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THE BREEDING ECOLOGY OF WHIMBREL (NUMENIUS PHAEOPUS) IN SHETLAND; WITH PARTICULAR REFERENCE TO THE EFFECTS OF AGRICULTURAL IMPROVEMENT OF HEATHLAND NESTING HABITATS

by

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A thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, May 1989.

ABSTRACT

The effect of re-seeding of heathland on the breeding ecology of whimbrel in Shetland was studied from 1986-1988, on five study sites located on the islands of Unst and Fetlar. A total of 36-45 pairs bred on these study sites in each year, and a large proportion of the breeding adults were individually colour ringed. Heathland was the main nesting habitat for whimbrel. Established pastures and areas ploughed or harrowed before re-seeding were avoided as nesting habitats, but some pairs nested on areas subjected only to surface re-seeding. Avoidance of ploughed or harrowed re-seeds was associated with changes in vegetation composition and structure, and such re-seeds lacked attributes important in the selection of nest-sites by whimbrel. Habitat change was less marked in surface re-seeds. Ploughed or harrowed re-seeds were used extensively as feeding habitat by adults during the pre-laying period, and evidence was obtained to indicate that re-seeding improved feeding conditions for adults. Measures of breeding success were positively correlated with egg volume, and negatively correlated with laying date. However, the improved feeding conditions on re-seeds for females prior to laying were unlikely to have provided major benefits for breeding success via effects on either egg volume or laying date. Approximately 30% of all broods studied used re-seeds at some stage prior to fledging. Although some broods did show preferences for this habitat, there was little evidence that this was associated with either, decreasing the risk of predation on chicks, or improving chick food supply. The survival of chicks to fledging did not vary according to the habitat-use of broods. Both nesting densities and productivity varied between study sites. The possibility that areas of heathland differ in their suitability as breeding habitat for whimbrel is considered, and the implications of this in assessing the effects of re-seeding heathland are discussed. Over the study period the overall production of fledglings from study sites was probably in excess of that required to balance adult mortality. This result is consistent with the current increase of the whimbrel population in Shetland.

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.

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The study was funded by N.E.R.C. in conjunction with N.C.C. and I am grateful to both organisations. The Department of Biological Sciences at Durham University provided facilities during the course of the study.

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Special thanks are due to the many crofters on Fetlar and north Unst who kindly allowed me access to their land. Considerable amounts of intensive work were carried out on land belonging to Jimmy Thomason, Neill Coutts, Frank and Peter Coutts, Nick Baisley, Will Henderson, and Bill Spence. The hospitality of the islanders made my time on Fetlar especially enjoyable and in this respect Grace Anderson and Lolly Brown deserve special mention.

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1. GENERAL INTRODUCTION

1.1 AGRICULTURAL IMPROVEMENT

This thesis is concerned with the effects of changes in agricultural practice in the Shetland Isles on the breeding ecology of one species of wading bird, the whimbrel (Numenius phaeopus).

Agricultural improvements and intensification have proceeded at a rapid rate in Britain and most other West European countries during the post war period (Gardner 1983, O'Connor and Shrubb 1986). The consequences of this for breeding bird populations are wide ranging and include the lethal, or sub-lethal, effects which resulted from the use of organo-chlorine pesticides in the 1960's (Newton 1979, Cooke et al. 1982) and the more subtle effects which result from habitat changes.

With regard to the effects of habitat change, to date the majority of studies have been concerned with breeding birds on relatively fertile farmland which is typical of lowland areas, and where notable habitat changes include losses of hedgerows and increases in cereal acreages (e.g. Bull et al. 1976, Moller 1983, Osbourne 1984, and O'Connor and Shrubb 1986). This reflects the fact that agricultural intensification, and hence habitat change, has proceeded most rapidly in the lowlands, and more specifically in those areas which are suitable for cereal production (O'Connor and Shrubb 1986). However, the extent of improvement in upland and northern regions of Britain, where agricultural activities are of a low intensity, has also increased in recent years (R.S.P.B. 1984, Fig.

1.1) and this is particularly so in several remote areas where Agricultural Development Plans have been initiated (e.g. the Western Isles and Northern Isles of Scotland). The habitats affected by these changes include marginal farmland (e.g. rough grazings) heathland and moorland; habitats which are of particular importance for many species of ground nesting birds (R.S.P.B. 1984, Galbraith et al. 1984, Peacock et al. 1985).

1.2 AGRICULTURAL CHANGES IN SHETLAND

Occurring at a latitude of 60° N the Shetland Islands experience a short growing season, with considerable exposure to winds and salt (Berry and Johnston 1980). These factors, together with the inherent infertility of most soils, result in crofting agriculture being the main land-use in Shetland. This consists almost exclusively of stock-rearing, primarily of sheep but also of beef cattle. To increase stocking densities heathland (which is used as common grazing land) can be re-seeded with high quality grass-seed mixtures (usually dominated by such species as; ryegrass, Lolium perenne; timothy grass, Phleum pratense; meadow grasses, Poa spp.; and clover, Trifolium repens). This is carried out when the common grazing is apportioned so that each crofter "fences off" the area of land which is equivalent to his share in the common grazing. Once apportioned the heathland is re-seeded by one of two basic methods:-

(i) Lime, grass-seed, and inorganic fertilisers are applied directly to the ground surface without any prior removal of the existing vegetation. This is known as surface re-seeding and is often carried out on land where the occurrence of such features as large stones or steep slopes prevent ready use of heavy machinery.

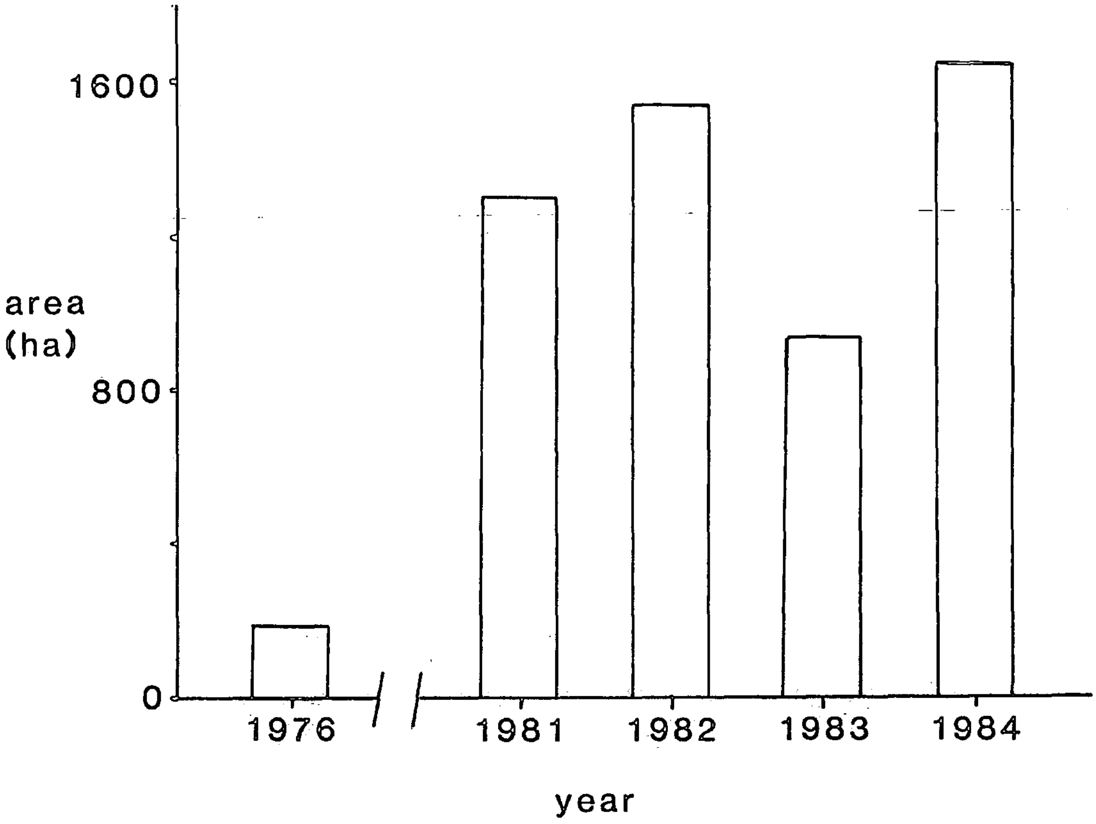
(ii) Prior to applying lime, grass-seed, and fertiliser the land is first ploughed or harrowed to remove the existing vegetation. This usually produces a higher quality of pasture than by surface re-seeding (see 4.2.3) and can allow stocking densities to be increased by a factor of x10 (various crofters, pers. comm.).

Following increases in the availability of grant aid to Shetland crofters (e.g. from the Crofters Commission and the Shetland Islands Council) the extent of re-seeding of heathland increased considerably in the years immediately prior to the start of this study; e.g. between 1957 and 1970, 3238ha of common grazing land were re-seeded (Berry and Johnston 1980) whilst in just four years from 1980 to 1984, 5422ha were apportioned for re-seeding (figures derived from Annual Reports of the Crofters Commission, after Richardson 1989), and see Fig. 1.1. Since breeding bird surveys (Herfst and Richardson 1982, and Fisher and Richardson 1983) indicated that heathland is the major nesting habitat for whimbrel in Shetland, re-seeding was considered to be a potential threat to the conservation of the Shetland population.

1.3 THE STUDY SPECIES AND ITS STATUS IN SHETLAND

The whimbrel breeds in the boreal and subarctic zones. Four subspecies are recognised of which it is the nominate subspecies (*N. phaeopus phaeopus*) that breeds in Britain (the breeding range of this subspecies extending from Iceland in the west to Western Siberia in

<u>Figure</u> <u>1</u>.<u>1</u>. Recent increases in the areas of common grazing land apportioned annually in Shetland. (Figures derived from the Annual Reports of the Crofters Commission, after Richardson 1989).



1600
800
0
area
(ha)
1976
1981
1982
1983
1984
year

the east - Cramp and Simmons 1983). Ringing recoveries of breeding birds from western Europe indicate that the main wintering areas for these populations occur in West, and possibly southern, Africa (e.g. Ferns et al. 1979).

Within Europe, Britain represents the southern limit of the species breeding range and as such breeding only occurs in northern areas of Britain. Based on the most recent survey data, Richardson (1989) estimates that Shetland currently holds 413 to 471 breeding pairs of whimbrel, representing c.95% of the total British population (small numbers also breed in Orkney, The Western Isles, and the north mainland of Scotland). It is evident that the Shetland population is of considerable conservation importance at a national level. Internationally this population is of much less importance, as the estimated breeding populations for the Faeroe Islands and Iceland are 3000 and 200000 pairs respectively (Piersma 1986).

The abundance of breeding whimbrel in Shetland has fluctuated markedly in the past. Based on the anecdotal records of mid. to late 19th Century naturalists (reviewed by Richardson 1989) the whimbrel appears to have been "numerous" in Shetland in the mid. 1800's, but to have become "scarce" by the late 1800's. In the early 1950's Venables and Venables (1955) estimated the population to be 50-55 pairs, whilst by the 1970's the population was thought to number c.150 pairs (Sharrock 1976). Comparisons with the current estimate indicate a considerable increase, which has been occurring since at least the 1950's. The increase may be due in part to the more extensive coverage of land area in the latest surveys but monitoring of numbers on two specific sites in Shetland demonstrates increases of a similar magnitude over the same period (Richardson 1989). Several possibilities for the cause of the current increase (e.g. changes in the abundance of potential competitor species and changes in climate) are discussed by Richardson (1989) but little, or no, evidence exists to support any of these. Further, the causal factors may occur outwith Shetland; e.g. improved conditions in other breeding grounds or in wintering areas could provide a "surplus" of birds to colonise Shetland.

1.4 SPECIFIC AIMS

The main aims of this study were to determine the ecological requirements of whimbrel so that the effects that further re-seeding of heathland would have on the whimbrel population could be predicted. Fieldwork was carried out in the months of April to August, 1986-88, with the following specific aims:-

(i) To identify whether re-seeding of heathland results in a loss of suitable nesting habitat for whimbrel and, if so, the changes in vegetation structure and composition which are responsible for this.

(ii) To determine whether whimbrel make use of re-seeds in other respects (e.g. as feeding sites for adults and as chick-rearing habitat) and, if so, the extent to which this could benefit breeding success.

(iii) To determine whether different breeding sites vary in quality, as assessed by nesting densities and breeding success of whimbrel, and, if so, to identify the cause of these differences and the implications this has for assessing the effects of re-seeding.

(iv) To obtain information on other, more general, aspects of the breeding ecology of this species (aspects such as site fidelity were likely to be of importance in interpreting the results from aims (i) to (iii); also few breeding studies have previously been carried out on whimbrel, and none in Britain).

2. STUDY AREAS

Within Shetland the main concentrations of breeding whimbrel occur in the Northern Isles, namely Fetlar and Unst (Richardson 1989). On both islands considerable re-seeding had occurred prior to the start of the study and whimbrel were known to nest on a range of different heathland types. For these reasons it was on the Northern Isles that this study was carried out, using the five study sites shown in Fig. 2.1. It was thought that re-seeding would also occur on certain sites during the course of the study. However, just prior to the start of fieldwork in 1986 management agreements were reached between the crofters and the Nature Conservancy Council (N.C.C.) and consequently re-seeding occurred to only a limited extent during the study (see 4.2).

In addition to heathland and re-seeds, study sites also included established pasture and mire habitats. Established pastures were the main constituent of the enclosed land which occurs around the crofting townships and were often the result of past improvement. They were distinguished from the recently re-seeded habitats on the basis of their greater age. At the start of the study in 1986 the most recent field on any study site which was classed as an established pasture had been improved approximately 12 years previously (according to the crofter concerned) whilst the oldest re-seed had first been improved in 1982.

