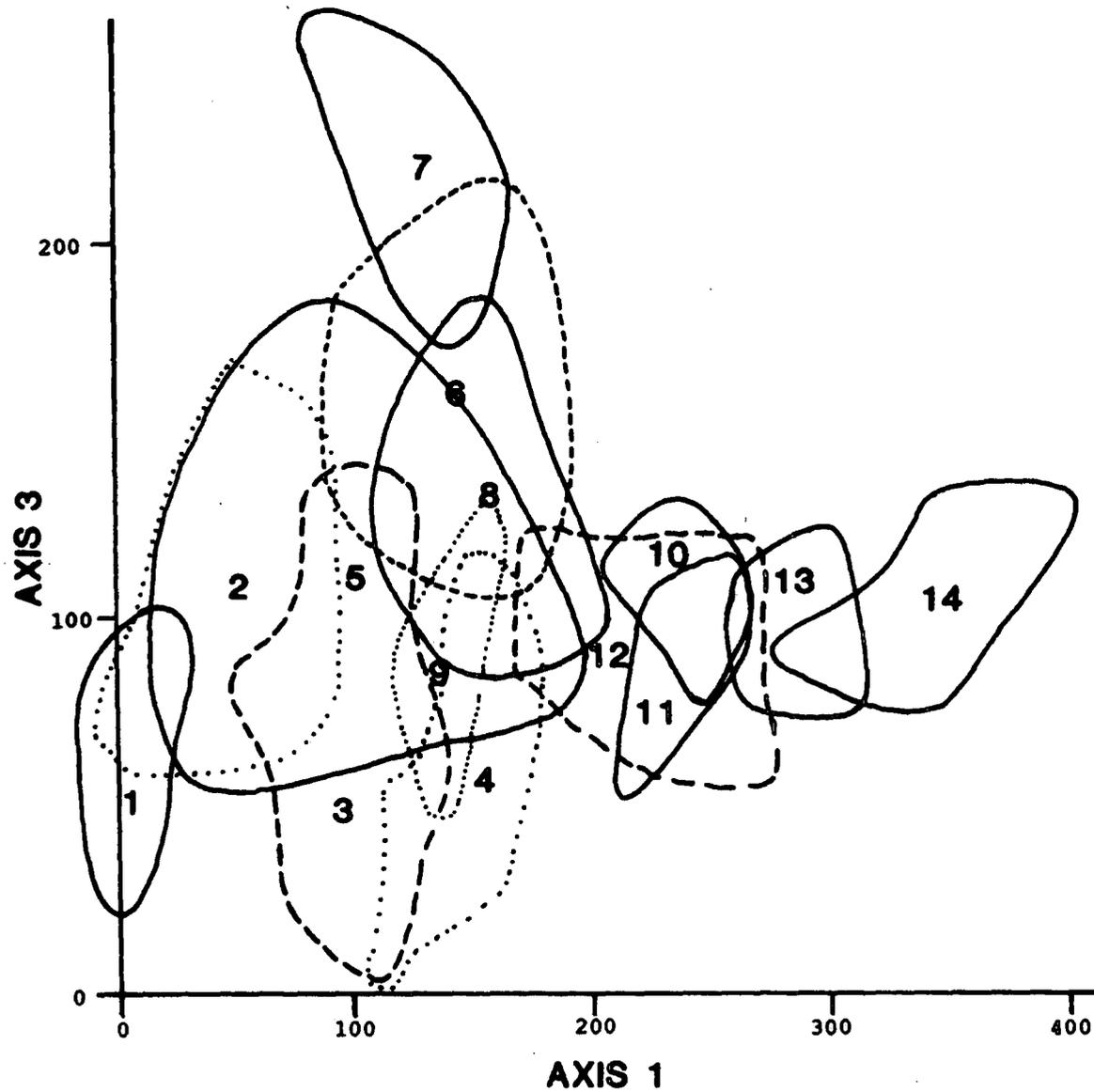


Figure A.3: DECORANA ordination plot (Axis 1 vs. Axis 3) of data from 281 vegetation quadrats sampled on the breeding-wader study-sites on South Uist. The areas labelled 1-14 show the areas covered by the cluster of quadrat points corresponding to each of the 14 stand types identified by the TWINSpan analysis.

with the stand-type number.

Axis 1 clearly corresponds to soil type. Peaty soils appear near the origin (e.g. stand-type 1) and the sandy soils of the machair and dunes appear on the right of the plot. Stand-types 1 and 2 occur on peat, stand-types 3 to 9 occur on peaty loams, the typical soil of the more fertile blackland and marshes, whilst stand-types 10 to 14 occur on the sandy soils of the machair. Axis 1 can also be considered to reflect a gradient from acidic soils on the left, through neutral conditions in the centre to the calcareous soils of the machair on the right.

Axis 2 does not clearly correspond to any single environmental gradient. Wetness appears to be the main factor, stand-types found on dry areas occur close to the origin whilst those of the wettest conditions occur towards the top of the plot. However, the orientation of this wetness gradient is clearly angled somewhat to Axis 2 with the maximum wetness (wet marsh, stand-type 5) in the top left of the plot and the maximum dryness (sand-dunes, stand-type 13) in the bottom right. A similar ordination plot of the species suggest that two other environmental gradients are involved in Axis 2, but these are restricted to only certain areas of the plot. Firstly, on the most peaty soils, i.e. the far left of the plot, there appears to be a gradient from base poor conditions close to the origin to less base poor conditions at higher Axis 2 scores. Secondly, on the most sandy soils, i.e. the far right of the plot, there appears to be a gradient of soil disturbance. Sand-dune quadrats (stand-type 13), which are undisturbed, have low scores on Axis 2 whilst the quadrats from the highly disturbed and unnatural

reseeded machair (stand-type 14) generally score high values. The corresponding ordination plot of the species shows that various agricultural ruderals such as *Odonites verna*, *Sinapis arvensis* and *Polygonum aviculare* are positioned in the top right corner.