Mires were unimproved habitats present in areas of study sites which were poorly drained and/or where a high water table occurred. In such habitats plant species typical of heathland (e.g. *Calluna* vulgaris and Erica spp.) were scarce or absent and the vegetation was characterised by such species as Juncus articulatus, J. effusus, Eriophorum angustifolium, and Sphagnum spp. (detailed descriptions and classification of such communities are provided by Lewis 1977, and Slingsby et al. 1983). Being natural, rather than artificial, the boundaries between mires and heathland were not discrete and some subjectivity was necessarily involved in plotting these onto maps. However, the locations and extent of mires as determined by mapping in the field coincided closely with those ascertained by using 1967 aerial photographs of study sites (obtained from Shetland N.C.C.).

Since the basic heathland types on which study sites were located showed considerable variation, details of factors determining the nature of these heathlands are given below. (Information on underlying geology has been derived from Mykura 1976, and for soil type from Dry and Robertson 1982):-

Site 1:- heathland on this site forms part of the main area of Fetlar heath which is located on the ultra-basic serpentine rock. Soils consist of magnesian gleys with some brown magnesian soils. Unlike areas of serpentine debris, which are almost devoid of vegetation, serpentine heaths on Fetlar and Unst are usually more fertile than other heaths on these islands. Such heathland is characterised by low levels of calcium but has a high base status due to the high magnesium content (Slingsby et al. 1983).

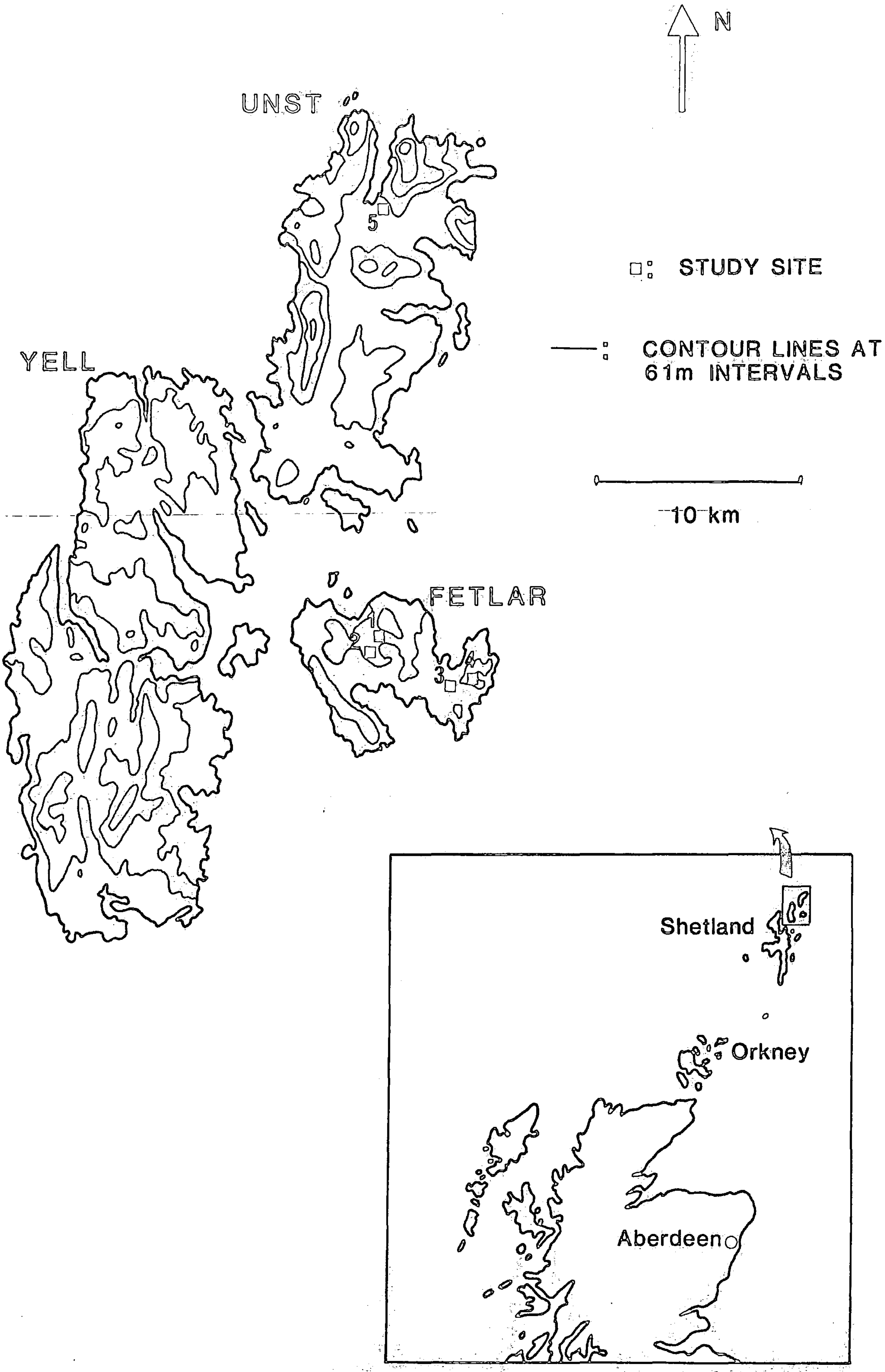
Site 2 :- although almost adjacent to site 1, the heathland on this site is markedly different. It is located on weakly metamorphosed argillaceous rocks and soils consist of peaty gleys, peaty podzols, and some peat.

Site 3 :- underlying rock and soil types are as for site 1. However, this site is located on a smaller area of serpentine heath, separated from the main Fetlar block by areas of improved land.

Site 4:- located on a relatively large block of conglomerate rock which includes quartzite, granite, and some basic igneous rock. Soils in this area are comprised mainly of peaty podzols and peaty gleys.

Site 5:- occurring on the relatively large geological block which forms the northern hills of Unst, the main rock types are schists and flags. Soils comprise peat and associated soils but, having been used for peat cuttings in the past, areas of deep peat are not present.

Figure 2.1. The location of study sites.

N
UNST
YELL
FETLAR
1
2
3
4
5
□: STUDY SITE
——: CONTOUR LINES AT 61m INTERVALS
10 km
Shetland
Orkney
Aberdeen

3. GENERAL METHODS OF DATA ANALYSIS

In carrying out the analysis of data in this study Sokal and Rolhf (1969) and Norusis (1983) were referred to for statistical methods. Data were entered into the mainframe computer at Durham University and most analyses were carried out using the SPSSX statistical package. Parametric tests have been used where possible but in cases where the data violated the necessary assumptions nonparametric tests have been used. Pooled variance t-tests have been used in all cases, except where the two population variances appear to differ (ie. $p \leqslant 0.05$ for the F-value) and in such cases a t-test based on a separate variance estimate has been calculated (such cases are indicated in the text). All 2x2 X^2 tests have been calculated using Yates' correction factor and all probability values given for statistical tests are 2-tailed unless stated otherwise.

Throughout the text results are referred to as being significant or not. This concerns statistical significance at the 5% level.

4. FACTORS DETERMINING THE DISTRIBUTION AND SELECTION OF NEST-SITES WITHIN YEARS

4.1 METHODS

4.1.1 Preparation of Study Sites

Due to the fact that the heathlands on study sites were devoid of landmarks a grid system was established on the most extensive areas (ie. on site 1, site 3, and parts of sites 2 and 5). Prior to the arrival of whimbrel on the breeding grounds in late April each year, flagged canes (0.3 to 0.6m high) were set into the ground at 200m intervals across the heathland area. These were subsequently used as nest markers, allowing nests to be marked at random distances and directions, and therefore preventing the possibility that marking would cause artificially high predation rates (e.g. Picozzi 1975). Apportionments (ie. fenced areas which had been improved) and some areas of heathland on sites 2, 4, and 5, did not require gridding due to the presence of fence lines and other landmarks which could be used for nest marking.

4.1.2 Distribution of Nests

Attempts were made to locate all nests within the study sites in each year of the study.

After the onset of incubation whimbrel become vigorous in their defence of the nest, with the incubating adult usually leaving the nest to alarm-call at any intruder who approaches the nesting territory. Most nests were found by locating such "active" birds and subsequently watching the incubating adult return to the nest from a position of cover (usually a hide or vehicle). A few birds were less conspicuous in their behaviour but any areas within which no nests had been located were re-checked throughout the incubation period using a combination of observations and ground searches.

To test for differential habitat-use, the area of each habitat which had been searched for nests was calculated. This allowed the observed distribution of nests between habitats to be compared with that which was expected on the basis of the relative area of each habitat which was available.

After studies of whimbrel breeding success had been completed for that year (see 6.1) each nest was revisited. Using a prismatic compass and 50m tape, bearings and distances were measured to at least one (usually two) landmark which occurred on the O.S. 1:10000 maps for the site, or to grid markers where no other landmarks could be used. Nest positions were later plotted onto 1:3500 scale maps (enlarged from the O.S. 1:10000 maps) and the nearest neighbour distances were measured for each nest (positions of any relays were omitted from these measurements).

4.1.3 Nest-Site Selection and the Effects of Re-seeding on the Structure and Vegetation Composition of Habitats

For each nest located in 1986 and 1987 the plant species or taxa, on which it occurred, and whether it was on a hummock or not, were recorded. Identification of a hummock was considered to be a somewhat subjective process during this work in 1986, so that in 1987 measurements were taken to quantify hummock sites. At each nest in

1987 the maximum height of the edge of the nest cup above the ground within a 0.5m distance was measured to the north, south, west, and east of the nest cup. Nests which were higher than the surrounding ground for at least two of these measurements were classed as being on hummocks.

In late July and early August 1987 the same information was recorded for a number of random points on heathland and re-seed habitats. Heathland points were selected such that the proportion of total points from any one site was approximately equal to the proportion of total nests on that site. Re-seed points were taken from five different fields (three being surface re-seeds and two being ploughed or harrowed re-seeds). In the two most recent surface re-seeds, and in another apportionment which was surface re-seeded in June 1987, sampling was repeated in 1988.

Since this sampling was carried out after the main period of vegetation growth it could not be used to assess differences in the vegetation heights of habitats when whimbrel selected their nesting areas (ie. in early to mid. May). During the pre-laying and incubation periods no time was available for vegetation sampling due to other priorities of the study (see 6.1 and 7.1). A series of three photographs taken from late April to mid. May in 1987 at each of seven permanent heathland and four permanent re-seed locations revealed little, or no, change in vegetation heights over this period. In each photograph two canes, placed 1m apart and marked at 5cm intervals, were used to assess vegetation heights at the location, and each location was photographed from the same direction on each occasion. It was therefore assumed that measurements of vegetation heights made in late April, just prior to the arrival of whimbrel, could be taken to represent the situation which existed at laying in early to mid. May.

Vegetation heights were measured during this period in 1987, selecting a number of random points from heathland on three sites (ie. 1, 2, and 3) and from two re-seeded fields, representing the two different types of re-seed. The number of points measured on each heathland site was approximately proportional to the area of heathland on that site.

4.2 RESULTS

4.2.1 The Distribution of Nests in Relation to Habitat-Type

In each year of the study heathland provided the major nesting habitat for whimbrel, holding 89% of all nests found (Table 4.1). The observed distribution of nests between habitats differed significantly from that which was expected on the basis of the availability of each habitat (Table 4.2). Following the methods of Neu et al. (1974), 95% confidence intervals were calculated for the proportion of all nests which were found in each habitat. Comparing these with the expected proportion (ie. the proportion of the total area searched which was represented by each habitat) demonstrated that heathland held significantly more nests than predicted by its availability (Table 4.2). Significantly fewer nests than predicted by availability occurred in both ploughed or harrowed re-seeds and established pastures.

Table 4.1. The distribution of whimbrel nests in relation to habitat-type

		HABITAT-TYPE				
YEAR		HEATHLAND	MIRE	SURFACE RE-SEED	PLOUGHED/HARROWED RE-SEED	ESTABLISHED PASTURE
	NO. OF NESTS	34+	2	0	0	0
1986	APPROX. AREA SEARCHED (ha)	220	20	15	23	29
	NO. OF NESTS	37+	0	4	0	0
1987	APPROX. AREA SEARCHED (ha)	250	20	20	33	34
	NO. OF NESTS	40	2	4+	2+	0
1988	APPROX. AREA SEARCHED (ha)	230	20	33	42	34

Notes: +these figures include 2 nests from a single pair which re-laid in the same habitat, after failure of the first clutch.

Table 4.2. Occurrence of whimbrel nests in relation to habitat availability

HABITAT	AREA SEARCHED OVER 3 YEARS (ha)	PROPORTION OF TOTAL AREA SEARCHED (P)	TOTAL NO. OF NESTS OVER 3 YEARS	EXPECTED NO. OF NESTS+	PROPORTION OF NESTS IN EACH HABITAT	95% CONFIDENCE INTERVAL ON PROPORTION OF OCCURRENCE
HEATHLAND	697	0.683	111	85	0.888	0.816-0.960
MIRE	60	0.059	4	7	0.032	0.008-0.072
SURFACE RE-SEED	68	0.067	8	9	0.064	0.008-0.120
PLOUGHED/HARROWED RE-SEED	98	0.096	2	12	0.016	0.000-0.045
ESTABLISHED PASTURE	97	0.095	0	12	0	0-0
TOTAL	1020		125	125		

The difference between the observed and expected numbers of nests in each habitat is significant; $X^2 = 29.6$, d.f. = 4, $p<0.001$.

Notes: +calculated by multiplying P for each habitat by the total number of nests (i e. 125)

4.2.2 Nest-Site Selection

Of the 77 nest-sites studied, 75% were located on *Calluna vulgaris*, and no more than 7% occurred on any other plant species, or combination of species (Table 4.3). Approximately 80% of nests were defined as being located on hummocks. Overall, 64% of nests occurred on both, and 92% on at least one, of these attributes. Selection for these attributes was tested by comparing the results for nests with those from the random points taken on heathland. For both *C. vulgaris* and hummocks, a significantly greater proportion of nest-sites occurred on the attribute than did random heathland points (Figs. 4.1 and 4.2) demonstrating that selection did occur in both cases.

The heights of nests in 1987 and of random heathland points located on hummocks were compared by calculating the average of; (i) the maximum; and (ii) the mean; of all four measurements taken at each hummock. By both calculations nests occurred on hummocks which were significantly higher than those selected randomly on heathland (Table 4.4).

4.2.3 The Effects of Re-seeding on the Structure and Vegetation Composition of Habitats

The abundance of hummocks on different sites, or fields, within any one of the three habitat-types sampled did not differ significantly (ie. for heathland, $X^2=3.02$, d.f.=4, $p>0.10$; surface re-seeds, $X^2=4.76$, d.f.=3, $p>0.10$; ploughed or harrowed re-seeds, $X^2=0.13$, d.f.=1, $p>0.10$). Data from the different sites or fields were therefore clumped to test for between habitat differences.

Table 4.3. Vegetation on which whimbrel nest-sites were located

PLANT SP./TAXA ON WHICH NEST LOCATED	% OF NESTS (n=77)
Calluna vulgaris	75.3
C. vulgaris & others	3.9
Gramineae spp.	5.2
Gramineae spp. & others	6.5
Juncus squarrosus	3.9
Rhacomitrium spp.	2.6
Rhacomitrium spp. & Empetrum nigrum	1.3
Juncus effusus	1.3

Figure 4.1. The proportions of whimbrel nests and of randomly selected heathland points located on *Calluna vulgaris*.

$X^2=26.5$, d.f.=1, $p<0.001$.

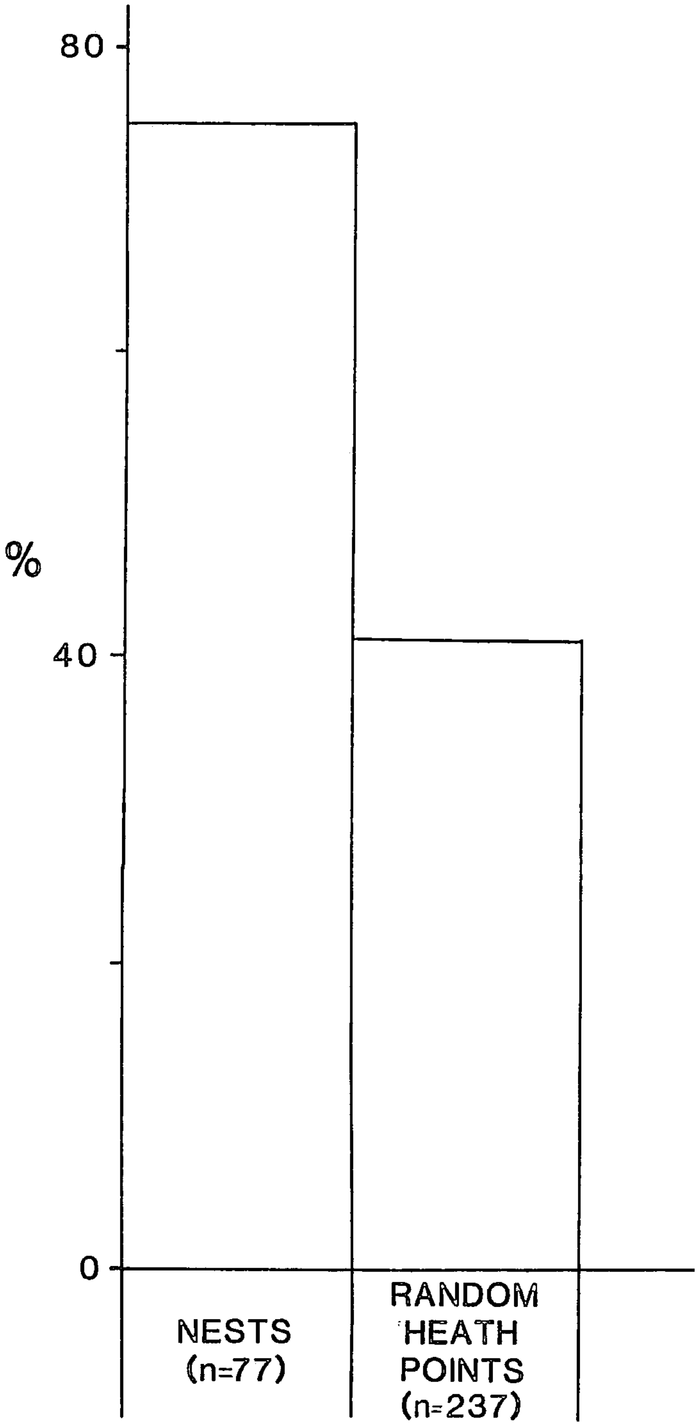

80
%
40
0
NESTS (n=77)
RANDOM HEATH POINTS (n=237)

Figure 4.2. The proportions of whimbrel nests and of randomly selected heathland points located on hummocks.

$X^2=61.2$, d.f.=1, $p<0.001$.

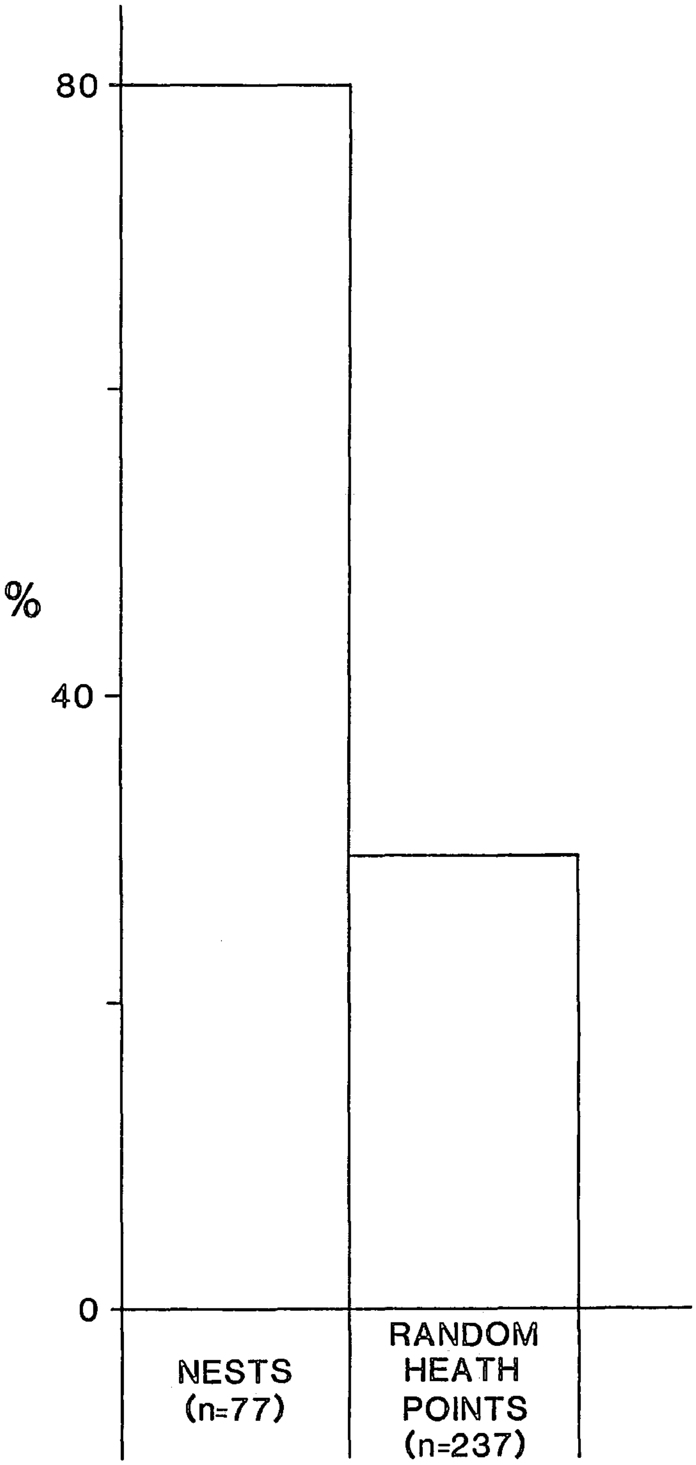

80
%
40
0
NESTS
(n=77)
RANDOM
HEATH
POINTS
(n=237)

Table 4.4. Comparisons between the heights of hummocks used as whimbrel nest-sites and randomly located hummocks on heathland

	HUMMOCK HEIGHT (mm)			
	MAXIMUM		MEAN	
NEST-SITES (n=34)	153.2±7.1	t=3.51***	112.0±6.8	t=3.09**
RANDOM HUMMOCKS (n=70)	121.9±5.2		89.5±3.8	

Note: heights are mean ± 1S.E. (see text for details of calculation)

**p<0.01 ***p<0.001

Figure 4.3. The proportions of randomly selected points located on hummocks on, heathland, surface re-seeds, and ploughed or harrowed re-seeds.

Differences:-

(i) Heathland vs. surface re-seeds;

$X^2=0.1$, d.f.=1, $p>0.10$.

(ii) Heathland vs. ploughed/harrowed re-seeds;

$X^2=13.2$, d.f.=1, $p<0.001$.

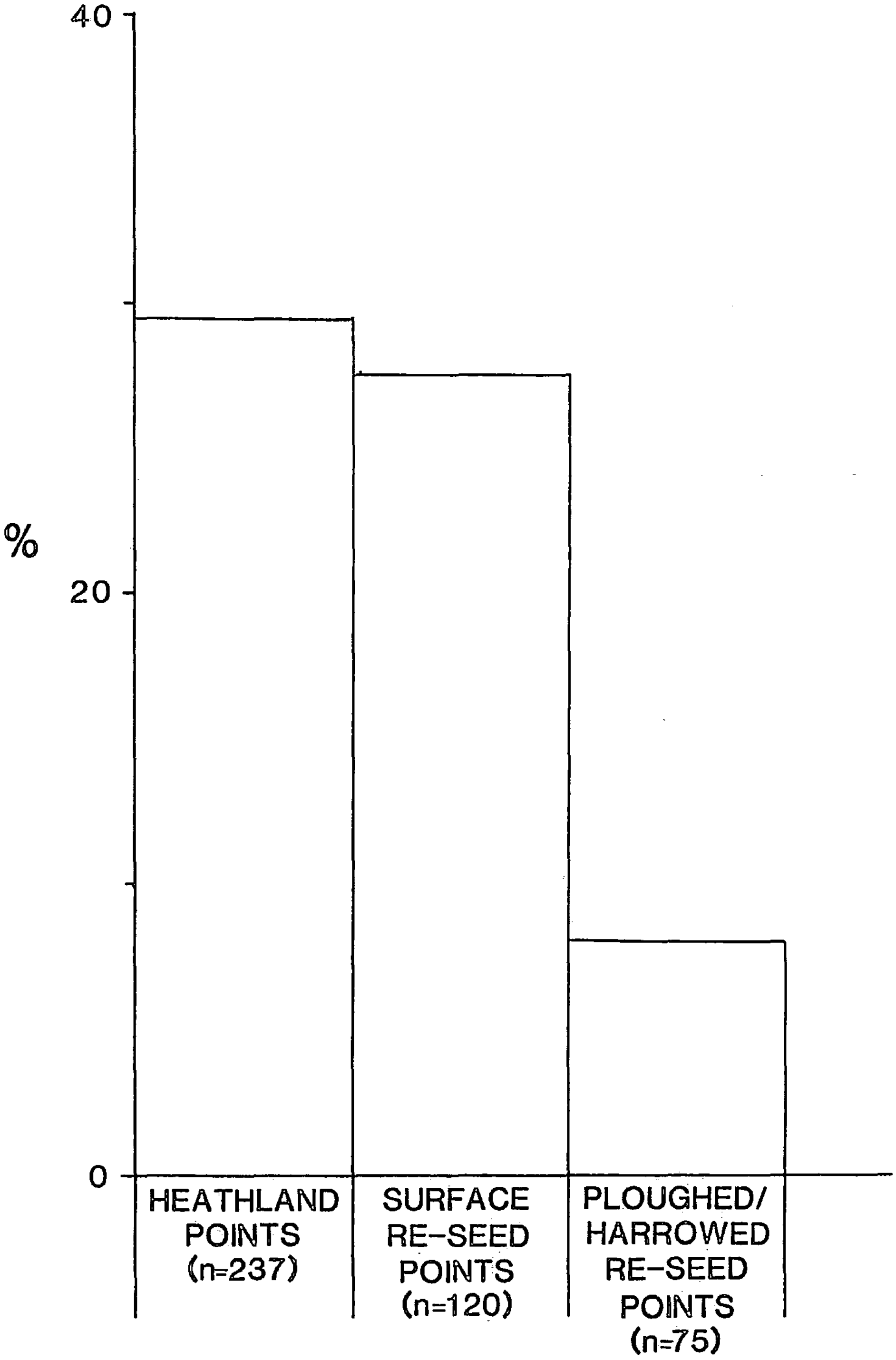

40
%
20
0
HEATHLAND POINTS (n=237)
SURFACE RE-SEED POINTS (n=120)
PLOUGHED/ HARROWED RE-SEED POINTS (n=75)

Table 4.5. Comparisons between the heights of randomly selected hummocks on heathland, surface re-seeds and ploughed/harrowed re-seeds

		HUMMOCK HEIGHT (mm)					
		MAXIMUM			MEAN		
HEATHLAND	(n=70)	121.9±5.2	t=0.35 NS	t=2.34*	89.5±3.8	t=0.90 NS	t=2.70**
SURFACE RE-SEEDS	(n=33)	125.1±7.2			83.2±6.1		
PLOUGHED/HARROWED RE-SEEDS	(n=6)	80.0±9.3			53.7±4.1		

Note: heights are mean ± 1 S.E. (see text for details of calculation)

NS $p>0.10$ *$p<0.05$ **$p<0.01$

Hummocks were significantly more abundant on heathland than on ploughed or harrowed re-seeds but there were no significant differences between heathland and surface re-seeds in this respect (Fig. 4.3). Data from the three most recent surface re-seeds showed no significant changes in the abundance of hummocks between 1987 and 1988. Hummocks were also significantly higher on heathland than on ploughed or harrowed re-seeds, but again no differences occurred between heathland and surface re-seeds (Table 4.5).