The ordination plot of Axis 1 vs. Axis 2 fails to adequately separate stand-types 4, 6, 7, 8 and 9. These stand-types all occur on areas with damp peaty-loam soils. These five stand-types separate out to some extent along the third ordination axis, Axis 3, as illustrated in Figure A.3. There is no obvious environmental gradient that corresponds to this axis. The ordination plot of species suggests that a combination of grazing pressure and salinity are probably involved. Species indicative of low grazing pressure such as *Iris pseudacorus* and *Juncus effusus* have high scores on Axis 3 whilst species that can tolerate intensive grazing such as *Cynosurus cristatus* and *Trifolium pratense* tend to have low scores on this axis. Species that indicate high salinities, for instance many of the species found in maritime pasture (stand-types 8 and 9) such as *Plantago coronopus*, also have low scores on Axis 3.

Table A.1: Indicator-species criteria for the TWINSPAN stand types.

The figures in the lefthand column indicate the level and direction of the division. The cover percentage thresholds for individual species, and the indicator score thresholds for the groups are given (+ = present), with the latter appearing first in bold type. The stand type indentivity numbers appear at the right in italic.

1-ve	-1		
		<i>Carex nigra</i> +	
		<i>Anthoxanthum odoratum</i> +	
		<i>Senecio aquaticus</i> +	
		<i>Lychnis flos-cuculi</i> +	
		<i>Hydrocotyle vulgaris</i> +	
2-ve	0		
		<i>Succisa pratensis</i> +	
		<i>Molinia caerulea</i> +	
3-ve	-1		
		<i>Carex echinata</i> +	
		<i>Potentilla erecta</i> +	
4-ve	-1		
		<i>Nardus stricta</i> +	
		<i>Potentilla erecta</i> >4	
		<i>Calluna vulgaris</i> +1
4+ve	0		
		<i>Holcus lanatus</i> >42
3+ve	0		
		<i>Vicia cracca</i> +	
		<i>Trifolium pratense</i> +	
4-ve	-2		
		<i>Molinia caerulea</i> +	
		<i>Vicia cracca</i> +	
5-ve	0		
		<i>Molinia caerulea</i> >10	
		<i>Senecio aquaticus</i> +	
		<i>Ranunculus flammula</i> +	
		<i>Pedicularis palustris</i> +3

continued.

Table A.3 continued:

5+ve	1		
		<i>Cynosurus cristatus</i> >4	
		<i>Trifolium pratense</i> >4	
		<i>Festuca rubra</i> >104
4+ve	-1		
		<i>Caltha palustris</i> >4	
		<i>Epilobium palustre</i> +5
2+ve	1		
		<i>Rumex acetosella</i> +	
		<i>Juncus effusus</i> >4	
3-ve	0		
		<i>Potentilla anserina</i> +	
		<i>Iris pseudacorus</i> +	
4-ve	-1		
		<i>Anthoxanthum odoratum</i> +	
		<i>Rumex acetosella</i> +	
		<i>Cynosurus cristatus</i> +	
		<i>Juncus effusus</i> >306
4+ve	0		
		<i>Iris pseudacorus</i> >30	
		<i>Hydrocotyle vulgaris</i> >47
3+ve	1		
		<i>Bellis perennis</i> +	
		<i>Nardus stricta</i> >10	
		<i>Danthonia decumbens</i> +	
		<i>Prunella vulgaris</i> >4	
4-ve	0		
		No indicator species8
4+ve	1		
		<i>Carex flacca</i> >49
1+ve	0		
		<i>Festuca rubra</i> >30	
		<i>Cerastium fontanum</i> +	
2-ve	-1		
		<i>Festuca rubra</i> >4	
		<i>Euphrasia officinalis</i> +	
		<i>Plantago lanceolata</i> +	
		<i>Vicia cracca</i> +	

continued.

Table A.3 continued:

3-ve	0 <i>Potentilla anserina</i> >10 <i>Vicia cracca</i> + <i>Carex flacca</i> + <i>Agrostis stolonifera</i> >10	
4-ve	0 No indicator species10
4+ve	1 <i>Poa pratensis</i> +	
5-ve	0 <i>Carex flacca</i> + <i>Potentilla anserina</i> >1011
5+ve	1 <i>Senecio jacobaea</i> + <i>Lotus corniculatus</i> + <i>Honkenya peploides</i> + <i>Galium verum</i> + <i>Carex disticha</i> +12
3+ve	1 <i>Galium verum</i> + <i>Senecio jacobaea</i> + <i>Achillea millifolium</i> +13
2+ve	0 <i>Lolium perenne</i> >414

Appendix A.2: Constancy values of species in each vegetation stand type.

1 = 1-20% of quadrats 3 = 41-60% of quadrats 5 = 81-100% of quadrats
 2 = 21-40% of quadrats 4 = 61-80% of quadrats

Species that, when present, tend to dominate are shown in bold (i.e. their average cover score is atleast 3).