Significant differences did occur in the abundances of certain plant species, or taxa, between the sites, or fields, within each habitat-type (e.g. for *Carex* spp. on heathland, $X^2=25.50$, d.f.=4, $p<0.001$; for *C. vulgaris* on surface re-seeds, $X^2 =23.50$, d.f.=3, $p<0.001$; and for *Trifolium repens* on ploughed or harrowed re-seeds, $X^2 =9.03$, d.f.=1, $p<0.01$). Therefore differences in vegetation composition were assessed by comparing the data for each improved field with that for the heathland on the same study site. Re-seeds re-sampled in 1988 were included in these analyses so that comparisons were made for the apportionment over two consecutive years, as well as with the adjacent heathland.

Since the aim of these comparisons was to detect broad changes in vegetation composition, only those plant species, or taxa, which occurred in at least 10% of the random points taken in either of the sites involved in each comparison were considered.

Fundamental differences in vegetation composition occurred between heathland and both of the ploughed or harrowed re-seeds which were sampled (Table 4.6). *C. vulgaris* was almost absent from these re-seeds, whilst grasses (Gramineae spp.) and *T. repens* increased considerably (*T. repens* being absent from all heathland sites). The increase in the abundance of grasses was also associated with a change in species composition, though this was not measured. Typical heathland grasses such as, *Nardus stricta*, *Molinia caerula*, and *Festuca* spp. were replaced by such species as, *Lolium perenne* and *Phleum pratense*. Other changes included a loss of sedges (Carex spp.) from the re-seeds, whilst *Juncus squarrosus* had become abundant in one re-seed.

Although both of these ploughed or harrowed re-seeds were three years old at the time of sampling it is evident from Fig. 4.4 that these changes in vegetation composition can occur within a year of re-seeding by this method.

Only the oldest surface re-seed sampled (ie. four years at the time of sampling) showed differences with heathland similar to those recorded for ploughed or harrowed re-seeds (Table 4.7). For the other three surface re-seeds the only significant difference with heathland was a greater abundance of grasses in the most recent of the two fields on site 5. None of the changes recorded for these three fields between 1987 and 1988 were significant.

There were no significant differences between the vegetation heights measured on three heathland sites. Overall, vegetation heights for heathland were not significantly different from those measured in the two re-seeds (Table 4.8).

Table 4.6. Differences in abundance of the main vegetation components on heathland and individual ploughed/harrowed re-seed fields on two sites

	% OCCURRENCE			
	SITE 1		SITE 4	
PLANT SP. OR TAXA	HEATH (n=77)	3-YEAR RE-SEED (n=40)	HEATH (n=77)	3-YEAR RE-SEED (n=35)
Calluna vulgaris	32	2	47	0
	X^2_1 = 12.0***		X^2_1 = 18.1***	
Juncus squarrosus	0	15	-	-
	X^2_1 = 9.3**			
Gramineae spp.	17	47	27	37
	X^2_1 = 10.9***			
Carex spp.	31	0	-	-
	X^2_1 = 13.8***			
Trifolium repens	0	22	0	46
	X^2_1 = 15.8***		X^2_1 = 15.8***	
Bare ground	6	10	-	-

**p<0.01 ***p<0.001 (other differences are not significant)

Notes: - denotes sites in which the plant sp./taxa occurred with a frequency of <10% in all plots.

Figure 4.4. Photographs of; a) heathland being harrowed, prior to re-seeding in April 1987; and b) the same apportionment one year later, in May 1988.

a)

b)

Table 4.7. Differences in abundance of the main vegetation components on heathland and individual surface re-seed fields on three sites

% OCCURRENCE

	SITE 2		SITE 3			SITE 5			SITE 5		
		4-YEAR		RE-SEED			RE-SEED			RE-SEED	
PLANT SP./ TAXA	HEATH (n=40)	RE-SEED (n=40)	HEATH (n=30)	0-YEARS (n=42)	1-YEAR (n=30)	HEATH (n=60)	1-YEAR (n=25)	2-YEARS (n=25)	HEATH (n=60)	2-YEARS (n=25)	3-YEARS (n=25)
Calluna vulgaris	37	2	43	40	23	50	36	32	50	52	56
	X_1^2 = 14.7***										
Empetrum nigrum	-	-	-	-	-	13	8	4	13	12	0
Juncus squarrosus	2	25	-	-	-	5	12	8	5	8	20
	X_1^2 = 6.7**										
Gramineae spp.	17	40	23	24	40	3	28	52	3	12	12
	X_1^2 = 3.9*					X_1^2 = 8.8**					
						X_1^2 = 25.5***					
Carex spp.	15	0	-	-	-	-	-	-	-	-	-
	X_1^2 = 4.5**										
Trifolium repens	0	27	-	-	-	-	-	-	-	-	-
	X_1^2 = 10.5**										
Bare ground	12	2	-	-	-	-	-	-	7	16	12

*p<0.05 **p<0.01 ***p<0.001 (other differences are not significant)

Notes: - denotes sites in which the plant sp./taxa occurred with a frequency of <10% in all plots.

Table 4.8. Vegetation heights in heathland and re-seeded habitats prior to the laying period of whimbrel

HABITAT	n	AVERAGE VEGETATION HEIGHT (mm) ± 1 S.E.		
HEATHLAND	60	83±6	Ƶ = 0.12 NS	Ƶ = 0.24 NS
SURFACE RE-SEED	20	104±21		
PLOUGHED RE-SEED	20	107±22		

NS p>0.10

Notes: Ƶ - values are calculated from the Mann-Whitney test.

4.2.4 Nesting Density and Dispersion

Due to the differential use of habitats as nesting areas, to calculate nesting densities areas of non-heathland habitat which were present on study sites were excluded, unless;

(i) nests occurred in these areas; or

(ii) the area occurred within (rather than adjacent to) a nesting area, such that it lay between two, or more, areas of heathland in which nests were present.

The reliability of the density calculations are dependent on the efficiency with which nests were found. It is possible that a small proportion of pairs remained unrecorded each year, particularly if they failed during laying or in the early stages of incubation. However, most nests were found within a few days of first laying and nest losses were relatively low, so that this possibility is unlikely (see also 6.1.1).

Nesting densities were consistently highest on site 1., where nests were dispersed in a significantly regular pattern in each year (Table 4.9). Nest distributions on other sites were not consistently regular in each year, and on site 5 the distribution did not differ significantly from a random pattern in any year. Thus, despite the higher nesting densities on site 1, nearest neighbour distances were not significantly less than on other study sites.

Table 4.9. Nesting densities and nest dispersion on study sites

SITE	YEAR	NO. KNOWN PAIRS	NESTING AREA (ha)	DENSITY (NO. PAIRS/100ha)	MEAN NEAREST NEIGHBOUR DISTANCE; r(m) ± 1 S.E.	EXPECTED NEAREST[b] NEIGHBOUR DISTANCE; E(r)	R(=r/E(r))[c]
1.	1986	[a]14	65	21.4	155±22	108	1.43**
	1987	14	71	19.7	175±25	113	1.55***
	1988	13	71	18.3	189±28	117	1.61***
2.	1986	5	40	12.5	185±12	-	-
	1987	[a]7	61	11.4	226±60	148	1.52**
	1988	7	61	11.4	185±10	148	1.25NS
3.	1986	5	40	12.4	143±36	142	1.01NS
	1987	6	44	13.5	213±43	136	1.56***
	1988	8	44	18.1	87±17	118	0.74NS
4.	1986	3	28	10.8	295±67	-	-
	1987	3	28	10.8	290±94	-	-
	1988	4	28	14.4	321±86	-	-
5.	1986	9	82	11.0	157±30	151	1.04NS
	1987	[a]12	87	13.7	140±25	135	1.04NS
	1988	13	87	14.9	124± 8	130	0.95NS

NS p>0.05 **p<0.01 ***p<0.001

Notes: a. Figures include a single pair for which the nest was not found. In 2 cases pairs were found with young chicks, in the third the nest was observed being predated.

b. This is calculated following the method of Clark and Evans (1954); i.e. $E(r) = \frac{1}{2\sqrt{density}}$

c. R is a measure of departure from a random distribution and can vary from 0 to 2.149. Values of >1 indicate a regular dispersion, and of <1, aggregation. Significance levels are calculated using a standardised normal variate, as in Clark and Evans (1954). No measures of dispersion are made for site 2 in 1986 or site 4 (all years) due to small sample sizes.

Within any one year, differences between sites in mean nearest neighbour distances are significant only in 1988 (F = 7.32, d.f. = 4,40, p<0.001). This difference is due to significantly greater nest spacing at site 4 than at sites 3 and 5.

Between years, mean nearest neighbour distances differed only at site 3 (F = 4.50, d.f. = 2, 16, p<0.05). This difference is due to significantly greater spacing in 1987 than in 1988.

4.3 DISCUSSION

4.3.1 Re-seeding and the Distribution of Nests

Results from this study demonstrated that both of the improved grassland habitats present on study sites (ie. ploughed or harrowed re-seeds and established pastures) were avoided as nesting areas by whimbrel. Similar results have also been obtained from extensive surveys throughout Shetland (carried out at times to coincide with the main incubation period of whimbrel) in which less than 1% of 353 locations of whimbrel pairs occurred on improved grasslands of any type (Richardson 1989).

Despite these results, evidence that re-seeding actually displaces whimbrel from a nesting area is lacking, and during this study the opportunity did not arise to determine whether or not displacement occurred following re-seeding with prior ploughing or harrowing. In this respect the fact that adult whimbrel are highly faithful to their nesting territories between years (see 5.2.2) may be important, and this could cause birds to continue nesting in areas even after detrimental habitat changes have taken place.

4.3.2 Factors Causing the Avoidance of Ploughed or Harrowed Re-seeds

The fact that ploughed or harrowed re-seeds were avoided as nesting habitat, whilst surface re-seeds were not, was associated with the extent of the habitat change following re-seeding. In particular, within ploughed or harrowed re-seeds there was a considerable loss of attributes important in nest-site selection; ie. *C. vulgaris* and hummocks. Of the few hummocks which remained in these re-seeds, their suitability as nest-sites was probably reduced since they were lower in height than those on heathland; whimbrel having selected nest-sites on hummocks which tended to be higher than average.

Both C. vulgaris and hummocks were retained to a greater degree within surface re-seeds. However, within the oldest surface re-seed (ie. four years old at the time of sampling) C. vulgaris had virtually disappeared, and in other surface re-seeds this species had begun to "die-off", so that only the woody stems remained in places. Such gradual "dying-off" of C. vulgaris was presumably a result of liming, though the increased grazing pressures which follow re-seeding may also have contributed. Thus, it is predicted that with time, noticeable declines in the abundance of C. vulgaris will occur in most of these surface re-seeds.

Extensive use of hummocks as nest-sites by whimbrel has been noted previously (e.g. in Iceland - Gudmundsson 1957, and at Churchill, Manitoba - Skeel 1976, 1983). One possible advantage of nesting on hummocks in such open habitats is that visibility for the incubating adult will be increased, thus allowing earlier detection of approaching predators. Selection for this attribute may also be important in keeping the eggs on dry ground if the surrounding area is poorly drained (see Skeel 1976).

The use of C. vulgaris as a nest-site will be a less widespread occurrence since this species is not abundant throughout the whimbrels' breeding range (e.g. see Williamson 1946, and Dementiev et al. 1969, for descriptions of the vegetation on which nests are located in other areas). Selection for C. vulgaris in this study was probably due to certain structural attributes possessed by this plant species (rather than selection for the plant species per se) and, in part, possibly because it often grew in discrete clumps, thereby creating hummocks.

In addition to the scarcity or absence of attributes important in nest-site selection, other factors which may have caused whimbrel to avoid nesting in ploughed or harrowed re-seeds include:-

(i) Increased risk of nest predation:- re-seeding with prior ploughing or harrowing produced a relatively uniform habitat within which both an incubating whimbrel, and its eggs, were likely to be more visible than on the more heterogeneous heathland. This could increase the liklihood of nest detection by predators and hence lead to increased rates of nest predation. Preferences for more heterogeneous nesting habitats (as assessed by differences in nesting densities) have been noted in several other wader species (Howe 1982, Redfern 1982, Skeel 1983, and Baines 1988) and in certain studies this has been associated with greater nest predation in the more uniform habitat (Skeel 1983, and Baines 1988).