SPECIES	STAND TYPE													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Monocotyledones														
<i>Narthecium ossifragum</i>	1	1
<i>Carex pulicaris</i>	2	3	1	1
<i>Carex flava</i>	1	1	1	.	2
<i>Triglochin maritima</i>	2	1	4	3	2
<i>Carex echinata</i>	4	5	1	1	1	1
<i>Eriophorium angustifol.</i>	3	4	2	.	3	1	1	1
<i>Eleocharis palustris</i>	.	2	1	1	3
<i>Schoenus nigricans</i>	.	1	.	.	1
<i>Carex ovalis</i>	.	1	1	.	1	1
<i>Juncus balticus</i>	.	.	3	1
<i>Phragmites australis</i>	.	1	1	1	1	.	1	.	.	1
<i>Triglochin palustris</i>	.	1	1	.	1	1	1	.	.	.
<i>Carex dioica</i>	4	.	1	1
<i>Nardus stricta</i>	5	1	1	4	5
<i>Carex panicea</i>	5	5	4	4	2	1	1	2	.	.	.	1	.	.
<i>Luzula multiflora</i>	5	4	3	3	1	1	.	2	3	1	.	2	2	.
<i>Molinia caerulea</i>	5	5	5	3	1	1	3	3	1	.
<i>Anthoxanthum odoratum</i>	5	5	5	3	2	4	1	3	4	3	.	1	1	.
<i>Iris pseudacorus</i>	.	.	1	.	1	1	5
<i>Cynosurus cristatus</i>	1	1	2	5	2	3	.	1	.	2	1	1	.	.
<i>Juncus effusus</i>	2	4	1	1	.	5	5	5	.	.	.	1	.	.
<i>Carex nigra</i>	5	5	5	5	5	5	5	5	4	3	1	1	1	.
<i>Holcus lanatus</i>	5	5	5	5	5	5	5	5	5	5	5	5	5	3
<i>Agrostis stolonifera</i>	3	4	5	4	5	5	5	5	3	5	5	5	4	4
<i>Juncus acutiflorus</i>	3	5	3	4	5	1	1	4	3	3	2	1	.	2
<i>Festuca rubra</i>	2	3	4	5	2	5	5	5	5	4	5	5	5	2
<i>Poa pratensis</i>	1	1	1	2	2	3	3	2	.	.	5	5	4	2
<i>Dactylis fuchsii</i>	1	1	2	3	1	1	1	1	2	.	1	.	1	.
<i>Danthonia decumbens</i>	1	1	1	.	1	1	.	2	4	.	.	1	1	.
<i>Carex flacca</i>	1	1	1	2	1	1	.	1	5	2	4	2	.	.
<i>Plantago lanceolata</i>	1	.	3	3	1	2	2	3	4	3	5	4	5	1
<i>Plantago maritima</i>	.	.	2	2	1	.	.	1	2	1	.	.	1	.
<i>Plantago coronopus</i>	1	2	.	.	1	.	.
<i>Aira praecox</i>	2	.	.	1	.	.
<i>Listera cordata</i>	1	.	.	.
<i>Bromus mollis</i>	.	.	.	1	1	1	1	.
<i>Carex disticha</i>	1	2	3	.
<i>Ammophila arenaria</i>	2	.
<i>Poa annua</i>	1	.	.	1	2	.	.	.	1	3
<i>Poa trivialis</i>	.	.	.	1	1	3	.	.	1	2
<i>Juncus bufonius</i>	.	.	.	1	1	4	.	.	.	3
<i>Lolium perenne</i>	.	.	.	1	1	1	1	1	5
<i>Alopecurus pratensis</i>	2

Appendixa A.2 continued:

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Dicotyledones														
<i>Drosera anglica</i>	1	1
<i>Drosera rotundifolia</i>	1	1
<i>Potamogeton</i> sp.	.	1
<i>Veronica scutellata</i>	.	1	1
<i>Calluna vulgaris</i>	4	.	1
<i>Potentilla erecta</i>	5	3	1	2	.	.	1	.	.
<i>Gentianella campestris</i>	.	.	1	1
<i>Angelica sylvestris</i>	.	.	1	1
<i>Menyanthes trifoliata</i>	.	.	1	.	1
<i>Myosotis scorpioides</i>	.	1	1	.	1
<i>Pedicularis palustris</i>	4	2	3	.	2
<i>Pinguicula vulgaris</i>	1	1	1	1	1
<i>Succisa pratensis</i>	4	3	4	4	2	1
<i>Epilobium palustre</i>	1	2	2	1	3	1	1
<i>Caltha palustris</i>	1	1	3	2	4	1	1
<i>Potentilla palustris</i>	2	4	1	.	3	1	1
<i>Galium palustre</i>	.	1	1	.	2	.	1
<i>Polygonum amphibium</i>	.	1	1	1	1	1	1	.	.	2
<i>Sagina nodosa</i>	.	1	1	1	2	.	1	2	3	.	2	.	.	.
<i>Senecio aquaticus</i>	2	3	4	1	3	4	5	4
<i>Lathyrus pratensis</i>	1	1	2	3	1	1	.	.	.	2	1	.	.	.
<i>Hydrocotyle vulgaris</i>	2	4	4	3	4	1	5	3	3	2
<i>Lychnis flos-cuculi</i>	3	4	4	4	5	2	4	4	.	1	1	1	.	.
<i>Ranunculus flammula</i>	2	4	3	1	3	1	1	2	4	.	1	1	.	.
<i>Hypochaeris radicum</i>	2	1	1	1	.	1	1	2	3	.	1	1	1	.
<i>Cardamine flexuosa</i>	1	3	2	2	3	3	3	2	2	1	1	.	1	.
<i>Prunella vulgaris</i>	1	2	2	3	2	4	3	5	5	3	4	4	3	1
<i>Ranunculus acris</i>	1	2	4	4	3	3	4	5	5	4	5	5	4	2
<i>Trifolium pratense</i>	1	1	3	5	2	1	1	1	2	3	2	4	3	2
<i>Leontodon autumnalis</i>	1	1	3	2	1	2	1	3	3	3	4	3	3	1
<i>Cerastium fontanum</i>	1	1	2	3	2	1	1	2	2	5	4	5	5	4
<i>Trifolium repens</i>	2	4	4	4	3	5	5	5	4	3	5	5	5	3
<i>Euphrasia officinalis</i>	1	1	2	4	2	3	4	4	5	1
<i>Rhinanthus minor</i>	1	1	2	3	2	1	.	.	.	3	5	4	3	2
<i>Rumex acetosella</i>	.	1	.	1	.	5	3	4	3	2	4	3	1	1
<i>Bellis perennis</i>	.	1	1	2	1	1	1	3	5	3	3	3	5	4
<i>Potentilla anserina</i>	.	2	3	4	3	4	3	2	.	5	5	4	3	3
<i>Ranunculus repens</i>	.	1	3	3	3	3	3	2	.	3	4	3	1	3
<i>Lotus corniculatus</i>	.	1	2	3	1	1	.	1	.	3	2	4	5	.
<i>Vicia cracca</i>	.	1	3	5	1	4	5	5	2	1
<i>Linum catharticum</i>	.	1	1	1	1	.	1	.	.	.	4	4	4	1
<i>Oenanthe lachenalii</i>	.	.	1	1	2	1	2	.	.
<i>Senecio jacobaea</i>	.	.	.	1	.	.	.	1	.	1	1	4	5	1
<i>Galium verum</i>	.	.	.	1	1	.	3	4	.
<i>Odonites verna</i>	.	.	.	1	3	1	1	.	2
<i>Achillea millefolium</i>	1	.	.	.	1	.	1	4	1
<i>Sagina procumbens</i>	1	.	3	1	1	.	2
<i>Viola tricolor</i>	1	.	.	2	1
<i>Myosotis arvensis</i>	1	.	.	1	2

Appendix A.2 continued:

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Stellaria media</i>	1	.	.	1	1
<i>Polygonum aviculare</i>	1	.	.	.	1
<i>Honkenya peploides</i>	1	3	2	1
<i>Thalictrum minus</i>	1	1	1
<i>Heracleum sphondylium</i>	1	.	.
<i>Centaurea nigra</i>	1	.	.
<i>Polygala vulgaris</i>	1	.
<i>Anthyllis vulneraria</i>	1	.
<i>Erodium cicutarium</i>	1	1
<i>Ranunculus bulbosus</i>	1
<i>Daucus carotus</i>	1
Lower plants and lichens														
<i>Selagenella selagin.</i>	1	.	.	1
<i>Anagallis tenella</i>	1	1	1	1
<i>Equisetum fluviatile</i>	1	1	2	3	4
<i>Acrocarpus sp</i>	1	1	1	1	1	1
<i>Mnium hordeum</i>	2	1	1	.	1	.	.	2	3	.	.	1	.	.
<i>Peltigra canina</i>	2	1	1	.	.	1	.	1	3	.	.	1	.	.
<i>Polytrichum juniperi</i>	2	1	2	.	.	1	.	.
<i>Equisetum arvense</i>	.	.	1	2	3	1	.	1	1
<i>Cladonia squamosa</i>	1	1	.	.	.	1	.	.
<i>Ophioglossum vulgatum</i>	.	.	.	1	1	2	1	3	2	1	1	2	1	.
<i>Rhytidiadelphus squar.</i>	3	3	1	1	1	4	3	4	3	.	4	5	4	.
<i>Moss spp.</i>	3	2	3	2	2	1	2	2	.	2	3	4	3	3

Table A.3: Habitat types recognised on the breeding-wader study-sites on South Uist.

Each of the twenty six habitats recognised is briefly described in terms of its floristic composition based on the TWINSpan analysis and its physical characteristics.