(ii) Increased risk of nest trampling by stock:- trampling by livestock can be a major cause of nest failure for waders nesting in agricultural habitats (Beintema et al. 1987, Green 1988). Stocking densities within re-seeded areas were considerably higher than on heathland (e.g. in 1988 stocking densities of 5-8 ewes plus lambs per ha occurred in three re-seeds during parts of the incubation period). Losses from trampling accounted for 1% of eggs found in nests in heathland or mires, but for 22% of those in nests in re-seeds (see 6.1.1 for methods of determining egg losses). However, whilst trampling may reduce the success rate of nests in re-seeds, compared to those on heathland, it is unlikely to cause the avoidance of ploughed or harrowed re-seeds since nests did occur in surface re-seeds, despite relatively high stocking densities.

4.3.3 Nesting Densities and Dispersion

The highest nesting densities in this study were associated with those sites located on serpentine heathland (ie. for site 1 in all years, and site 3 in 1988). An association between the distribution of nesting whimbrel and serpentine rock in Shetland has been noted in the past (e.g. Herfst and Richardson 1982) and despite its relative scarcity as a rock type, approximately 30% of the Shetland population nest on heathland overlying it (Richardson 1989). This may be partly due to a geographical coincidence; ie. the main blocks of serpentine are on Fetlar and Unst, as are the main concentrations of breeding whimbrel. However, within both islands the distribution of whimbrel closely mirrors that of serpentine heathland (Richardson 1989) and it appears likely that selection for serpentine heathland as a nesting area has occurred. Possible factors causing this and the associations between site and breeding success are considered further in 9.2.

That nesting densities were lowest on sites 2 and 4 was partly due to the presence of relatively extensive areas of ploughed or harrowed re-seeds within the nesting areas of those sites. However, even when all areas of this habitat were excluded from calculations, densities were still lower than on site 1.

Nesting densities recorded for whimbrel in other studies range from 1 pair per 100ha, on heathland in Norway (Aa Munkejord, after Cramp and Simmons 1983) to c.30 pairs per 100ha on heathland in the Faeroe Islands (M. Richardson, pers. comm.). The densities recorded on site 1 in this study are similar to those which occur on other areas of serpentine heath in Fetlar and Unst (Peacock et al. 1985, pers. obs.) and are higher than most of those recorded in the literature (e.g. see Cramp and Simmons 1983, and Skeel 1983).

Whimbrel actively defend nesting territories so that, within a nesting area, a regular distribution of nesting pairs would be expected (Patterson 1965, Krebs 1971). However, significantly regular distributions occurred consistently at site 1 only. The lack of a regular distribution on other study sites may have been due to the small sample size in some cases, but it is likely that the presence of unsuitable nesting habitat within the nesting areas of certain study sites was also important. In particular, suitable nesting habitat on site 2 was fragmented by the occurrence of ploughed or harrowed re-seeds, whilst on site 5 flat and gently sloping heathland was interspersed with steeply sloping heathland (ie. gradients of >30°). Whimbrel did not nest on such steep slopes and, within Shetland overall, whimbrel tend to avoid nesting on land with gradients of more than approximately 20° (Richardson 1989).

5. SITE AND MATE FIDELITY

5.1 METHODS

A total of 97 adults nesting on study sites were nest trapped (under N.C.C. licence) and individually colour ringed during the incubation periods of 1986-88 (see Appendix 1 for details of trapping methods). The sex of the marked adults was determined by the methods outlined in Appendix 1.

After the arrival of the first whimbrel on the breeding grounds in 1987 and 1988 systematic searches were carried out on each study site at one to three day intervals until laying began, to ascertain the arrival dates of marked birds. In all three years of the study the identity of any marked adult was recorded for each pair present on a study site.

Nests were located and plotted onto 1:3500 scale maps, as described in 4.1, and the distances between the nest-sites of individuals present on a study site in consecutive years were measured from these map locations. Measurements were taken from the nest-sites of first clutches and any relays are omitted from the results analysed below.

5.2 RESULTS

5.2.1 Arrival Patterns and Mate Fidelity

In both 1987 and 1988 males tended to arrive on the breeding grounds earlier than females (Fig. 5.1). Although the overall arrival dates (combined for both years) did not differ significantly between the sexes, males did arrive back first in a significantly greater proportion of those pairs in which both birds were marked and of known sex (Table 5.1).

Approximately 65% of pairs in which both birds were marked by the end of 1986 (n=17) and 68% of those marked by the end of 1987 (n=25) remained together in the following year. Only four cases (ie. 10%) were known in which both birds from a pair survived to the following year but did not re-mate in that year. In two of these cases the females, having been marked in 1986, were not re-sighted in 1987 but were observed in 1988, when one re-paired with its mate from 1986. The breeding status of those two females in 1987 was therefore unknown.

5.2.2 Site Fidelity

In both 1987 and 1988, a high proportion of both males (ie. 83% and 90% respectively) and females (ie. 71% and 70% respectively) returned to nest on the same study site as used in the previous year. In each of these years a few birds were also observed which did not re-nest on the study site used previously, though no intensive searches were made to locate such birds.

Expressed as a proportion of the total males or females marked

Figure 5.1. Timing of arrival of male and female whimbrel on the breeding grounds in Shetland (data combined for 1987 and 1988). Note; (i) the dates of first arrivals of marked adults were 24th and 26th April in 1987 and 1988, respectively; and (ii) any birds first sighted within a day of laying, or after, have been omitted.

The difference between the average date of arrival for males and females is not significant;

$t=1.74$, d.f.$=85$, $p>0.05$.

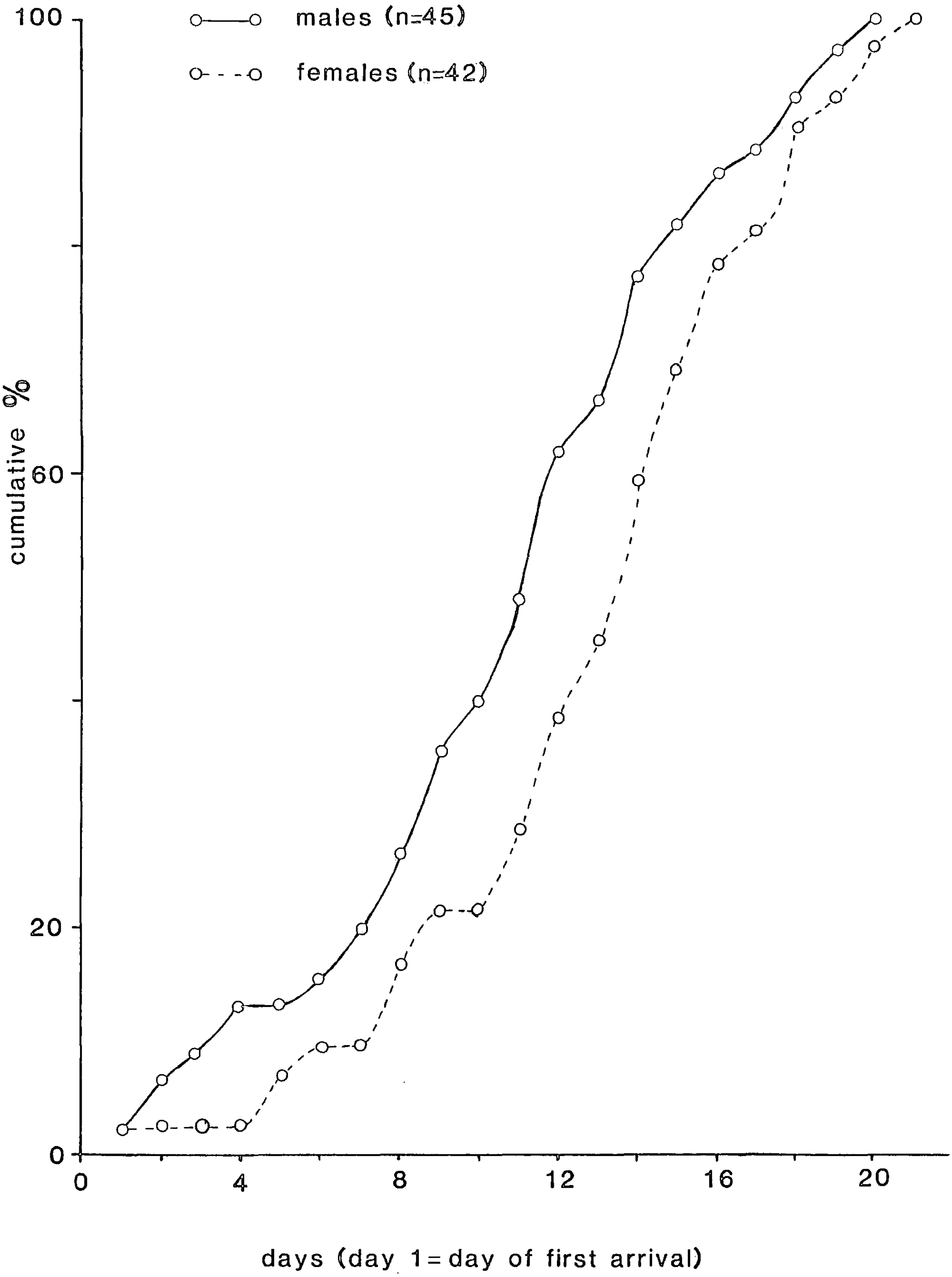

males (n=45)
females (n=42)
cumulative %
100
60
20
0
0
4
8
12
16
20
days (day 1 = day of first arrival)

Table 5.1. Relative timing of arrival of male and female whimbrel in pairs in which both birds were marked

YEAR	NO. OF PAIRS MALE SIGHTED FIRST	 FEMALE SIGHTED FIRST	 BOTH BIRDS FIRST SIGHTED TOGETHER
1987	5	0	7
1988	7	4	8
BOTH COMBINED	12	4	15

$X^2 = 4.0$*
d.f. = 1

*p<0.05

Table 5.2. Return rates to sites of previous breeding, and minimum estimates of annual survival, for male and female whimbrel

SEX	TOTAL NO. OF BIRDS MARKED BY END OF PREVIOUS BREEDING SEASON	NO. NESTING ON SAME STUDY SITE IN FOLLOWING BREEDING SEASON (%)		NO. KNOWN TO HAVE SURVIVED TO FOLLOWING BREEDING SEASON (%)	
MALE	54	47(87)	$X^2 = 3.5$NS d.f. = 1	49(91)	$X^2 = 0.0$NS d.f. = 1
FEMALE	54(56)[2]	38(70)		50(89)	
[1]ALL BIRDS	118(120)[2]	93(79)		107(89)	

NS $p>0.05$

Notes:
1. includes birds for which sex was not determined
2. figures in brackets include 2 females trapped in 1986 which were not observed in 1987 but were in 1988. Since their breeding status in 1987 was unknown they are excluded from estimates of fidelity, but are included in those for survival.

Table 5.3. Return rates of males and females to different study sites

SEX	SITE	NO. OF BIRDS MARKED AT END OF PREVIOUS BREEDING SEASON	NO. OF BIRDS NESTING ON SITE IN FOLLOWING YEAR (%)
MALE	1	17	14(82)
	2	8	5(62)
	3	10	9(90)
	4	6	6(100)
	5	13	13(100)
FEMALE	1	22	16(73)
	2	7	3(43)
	3	7	6(86)
	4	5	5(100)
	5	13	9(69)

For Males; $X^2 = 8.7$, d.f. = 4, $p>0.05$
Females; $X^2 = 4.7$, d.f. = 4, $p>0.10$

by the end of the previous year, the return rate of males was not significantly higher than that of females (Table 5.2). However, if expressed as a proportion of the total males or females known to have survived to the following breeding season the difference is significant (X^2=4.49; d.f.=1; $p<0.05$). Since searches were not made to locate marked birds breeding outside of the study sites this result may be biased; e.g. if males were less likely to be observed than females nesting outside of study sites. This could occur if males dispersed further than such females but this is unlikely. Detailed studies of dispersal in other species of monogamous waders have consistently shown that females disperse furthest (Soikelli 1970, Jackson 1988).

Neither males nor females showed any significant tendency to return at a higher rate to certain study sites than to others (Table 5.3). Clumping the data for both sexes and incorporating that from birds of unknown sex did not produce a significant result (X^2=8.10; d.f.=4; $p>0.05$). The magnitude of any differences between sites was not increased by expressing the return rates to sites as a proportion of the total number known to have survived.

No birds moved from one study site to another between years but one female trapped on site 2 in 1986 was observed on several occasions in 1987 in an area which was c.200m east of site 1 and on part of the same serpentine heathland nesting area as this site. The behaviour of this female indicated that it was nesting in this area. Another female (not included in calculations of fidelity) was nest trapped in 1986 outside of site 1, but again within the same heathland nesting area. This female subsequently nested on site 3 in

1988.

For males which returned to the same study site in consecutive years, 57% of nests (n=46) occurred within 100m and 91% within 200m of the previous years' nest-site. For females which were faithful to study sites (n=40), 50% nested within 100m and 88% within 200m of the previous years' nest-site. Comparing these movements in relation to sex and whether or not a change of mate had occurred revealed no significant differences (Table 5.4). However, the small sample size (ie. 2) available for females which were known to have changed mates prevents any firm conclusions on this aspect of site fidelity.

5.2.3 The Influence of Breeding Success

The outcome of a previous breeding attempt (determined by the methods in 6.1) did not appear to influence either mate fidelity or the site fidelity of males or females (Table 5.5). However, it should be noted that the data used include those birds not observed at all in following years, and therefore a proportion which would not have survived. Sample sizes were too small to allow comparisons of mate faithful and site faithful birds to be made with only those birds known to have survived and to have either "divorced" or nested outside of the previously used study site.