HABITAT TYPE (STAND-TYPE)	CODE	DESCRIPTION
Rough blackland pasture (1)	R	Moderately well drained and seasonally dry, but infertile, areas of blackland with a low heath-like sward. Soil very peaty. Dominated by <i>Nardus stricta</i> , <i>Molinia caerulea</i> and <i>Carex panicea</i> . Other species usually present are: <i>Luzula multiflora</i> , <i>Potentilla erecta</i> and short growing <i>Calluna vulgaris</i> .
Poor blackland pasture (2)	W	Low quality pasture on the less well drained areas of blackland which are water-logged for much of the year. Sward contains some dead material, is generally tussocky and rarely receives fertilizer. Dominated by <i>Carex nigra</i> , <i>Carex panicea</i> , <i>Molinia caerulea</i> and <i>Holcus lanatus</i> . Other frequent species are: <i>Anthoxanthum odoratum</i> , <i>Carex echinata</i> , and various broad-leaved marsh species.
Damp marsh (3)	M	Marsh with no surface water and an even surface. Typically a grazed sward with some tussocks. Dominated by <i>Carex nigra</i> , <i>Molinia caerulea</i> and <i>Triglochin maritima</i> . Other frequent species are <i>Succisa pratensis</i> , <i>Lychnis flos-cuculi</i> , <i>Hydrocotyle vulgaris</i> , <i>Caltha palustris</i> , <i>Carex panicea</i> , <i>Juncus balticus</i> and <i>Anthoxanthum odoratum</i> .
Good blackland pasture (4)	G	Good quality grass pasture on well drained, but not dry, fertile peaty-loam soils in blackland and blackland-machair transition zone. May have been reseeded and usually appears bright green with a short even sward lacking dead grass and proper tussocks. Typically given a spring top dressing of artificial fertilizer. Dominated by <i>Cynosurus cristatus</i> , <i>Carex nigra</i> , <i>Holcus lanatus</i> and <i>Trifolium pratense</i> . Other frequent species are <i>Vicia cracca</i> , <i>Potentilla anserina</i> and <i>Euphrasia officinalis</i> .

Continued.

Table A.3: continued.

HABITAT TYPE (STAND-TYPE)	CODE	DESCRIPTION
Wet marsh (5)	N	Marsh habitat with surface water usually present and soft peaty or muddy substrate. Typically, the vegetation is rank and tussocky. Dominated by <i>Carex nigra</i> and marsh plants such as <i>Lychnis flos-cuculi</i> , <i>Hydrocotyle vulgaris</i> , <i>Eriophorum angustifolium</i> , <i>Caltha palustris</i> , <i>Potentilla palustris</i> , and <i>Eleocharis palustris</i> .
Hummock marsh (3,5)	O	Marsh usually with no surface water, many small peaty hummocks of about 1m in diameter and 20cm high. Vegetation similar to damp marsh (3) but sometimes areas between hummocks may be of wet marsh (5).
Juncus pasture (6)	J	Areas having frequent clumps of <i>Juncus effusus</i> which often dominates large areas, particularly where grazing pressure is only moderate. Usually on damp areas of blackland, i.e. badly drained peaty soils. The other main species are: <i>Carex nigra</i> , <i>Holcus lanatus</i> , <i>Agrostis stolonifera</i> , <i>Festuca rubra</i> , <i>Anthoxanthum odoratum</i> , <i>Rumex acetosella</i> , <i>Prunella vulgaris</i> and <i>Senecio aquaticus</i> .
Iris beds (7)	I	All areas dominated by <i>Iris pseudacorus</i> . <i>Carex nigra</i> and <i>Hydrocotyle vulgaris</i> invariably present. Always in damp or wet areas, often adjacent to ditches. Typically on peaty loam soils where <i>Iris</i> may cover extensive areas.
Iris and Juncus (7)	K	Areas dominated by a mixture of <i>Juncus effusus</i> and <i>Iris pseudacorus</i> . Only a common habitat at Rubha Ardvule.
Maritime old damp fallow (8)	E	Occurred only at Rubha Ardvule where it was the predominant pasture type. Poorly drained areas of mineral soil in some ways resembling good blackland pasture (4) but lacking peaty soil species such as <i>Succisa pratense</i> . In other ways it resembles old damp fallow machair but lacking machair species such as <i>Potentilla anserina</i> . Dominant species are <i>Carex nigra</i> , <i>Holcus lanatus</i> and <i>Agrostis stolonifera</i> . Other common species are <i>Nardus stricta</i> , <i>Ranunculus acris</i> , <i>Prunella vulgaris</i> and <i>Rumex acetosella</i> .

Continued.

Table A.3: continued.

HABITAT TYPE (STAND-TYPE)	CODE	DESCRIPTION
Maritime dry pasture (9)	V	Occurred only at Rubha Ardvule. Well drained, short, old grassland close to the sea formed on poor mineral soil. Sward dominated by <i>Nardus stricta</i> , <i>Carex flacca</i> , <i>Prunella vulgaris</i> and <i>Festuca rubra</i> .
Old damp fallow machair (10,11)	E	All areas of closed sward machair grassland which may flood in winter and rarely experience drought summer. These areas have lain fallow for at least three, and usually more than ten, years. Dominant species are <i>Festuca rubra</i> , <i>Agrostis stolonifera</i> , <i>Holcus lanatus</i> , and <i>Potentilla anserina</i> . Other common species are: <i>Carex flacca</i> , <i>Poa pratensis</i> , <i>Vicia cracca</i> , <i>Plantago lanceolata</i> , <i>Trifolium repens</i> , <i>Ranunculus acris</i> and <i>Rhinanthus minor</i> . stand-types 10 and 11 are visually and floristically similar, the main difference appears to be that stand-type 10 is generally on wetter and less sandy ground and has usually lain fallow for longer.
Old dry fallow machair (12)	B	All areas of closed sward machair grassland which do not flood in winter and regularly experience drought in summer. Lain fallow for at least three years. Dominant species are the same as for old damp fallow with more emphasis on <i>Festuca rubra</i> . Other common species are: <i>Cerastium fontanum</i> , <i>Galium verum</i> , <i>Bellis perrenis</i> , <i>Honkenya peploides</i> , <i>Senecio jacobea</i> , and <i>Carex disticha</i> .
First year fallow machair (10,11,12)	F	All areas used for cereal cultivation in the previous year and in the process of being naturally re-colonised by machair grassland (dry or damp). Usually this habitat has about 50% bare ground.
Second year fallow machair (10,11,12)	S	Similar to first year fallow but one year older and therefore less bare ground, typically about 20%.

Continued.

Table A.3: continued.

HABITAT TYPE (STAND-TYPE)	CODE	DESCRIPTION
Mobile dunes (13)	A	All areas of sand dune hillocks. Dominated by <i>Festuca rubra</i> often in association with <i>Ammophila arenaria</i> . Other common species are: <i>Senecio jacobea</i> , <i>Achillea millefolium</i> , <i>Plantago lanceolata</i> , <i>Bellis perrenis</i> , <i>Lotus corniculatus</i> , <i>Carex disticha</i> , and <i>Galium verum</i> .
Reseeded machair (14)	U	All areas of close sward machair grassland which have been seeded with a commercial rye grass mixture. A very low species diversity is present which may include agricultural ruderals. Dominated by <i>Lolium perenne</i> . Other common species are <i>Agrostis stolonifera</i> , <i>Sagina procumbens</i> , <i>Juncus bufonius</i> <i>Alopecurus pratensis</i> and <i>Trifolium repens</i> .
Hay fields (2,4,3,10)	H	Any type of pasture allowed to grow tall and later cut for hay. Initially nearly always either good, or poor blackland pasture, but sometimes damp marsh or old damp fallow. Not recorded as hay until average height of vegetation reaches 15cm (ca. mid June).
Plough	P	All recently ploughed areas and very young cereals.
Short cereals	Q	Cereal crops from about three weeks after sowing up to when the plants are 15cm tall.
Tall cereals	C	Cereal crops over 15cm tall.
Track	T	All types of unmetalled track.
Seashore	X	All areas below maximum spring tide line.
Loch-edge	L	All types of loch shore, including areas exposed because of receding water levels.
Pool-edge	Z	The edge around any temporary freshwater pool including semi-permanent dune slack pools.
Ditch	D	All types of ditch.

Appendix B: Habitats used by Redshank for each activity at the northern study-sites.

NUMBER OF RECORDS					
HABITAT (CODE)	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	ROW TOTAL
Seashore (X)	0	3 0.4%	0	0	3 0.2%
Loch-edge (L)	27 21.3%	290 34.2%	21 3.1%	20 69.0%	358 21.2%
Pool-edge (Z)	3 2.3%	31 3.7%	0	0	34 2.0%
Ditch (D)	1 0.8%	49 5.8%	110 16.1%	1 3.4%	161 9.5%
Wet marsh (N)	3 2.3%	34 4.0%	110 16.1%	0	147 8.7%
Damp marsh (M)	23 18.1%	93 11.0%	148 21.7%	3 10.3%	267 15.8%
Hummock marsh (O)	0	11 1.3%	24 3.5%	0	35 2.1%
Iris beds (I)	0	0	17 2.5%	0	17 1.0%
Juncus pasture (J)	11 8.7%	6 0.7%	93 13.6%	0	110 6.5%
Iris & Juncus (K)	0	0	15 2.2%	0	15 0.9%
Hay field (H)	0	6 0.7%	26 3.8%	0	32 0.9%
Good blackland (G)	4 3.1%	142 16.7%	11 1.6%	1 3.4%	158 9.4%
Poor blackland (W)	14 11.0%	50 5.9%	17 2.5%	1 3.4%	82 4.9%
Rough blackland (R)	15 11.8%	28 3.3%	13 1.9%	2 6.9%	58 3.4%

continued.

Appendix B continued: Habitats used by Redshank for each activity at the northern study-sites

NUMBER OF RECORDS					
HABITAT (CODE)	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	ROW TOTAL
Old damp fall. (E)	22 17.3%	46 5.2%	31 4.5%	1 3.4%	100 5.9%
Old dry fall. (B)	2 0.2%	0	0	0	2 0.1%
2nd year fall. (S)	2 1.6%	12 1.4%	8 1.2%	0	22 1.3%
1st year fall. (F)	1 0.8%	6 0.7%	3 0.4%	0	10 0.6%
Bare plough (P)	0	1 0.8%	15 1.8%	0	16 0.9%
Short cereals (Q)	0	4 0.5%	24 3.5%	0	28 1.7%
Tall cereals (C)	0	1 0.1%	4 0.6%	0	5 0.3%
Reseeded machair (V)	0	20 2.4%	7 1.0%	0	27 1.6%
Total %	127 7.5%	849 50.3%	682 40.5%	29 1.7%	1687 100%