Table 5.4. Distances between the nest-sites in consecutive years of site faithful males and females in relation to mate fidelity

	MALES MEAN DISTANCE BETWEEN CONSECUTIVE NEST-SITES; ± 1 S.E. (m)	N	FEMALES MEAN DISTANCE BETWEEN CONSECUTIVE NEST-SITES; ± 1 S.E. (m)	N
KNOWN TO HAVE RETAINED PREVIOUS MATE	99.6±10.5	28	-	
UNKNOWN IF PREVIOUS MATE RETAINED	121.6±20.5	12	140.0±28.7	10
KNOWN TO HAVE OBTAINED NEW MATE	75.5±26.7	6	468.0 -	2

Excluding data for females known to have obtained a new mate (due to the small sample size); F = 1.53; d.f. = 3,52; p>0.10

Table 5.5. Fidelity to study sites (of males and females) and mates in relation to the outcome of the previous breeding attempt

		NO. OF BIRDS	NO. WHICH FLEDGED CHICKS IN PREVIOUS YEAR (%)	
MALES	RETURNED TO SAME STUDY SITE	44	23 (52)	$X^2 = 0.3$NS d.f. = 1
	NOT RETURNED TO SAME STUDY SITE	7	5 (71)	
FEMALES	RETURNED TO SAME STUDY SITE	36	20 (55)	$X^2 = 0.0$NS d.f. = 1
	NOT RETURNED TO SAME STUDY SITE	15	8 (53)	
	PAIR RETAINED	27	16 (59)	$X^2 = 0.0$NS d.f. = 1
	PAIR NOT RETAINED	14	9 (64)	

NS $p>0.10$

5.3 DISCUSSION

As with other monogamous wader species which exhibit biparental care (e.g. Oring and Lank 1984, Redmond and Jenni 1986, and Jackson 1988) whimbrel in Shetland showed high return rates to the previous breeding site. Return rates of whimbrel in Manitoba appeared to be similar to those obtained in the present study, but small sample sizes, and a different method of calculation (ie. Bailey's small-sample formula - Ricker 1975) for the results obtained in Manitoba, prevent direct comparisons with the present study (Skeel 1983). For birds (of both sexes) returning to the same habitat-type, Skeel (1983) found that the mean distance between successive nest-sites was 156.4±15.7m; S.E. (n=20). This is greater than the mean distance for either males or females which returned to the same study sites in the present study and may be due to the fact that nesting densities were generally lower (and hence potential territory size greater) in Manitoba.

The tendency for males to arrive on the breeding grounds earlier than females, and to show a slightly greater fidelity to the breeding area is also typical of other monogamous wader species in which it is the male that establishes and maintains the territory (Soikelli 1967, 1970, Oring and Lank 1984, Gratto et al. 1985, Jackson 1988).

There was no evidence to indicate that birds which returned to their previous territory had bred any more successfully than those which did not return. Therefore, with respect to whether or not re-seeding would displace birds from nesting habitat (see 4.3.1), it cannot be assumed that consistently poor breeding success in re-seeds (as might be expected to occur - see 4.3.1) would act as a mechanism for displacement.

6. THE INFLUENCE OF LAYING DATE AND EGG VOLUME ON BREEDING SUCCESS

6.1 METHODS

6.1.1 Determination of Laying Dates and Hatching Success

Nests on study sites were located and marked as described in 4.1.2. Those found during laying were usually re-visited daily until clutch completion to determine, the laying interval between successive eggs, the date (and egg) on which incubation started, and the final clutch-size. After this, and for all nests found after clutch completion, visits were kept to a minimum until the eggs began chipping. Visits were made if adults had to be trapped (5.1 and Appendix 1), it was thought likely that chipping had begun, or nest failure was suspected (e.g. if no birds were observed on the territory). The dates on which chipping would begin were assessed approximately in 1986 from the available information on whimbrel incubation periods (Williamson 1946, Jourdain 1962, Skeel 1976), but more precisely in later years from results obtained in this study (see Appendix 2).

Hatching often occurred asynchronously over one to two days, and the first hatched chicks often left the nest prior to the last egg hatching. As a result of this a proportion of chicks were not found, and ringed, in the nest (ie. 19% in 1986, 11% in 1987, and 5% in 1988). These were assumed to have hatched successfully since in all cases the eggs were last observed in an advanced stage of chipping, and later remains indicative of hatching (e.g. small shell fragments) were found in the nest. Also, during the whole study only five eggs were known to have been predated after the start of chipping so that any errors incurred by this assumption will be small.

Previous studies of breeding waders have frequently used the method proposed by Mayfield (1961, 1975) to estimate hatching success (e.g. Pienkowski 1984a, Galbraith 1988a). This method compensates for the possibility that some clutches may have failed before they could have been located and therefore prevents the calculation of artificially high hatching success. When estimates of nest survival for the current study were calculated using the Mayfield method, the results were found to be in close agreement with the observed survival rate of nests (the greatest discrepancy being in 1986 when observed nest survival was 78%, whilst that estimated by the Mayfield method was 75%). This suggests that few, if any, clutches failed prior to being located and thus the observed hatching success data has been used in all analyses.

Hatching success was not influenced by marking and visiting nests or by nest trapping adults (Appendix 3).

Predation of clutches, or of eggs from clutches, was identified by the disappearance of the eggs from a nest, though on a few occasions broken shells were also found close to the nest. Potential mammalian egg predators on both Unst and Fetlar were limited to otters (Lutra lutra), hedgehogs (Erinaceus europaeus), and feral cats. These were generally absent from study sites and no evidence was ever found to indicate predation by non avian predators (e.g. eggs having been eaten in the nest). Losses incurred from trampling by livestock were characterised by egg shell and yolk lying in the nest cup (or on remaining eggs), and/or the presence of partially crushed eggs.

Since most nests were found after clutch completion, laying dates had to be estimated by back-dating from the hatching date (taken as the date on which the first chick hatched). To do this it was assumed that incubation lasted 26 days and that the period from the laying of the first egg to the start of incubation was three days for three and four egg clutches but one or two days for smaller clutches (see Appendix 2 for justification of these assumptions).

Unless found during laying, the laying dates of clutches which failed could not be estimated with adequate precision (Appendix 2). Such clutches were therefore omitted from analyses involving laying dates. They represented 19%, 15%, and 10% of all clutches found in 1986, 1987, and 1988 respectively.

6.1.2 Egg Volumes and Chick Weights at Hatching

For each egg in a clutch, the length and breadth were measured to the nearest 0.1mm using vernier calipers, and the weight recorded to the nearest 2.0g using a 100g Pesola spring balance. Volume (in cm^3) was determined by filling 26 whimbrel eggs (collected earlier this century in Shetland) from the Royal Scottish Museum collection with measured quantities of alcohol solution. The lengths and breadths of these eggs were also measured. A regression of volume (V) against the length (L) multiplied by the square of the breadth (B^2) for these eggs gave the equation:-

$$V = 0.445LB^2 + 0.347$$

(L and B in cm)

The correlation coefficient for this equation was 0.950 ($p<0.001$) and the equation was subsequently used to estimate the egg volumes from the study population.

As detailed above, most chicks were found and ringed in the nest within 24 hours of hatching. On ringing, each chick was weighed to the nearest 0.5g (using a 50g Pesola spring balance) and the lengths of the right tarsus plus toe and the head plus bill were measured to the nearest 1.0mm (using a 300mm stopped rule and vernier calipers respectively). In 1987 and 1988 each of these chicks was also fitted with a single colour ring above the knee which allowed individual recognition within each brood, but not between chicks from different broods. Where possible the order in which these chicks hatched was recorded.

6.1.3 Chick Survival and Fledging Success

Due to the considerable time involved in studying brood movements (see chapter 8.) and chick survival it was necessary to obtain data on these aspects from a sample, rather than all, of the broods on study sites. This comprised 20, 24, and 28 broods in 1986, 1987, and 1988 respectively, and represented 70-75% of all the broods on study sites in each year.

Using a hide or vehicle, broods were re-located within seven days of hatching and thereafter at intervals of five to six days in 1986, and three to four days in later years, until the chicks had fledged or the brood had failed. Fledging was taken to occur at 28 days after hatching since work in 1986 demonstrated that chicks could fly by an age of 26 to 32 days. Both parents usually remained with their chicks until close to fledging, so that at each re-location the identity of the brood could be readily ascertained from that of the colour ringed adults (5.1 and Appendix 1). (Females usually departed a few days before or after the chicks fledged but males remained with the chicks for some time after this).

Whilst the number of chicks which finally fledged was determined for each of these broods, accurate counts were not possible at every re-location for some of them. Therefore, estimates of survival to various ages after hatching were based on a smaller sample of broods. (The reliability of chick counts was greatest in 1987 and 1988 because chicks were individually marked within broods in those years).

Failure of broods was usually determined by locating adults without chicks. Except in three cases, at least one (usually both) adult from each brood which had failed was observed on its territory following failure. The lack of vigilant behaviour and constant alarm-calling at any disturbances were usually indicative of failure but in each case observations were also carried out to confirm that chicks were no longer present. For the three cases where no adults were located it was assumed that they had left the territory soon after failure (all three having been late broods). In these cases an area of several hundred metres around the territory was searched. Since no broods in this study moved more than 1km from their original nest-site prior to fledging, and most remained within 400m of it (see 8.3), adults with chicks would have been located by such searches. This is particularly so, given the conspicuous behaviour of adult whimbrel with chicks; parents often flew 300 to 400m from their broods to alarm-call at approaching intruders.

6.2 RESULTS

6.2.1 Laying Date and Fledging Success

In each year of the study the first laying occurred on the 12th or 13th of May and the distribution of laying dates did not differ significantly between years (Kolmogorov-Smirnov 2-sample tests; $p>0.05$ for each comparison between any two of the three years).

Fledging success was significantly and negatively correlated with laying date in 1987 and 1988 but not in 1986 (Fig. 6.1). The maximum and modal clutch-size was four, comprising between 69-78% of all clutches found in each year. Clutches laid after the median laying date were less likely to comprise four eggs and also had a lower average hatching success than those laid on or before this date. These differences in clutch-size and hatching success were significant when data from all years were combined (Table 6.1). Predation and addling were the two main causes of egg loss (see 9.2.1). Both were more frequent in late clutches, but only significantly so for losses from predation (Table 6.2). Thus the observed seasonal difference in clutch-size was probably due, in part, to greater losses of eggs occurring in later clutches, before nests had been located.

These differences in clutch-size and hatching success were relatively minor and chick survival was the major factor determining the relationship between fledging success and laying date. No chicks survived in broods from clutches laid after the 19th of May in 1987

Figure 6.1. The relationship between laying date and fledging success for whimbrel clutches in each year of study.

Kendall's rank correlation coefficients:-

1986. $r_K=-0.23$, $n=13$, $p>0.10$

1987. $r_K=-0.53$, $n=13$, $p<0.05$

1988. $r_K=-0.63$, $n=18$, $p<0.001$

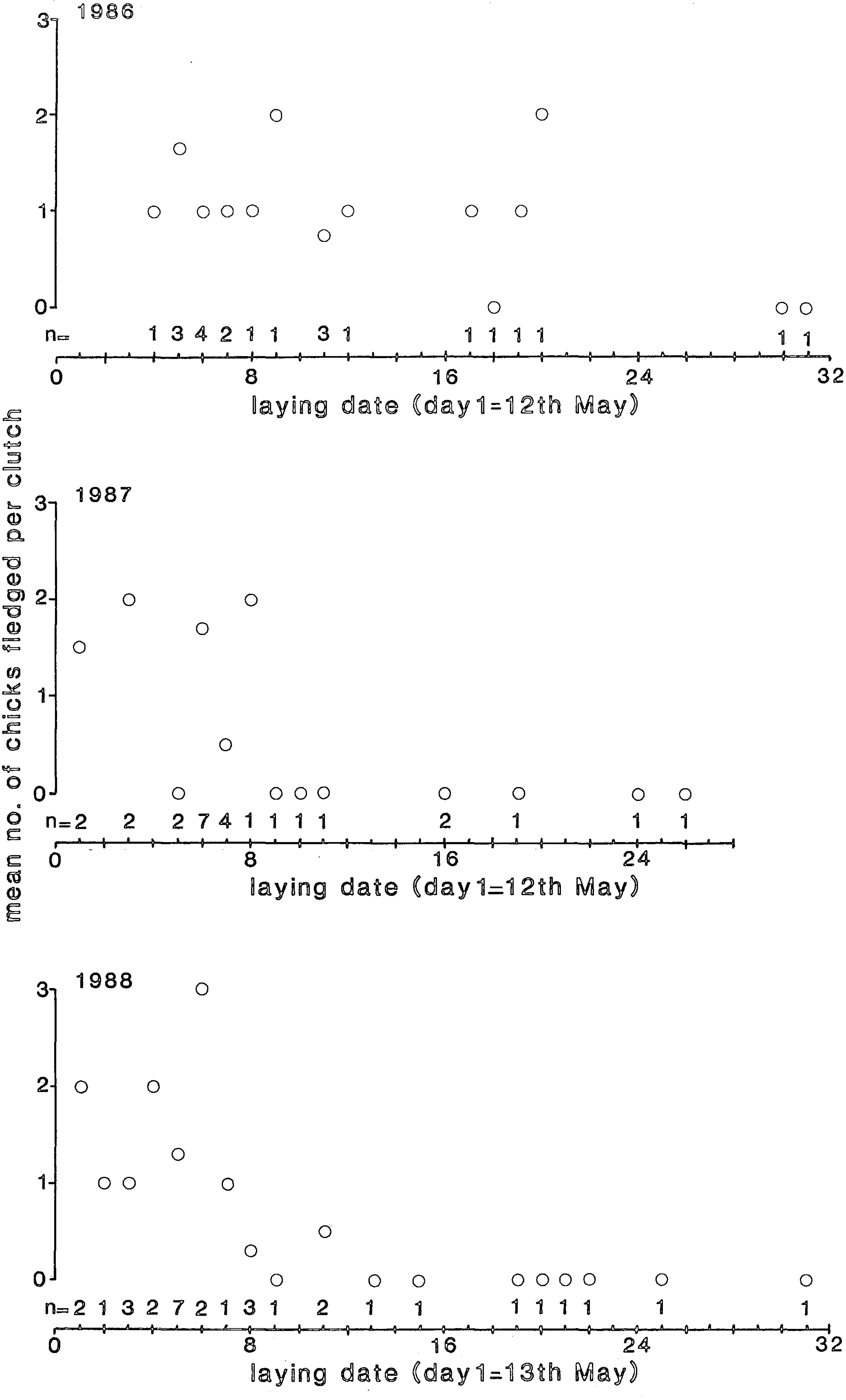

1986
1987
1988
mean no. of chicks fledged per clutch
0
1
2
3
n= 1 3 4 2 1 1 3 1 1 1 1 1 1 1
n=2 2 2 7 4 1 1 1 1 2 1 1 1
n=2 1 3 2 7 2 1 3 1 2 1 1 1 1 1 1 1 1
0
8
16
24
32
laying date (day1=12th May)
laying date (day1=12th May)
laying date (day1=13th May)