Appendix C: Habitats used by Redshank for each activity at Rubha Ardvule

HABITAT (CODE)	NUMBER OF RECORDS				TOTAL
	DISPLAY	FEEDING	CHICKS	RESTING	
Seashore (X)	8 19.4%	166 63.4%	3 2.9%	2 14.3%	179 42.4%
Loch-edge (L)	3 6.7%	53 20.2%	2 2.0%	6 42.9%	64 15.2%
Pool-edge (Z)	1 2.2%	3 1.1%	0	0	4 0.9%
Marsh (M,N)	4 8.9%	5 1.9%	1 1.0%	0	9 2.3%
Iris beds (I)	0	1 0.4%	37 36.3%	0	38 9.0%
Juncus (J)	1 2.2%	0	8 7.8%	0	9 2.1%
Juncus & Iris (J,I)	0	1 0.4%	16 15.7%	1 7.1%	18 4.3%
Maritime past. (U)	4 8.9%	2 0.8%	0	0	6 1.4%
Old damp fall. (E)	19 42.2%	24 9.2%	19 18.6%	4 28.6%	66 15.6%
Old dry fall. (B)	5 11.1%	6 2.3%	1 1.0%	1 7.1%	13 3.1%
Tall cereals (C)	0	0	15 14.7%	0	15 3.6%
Total %	45 10.7%	261 61.8%	102 24.2%	14 3.3%	422 100%

APPENDIX D: Habitats used by adult Dunlin for each activity at Stilligarry.

NUMBER OF RECORDS					
HABITAT (CODE)	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	ROW TOTAL
Seashore (X)	0	79 31.1%	0	0	79 18.1%
Loch-edge (L)	0	3 1.2%	0	6 54.5%	9 2.1%
Pool-edge (Z)	0	3 1.2%	0	0	3 0.7%
Damp marsh (M)	2 3.6%	15 5.9%	10 8.5%	0	27 6.2%
Old damp fall. (E)	41 74.5%	124 48.8%	89 76.1%	3 27.3%	257 58.8%
Old dry fall. (B)	0	2 .8%		0	2 .5%
1st year fall. (F)	1 1.8%	2 .8%	12 10.3%	0	15 3.4%
2nd year fall. (S)	6 10.9%	3 1.2%	3 2.6%	0	12 2.7%
Bare plough (P)	3 5.5%	20 7.9%	1 .9%	2 18.2%	26 5.9%
Short cereals (Q)	2 3.6%	3 1.2%	2 1.7%	0	7 1.6%
Total %	55 12.6%	254 58.1%	117 26.8%	11 2.5%	437 100%

APPENDIX E: Habitats used by Dunlin for each activity at Drimore Farm

NUMBER OF RECORDS					
HABITAT (COUNT)	DISPLAY	FEEDING	CHICK REARING	COMFORT ACTIVITY	ROW TOTAL
Seashore (X)	0	53 17.8%	0	0	53 9.2%
Loch-edge (L)	1 1.6%	10 3.4%	2 1.0%	21 84.0%	34 5.9%
Pool-edge (Z)	0	2 .7%	0	1 4.0%	3 .5%
Wet marsh (N)	4 6.6%	2 .7%	22 11.5%	0	28 4.9%
Damp marsh (M)	22 36.1%	55 18.5%	95 49.5%	0	172 29.9%
Hummock marsh (O)	25 41.0%	7 2.4%	39 20.3%	2 8.0%	73 12.7%
Old damp fall. (E)	3 4.9%	46 15.5%	22 11.5%	1 4.0%	72 12.5%
1st year fall. (F)	3 4.9%	62 20.9%	8 4.2%	0	73 12.7%
2nd year fall. (S)	2 3.3%	41 13.8%	3 1.6%	0	46 8.0%
Short cereals (Q)	1 1.6%	2 .6%	0	0	3 .5%
Reseeded mach. (V)	0	17 5.7%	1 .5%	0	18 3.1%
Total	61	297	192	25	575
%	10.6%	51.7%	33.4%	4.3%	100%

Appendix F: Habitats used by Ringed Plover at each study-site.

HABITAT (CODE)	N U M B E R O F R E C O R D S			
	DRIMORE FARM	RUBHA ARDVULE	STILLI- GARRY	ROW TOTAL
Seashore (X)	111 17.7%	171 47.8%	244 29.6%	526 29.1%
Loch-edge (L)	18 2.9%	20 5.6%	3 .4%	41 2.3%
Pool-edge (Z)	11 1.8%	3 .8%	1 .1%	15 .8%
Damp marsh (M)	11 1.8%	7 2.0%	3 .4%	21 1.2%
Blackland pastures (W,G)	17 2.7%	1 .3%	0	18 1.0%
Old damp fallow mach. (E)	39 6.2%	77 21.5%	165 20.0%	281 15.5%
Old dry fallow mach. (B)	29 4.6%	33 9.2%	44 5.4%	106 5.9%
2nd year fallow mach. (S)	140 22.4%	3 .8%	33 4.0%	176 9.7%
1st year fallow mach. (F)	211 33.7%	1 .3%	58 7.0%	270 14.9%
Bare plough (P)	6 1.0%	29 8.1%	162 19.7%	197 10.9%
Short cereals (Q)	3 .5%	4 1.1%	35 4.2%	42 2.3%
Tall cereals (C)	1 .2%	2 .6%	1 .1%	4 .2%
Reseeded machair (V)	9 1.4%	4 1.1%	0	13 .7%
Track (T)	20 3.2%	3 .8%	75 9.1%	98 5.4%
Total %	626 34.6%	358 19.8%	824 45.6%	1808 100%

Appendix G: Proportion of Redshank nests in each habitat

N U M B E R O F N E S T S					
HABITAT (CODE)	RUBHA ARDVULE	DRIMORE FARM	STILLI- GARRY	WEST GERINISH	TOTAL %
Ditch bank (D)	0	0	2 7.4%	0	2 1.0%
Wet marsh (N)	0	2 2.7%	0	3 6.7%	5 2.4%
Damp marsh (M)	0	10 13.5%	8 29.6%	14 31.1%	32 15.2%
Hummock marsh (O)	0	14 18.9%	0	11 24.4%	25 11.9%
Iris beds (I)	7 10.9%	0	0	0	7 3.3%
Juncus pasture (J)	27 42.2%	27 36.5%	0	1 2.2%	55 26.2%
Iris & Juncus (K)	23 35.9%	0	0	1 2.2%	24 11.4%
Hay fields (H)	0	0	0	1 2.2%	1 .5%
Wet blkcl.past. (W)	1 1.6%	6 8.1%	0	12 26.7%	19 9.0%
Rough blkcl.past. (R)	5 7.8%	10 13.5%	0	2 4.4%	17 8.1%
Old damp fallow (E)	1 1.6%	4 5.4%	15 55.6%	0	20 9.5%
1st year fallow (F)	0	1 1.4%	0	0	1 .5%
2nd year fallow (S)	0	0	2 7.4%	0	2 1.0%
TOTAL %	64 30.5%	74 35.2%	27 12.9%	45 21.4%	210 100.0%

Appendix H: Proportion of Dunlin nests in each habitat

HABITAT (CODE)	N U M B E R O F R E C O R D S		
	DRIMORE FARM	STILLI- GARRY	TOTAL %
Wet marsh (N)	6 7.7%	0	6 4.3%
Damp marsh (M)	24 30.8%	2 3.3%	26 18.8%
Hummock marsh (O)	28 35.9%	1 1.7%	29 21.0%
Juncus pasture (J)	2 2.6%	0	2 1.4%
Wet blkcl.past. (W)	1 1.3%	0	1 .7%
Rough blkcl.past. (R)	1 1.3%	0	1 .7%
Old damp fallow (E)	15 19.2%	46 76.7%	61 44.2%
Old dry fallow (B)	1 1.3%	8 13.3%	9 6.5%
2nd year fallow (S)	0	2 3.3%	2 1.4%
Sand dunes (A)	0	1 1.7%	1 .7%
TOTAL %	78 56.5%	60 43.5%	138 100%

Appendix I: Proportion of Ringed Plover nests in each habitat

HABITAT (CODE)	N U M B E R O F N E S T S			TOTAL %
	RUBHA ARDVULE	DRIMORE FARM	STILLI- GARRY	
Iris beds (I)	3 9.7%	0	0	3 2.0%
Iris & Juncus (K)	4 12.9%	0	0	4 2.6%
Old dry fallow (B)	0	2 4.2%	7 9.7%	9 6.0%
Old damp fallow (E)	13 41.9%	1 2.1%	29 40.3%	43 28.5%
2nd year fallow (S)	0	20 41.7%	3 4.2%	23 15.2%
1st year fallow (F)	1 3.2%	16 33.3%	5 6.9%	22 14.6%
Bare plough (P)	2 6.5%	2 4.2%	17 23.6%	21 13.9%
Short cereals (Q)	0	2 4.2%	1 1.4%	3 2.0%
Track (shingle) (T)	3 9.7%	5 10.4%	10 13.9%	18 11.9%
Seashore (shingle) (X)	5 16.1%	0	0	5 3.3%
TOTAL %	31 20.5%	48 31.8%	72 47.7%	151 100%

Appendix J: Rating system for attributes of nest-sites

Ground surface

- 1 Smooth surface; short sward, bare ground
- 2 Broken or nodular surface
- 3 Rough surface due to scraggy vegetation
- 4 Surface with well formed hummocks

Vegetation height

- 1 Bare ground
- 2 Bare ground and short vegetation (<5 cm.).
- 3 Short vegetation only.
- 4 Patchwork of short and medium vegetation (5-20cm.).
- 5 Medium height vegetation only.
- 6 Patchwork of short, medium and tall (>20cm.) vegetation.
- 7 Patchwork of medium and tall vegetation.
- 8 Tall vegetation only

The height of the vegetation refers to the maximum height of the bulk of the vegetation; usually there were a few shoots and flower heads that exceeded this general height but these are ignored.

Tussockiness

- 1 No tussocks or tufts of vegetation
- 2 Some small tussocks and tufts
- 3 A few well formed tussocks (<1 per m²)
- 4 Many well formed tussocks (>1 per m²)

Wetness of the ground

- 1 Very dry (dunes, shingle)
- 2 Dry, prone to summer drought
- 3 Damp, rarely dries out (typical soil)
- 4 Wet, soil wrings water (e.g. damp marsh)
- 5 Very wet, soil saturated, may be surface water (e.g. wet marsh)

Concealment of nest

- 1 Totally open, no side or top cover
- 2 Some side cover from vegetation or ground
- 3 Good all round side cover from vegetation
- 4 Good side cover and some top cover
- 5 Side and top cover totally obscures eggs.

continued

Appendix J continued: Rating system for attributes of nest sites

Camouflage of nest (Ringed Plover only)

- 1 Very poor (e.g. short green sward)
- 2 Poor (e.g. short sward with features)
- 3 Good (e.g. plough and recent fallow)
- 4 Very good (e.g. shingle)

Surface features (Ringed Plover only)

- 1 None
- 2 Stone or small rock, usually half buried.
- 3 Crumbling old cowpat
- 4 Piece of dry seaweed
- 5 Plastic litter.
- 6 Small patch of bare sand by rabbit hole