Table 6.1. Effect of laying date on the clutch-size and hatching success of whimbrel nests

		1986	1987	1988	ALL YEARS COMBINED	
CLUTCH-SIZE (MEAN ± 1 S.E.)	ON OR BEFORE MEDIAN LAYING DATE	3.79±0.15 (n=14)	3.81±0.14 (n=16)	3.77±0.11 (n=22)	3.79±0.07 (n=52)	Ƶ = 2.30*
	AFTER MEDIAN LAYING DATE	3.27±0.27 (n=15)	3.58±0.18 (n=19)	3.52±0.16 (n=21)	3.47±0.11 (n=55)	
HATCHING SUCCESS (MEAN ± 1 S.E.)	ON OR BEFORE MEDIAN LAYING DATE	3.50±0.25 (n=14)	3.37±0.27 (n=16)	3.18±0.28 (n=22)	3.33±0.16 (n=52)	Ƶ = 3.19***
	AFTER MEDIAN LAYING DATE	2.15±0.04 (n=15)	2.74±0.27 (n=19)	2.71±0.28 (n=21)	2.69±0.17 (n=55)	

*p<0.05 ***p<0.001

Notes: Ƶ - values are calculated from the Mann-Whitney test.

Table 6.2. Occurrence of predation and addling in whimbrel nests in relation to their laying dates

		% OF NESTS LOSING $\geqslant 1$ EGG (n)				
		1986	1987	1988	ALL YEARS COMBINED	
PREDATED	ON/BEFORE MEDIAN LAYING DATE	14 (14)	12 (16)	9 (22)	11 (52)	$X^2 = 4.0^*$ d.f. = 1
	AFTER MEDIAN LAYING DATE	27 (15)	21(19)	38(21)	29 (55)	
ADDLED	ON/BEFORE MEDIAN LAYING DATE	7 (14)	6 (16)	9 (22)	8 (52)	$X^2 = 0.7$NS d.f. = 1
	AFTER MEDIAN LAYING DATE	20 (15)	16 (19)	9 (21)	14 (55)	

NS $p>0.10$ *$p<0.05$

Notes: differences within any one year are not significant.

Figure 6.2. The relationship between laying date and chick survival for whimbrel clutches in each year of study.

Kendall's rank correlation coefficients:-

1986. $r_k = -0.30$, $n = 13$, $p > 0.10$

1987. $r_k = -0.48$, $n = 13$, $p < 0.05$

1988. $r_k = -0.71$, $n = 16$, $p < 0.001$

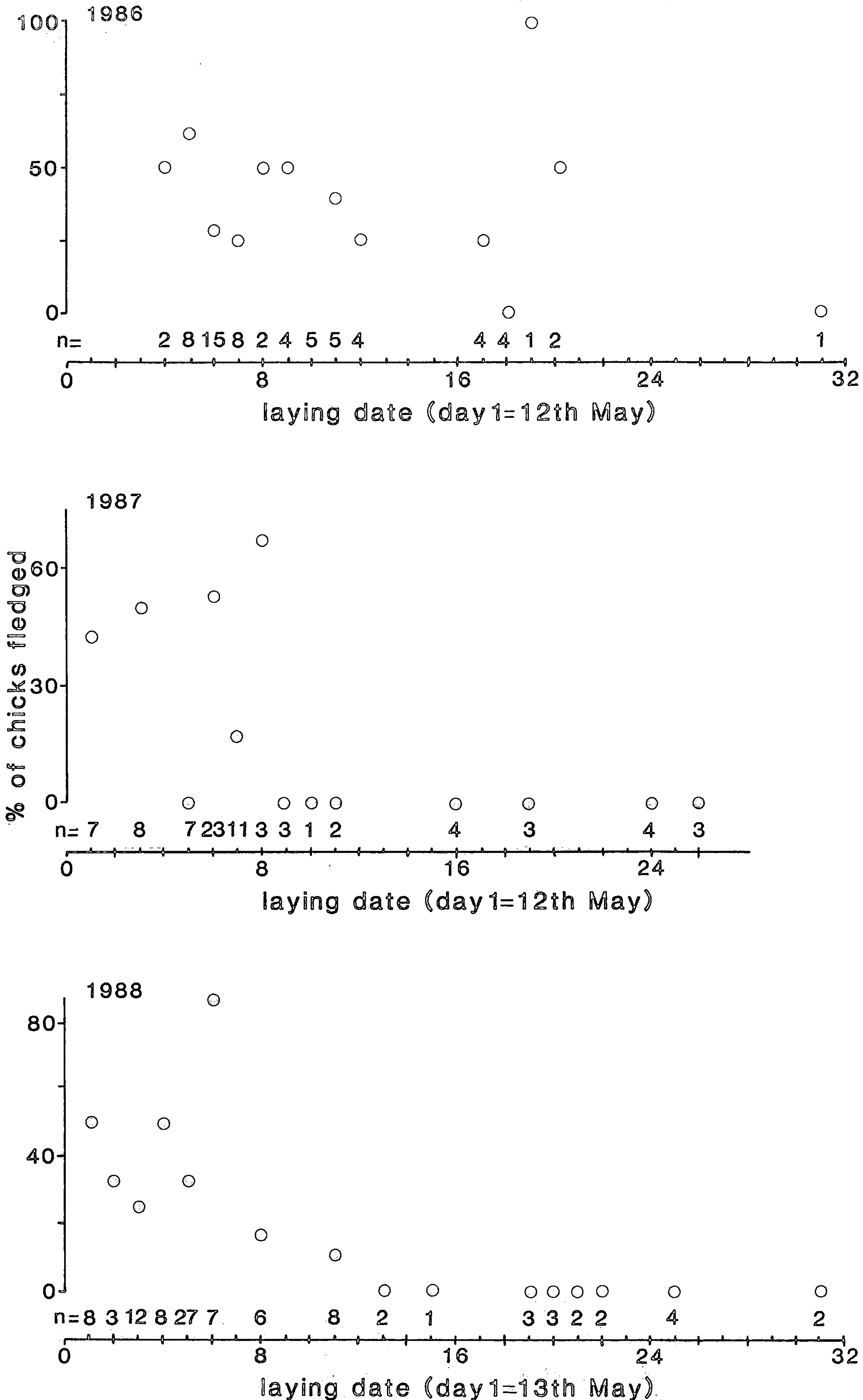
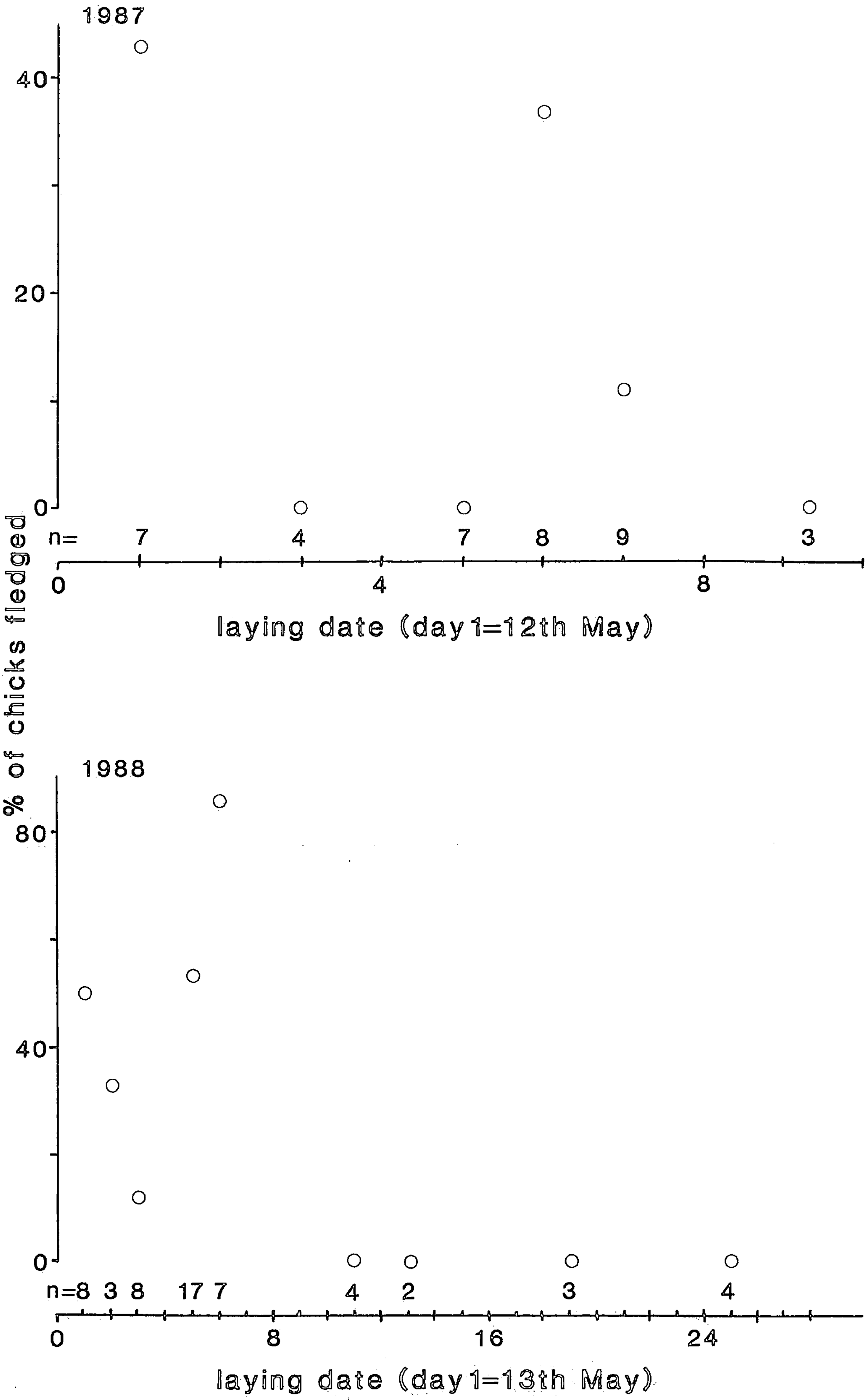

1986
100
50
0
n= 2 8 15 8 2 4 5 5 4 4 4 1 2 1
0 8 16 24 32
laying date (day 1=12th May)
1987
% of chicks fledged
60
30
0
n= 7 8 7 23 11 3 3 1 2 4 3 4 3
0 8 16 24
laying date (day 1=12th May)
1988
80
40
0
n= 8 3 12 8 27 7 6 8 2 1 3 3 2 2 4 2
0 8 16 24 32
laying date (day 1=13th May)

Figure 6.3. The relationship between laying date and chick survival for clutches of female whimbrel with previous breeding experience, in 1987 and 1988.

Kendall's rank correlation coefficients:-

1987. r_K=-0.11, n=5, p>0.10

1988. r_K=-0.49, n=9, p>0.05


1987
40
20
0
n= 7 4 7 8 9 3
0
4
8
laying date (day 1=12th May)
% of chicks fledged
1988
80
40
0
n=8 3 8 17 7 4 2 3 4
0
8
16
24
laying date (day 1=13th May)

or after the 25th of May in 1988, but in 1986 chicks did survive in such late broods (Fig. 6.2). Since females laid earlier as they became more experienced breeders (Table 6.7) the declines in chick survival in late broods might have reflected differences between experienced and inexperienced females. Therefore rank correlations between chick survival and laying date were carried out using data from known experienced females only. In neither 1987 nor 1988 was the relationship significant (Fig. 6.3). The possible seasonal decline in survival in 1988 was due largely to two re-laid clutches from which no chicks survived - ie. the two points at the latest laying dates in Fig. 6.3.

6.2.2 Chick Survival in Relation to Egg Volume and Chick Weight at Hatching

Variation between, rather than within, clutches was the main component of variation in egg volumes, accounting for 74-80% of this in each year. A similar result was obtained for between-brood variation in chick weights at hatching (Table 6.3). It was therefore valid to carry out analyses of these parameters using the mean values from each clutch or brood.

Neither egg volume nor hatchling weight were significantly correlated with laying date in any year (magnitude of $r<0.21$, $p>0.10$ in all cases) and only three of the five replacement clutches showed a decrease in egg volume when compared with the original clutch.

In each year mean hatchling weight from a brood was highly and positively correlated with the mean egg volume of the clutch (Fig. 6.4 and Table 6.4). Other measurements of hatchling size (ie. the mean tarsus plus toe length and head plus bill length) were also significantly but less highly correlated with mean egg volume (Table 6.4).

The proportion of chicks from a brood which survived to fledging increased significantly with mean hatchling weight in 1986 and 1987, but not in 1988 (Fig. 6.5). Weaker relationships (not significant in 1987) occurred between mean egg volume and chick survival in 1986 and 1987.

Colour ringing of chicks in both later years allowed survival of individual chicks within broods to be tested in relation to their weights at hatching. Survival up to seven, 14, and 28 days after hatching was studied for broods which suffered partial (but not complete) losses at each of these stages. Using paired t-tests the mean hatchling weights of surviving chicks were compared with those which had died (note, one-tailed probability levels were used as a result of the relationship which had occurred between broods). Since sample sizes were small and hatchling weights did not differ significantly between years (Table 6.7) data from both years were combined.

No difference was found between the mean hatchling weights of chicks which fledged and those which did not, but a progressively greater difference occurred when weights were compared between those which did and did not survive within a brood up to 14 days and up to seven days after hatching (Table 6.5).

Survival was not significantly related to chick hatching order. First hatched chicks did not have a significantly higher survival than others up to seven days after hatching (X^2=2.66, d.f.=1, p>0.10)

Table 6.3. The relative importance of between and within clutch variation in egg volume, and between and within brood variation in hatchling weight

		% OF TOTAL VARIATION					
		1986		1987		1988	
EGG VOLUME	BETWEEN CLUTCHES:	76	F = 8.10*** d.f. = 34, 35	74	F = 7.81*** d.f. = 39, 107	80	F = 10.36*** d.f. = 44, 115
	WITHIN CLUTCHES:	24		26		20	
HATCHLING WEIGHT	BETWEEN BROODS:	69	F = 3.97*** d.f. = 25, 45	65	F = 3.60*** d.f. = 32, 61	79	F = 8.01*** d.f. = 38, 82
	WITHIN BROODS:	31		35		21	

***p <0.001

Note: re-laid clutches and broods are omitted from analyses

Table 6.4. Correlations of measurements of mean hatchling size from broods with the mean egg volume of clutches

		CORRELATION COEFFICIENTS		
YEAR	N	BODY WEIGHT	TARSUS & TOE LENGTH	HEAD & BILL LENGTH
1986	27	0.86***	0.45*	0.44*
1987	33	0.83***	0.57***	0.60***
1988	39	0.86***	0.55***	0.58***

*p<0.05 ***p<0.001

Figure 6.4. Mean hatchling weight of broods in relation to the mean egg volume of clutches. (Data from 1988 used).

$r=0.86$, $n=39$, $p<0.001$

$y = 0.79x + 1.51$

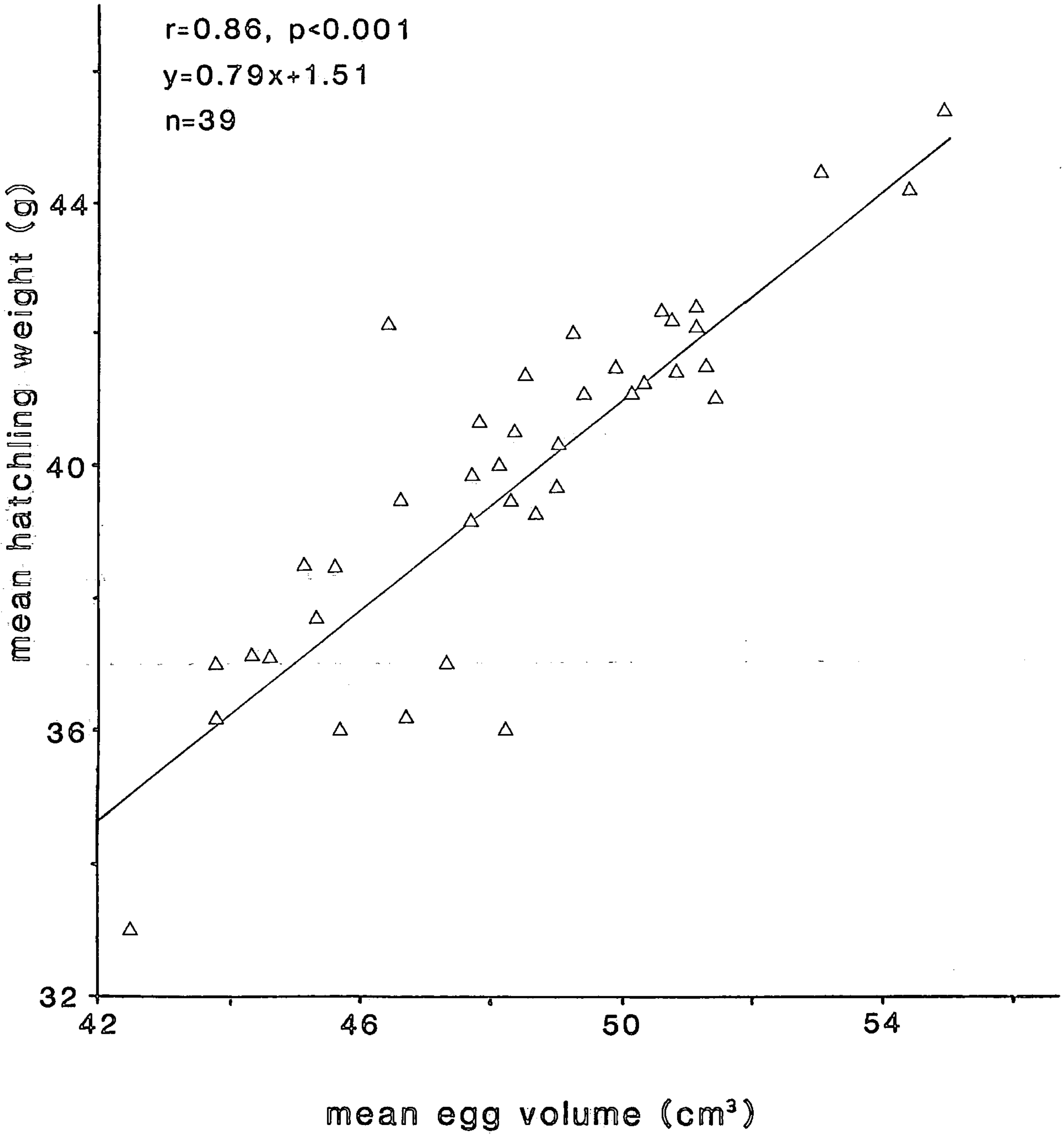

r=0.86, p<0.001
y=0.79x+1.51
n=39
mean hatchling weight (g)
44
40
36
32
42
46
50
54
mean egg volume (cm³)

Figure 6.5. Chick survival in relation to the mean hatchling weight of broods, in each year of study.

Kendall's rank correlation coefficients:-

1986. $r_K=0.49$, $n=20$, $p<0.01$

1987. $r_K=0.33$, $n=24$, $p<0.05$

1988. $r_K=0.17$, $n=28$, $p>0.10$

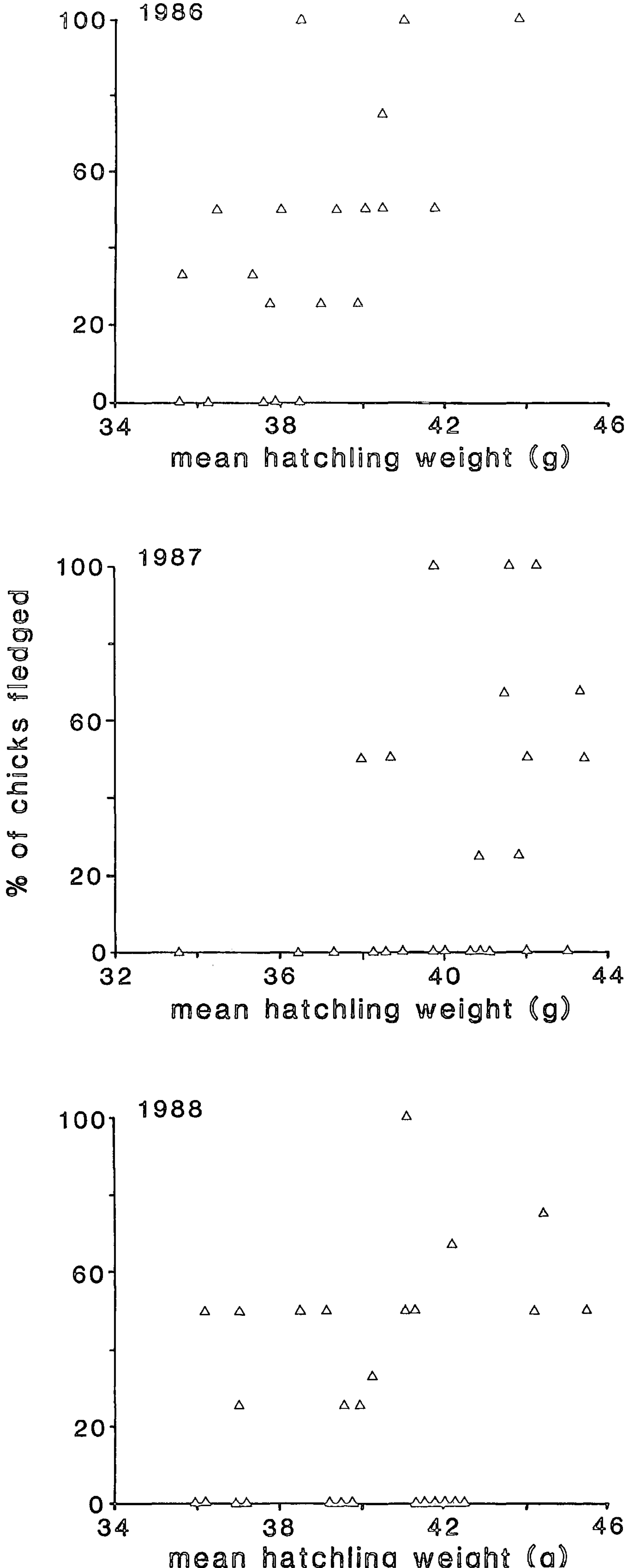

1986
100
60
20
0
34
38
42
46
mean hatchling weight (g)
1987
% of chicks fledged
100
60
20
0
32
36
40
44
mean hatchling weight (g)
1988
100
60
20
0
34
38
42
46
mean hatchling weight (g)

Table 6.5. Survival of individual chicks within broods to various stages of the chick-rearing period, in relation to their weights at hatching

DAYS AFTER HATCHING		MEAN WEIGHT AT HATCHING (g) ± 1 S.E.	[2]NUMBER OF BROODS	[1]PAIRED-t
7	SURVIVED	40.66±0.65	17	1.87*
	DIED	39.82±0.48		
14	SURVIVED	40.16±0.60	15	1.60NS
	DIED	39.52±0.41		
28	SURVIVED	40.64±0.68	19	0.48NS
	DIED	40.45±0.56		

NS $p>0.05$ $*p<0.05$

Notes:

1. one-tailed probability levels are used
2. numbers of broods at different stages vary due to complete failure (and hence exclusion from analysis) of some broods after 7 and 14 days, and to the fact that precise knowledge of which chicks had survived to 7 and 14 days was not obtained for all broods.

and such chicks were not heavier at hatching (paired-t=0.86, d.f.=35, p>0.10). Thus the relationship between hatchling weight and chick survival to seven days within broods was not attributable to an associated relationship with order at hatching.

6.2.3 Attributes of Females Influencing Laying Date, Egg Volume and Chick Weight at Hatching

Egg volumes and hatchling weights of individual females which bred in at least two consecutive years were highly correlated both between 1986 and 1987, and between 1987 and 1988, though the correlations were lower for hatchling weights (Table 6.6). The laying dates of individual females were significantly correlated between 1987 and 1988, but between 1986 and 1987 the correlation was weak and not significant (Table 6.6).

First laying became progressively earlier in each year for those females known to have been present throughout the study, so that their mean laying dates in 1986 and 1988 differed significantly. Over this period there was no associated advance in the mean laying dates of the overall study population (Table 6.7). Egg volumes of known females did not change significantly during the study period but a progressive increase in hatchling weights resulted in a significant difference between 1986 and 1988. However, over this same period there was a non significant increase of similar magnitude in hatchling weights for the whole study population, indicating that the increase for known females may not have been due to an effect of age (Table 6.7).

No significant correlations were obtained between egg volume, or hatchling weight, and any of the six biometric measurements taken from each colour ringed female (ie. body weight, and the lengths of wing, tarsus plus toe, head plus bill, bill, and tail - see Appendix 1 for methods of measurement). Positive correlations of laying date were obtained with, body weight in 1986 (ie. $r=0.51$, $n=20$, $p<0.05$), and tarsus plus toe length in 1988 (ie. $r=0.42$, $n=32$, $p<0.05$). However, since both of these relationships were significant in only one of the three years, and since several correlations had been carried out on each parameter (thereby increasing the probability of obtaining a significant result by chance) these results were considered to be inconclusive.

Table 6.6. Between year correlations of laying date, mean egg volume, and mean hatchling weight for individual female whimbrel

	YEARS	r	r^2	N
LAYING DATE	1986-87	0.22NS	0.05	14
	1987-88	0.79***	0.63	19
EGG VOLUME	1986-87	0.89***	0.79	17
	1987-88	0.88***	0.78	21
HATCHLING WEIGHT	1986-87	0.73***	0.53	13
	1987-88	0.78***	0.61	18

NS $p>0.10$ **$p<0.01$ ***$p<0.001$

Table 6.7. Changes in the laying date, mean egg volume, and mean hatchling weight of individual female whimbrel present throughout the study. Data from the overall study population in each year are provided for comparison

	LAYING DATES ± 1 S.E. (DAYS AFTER 11TH MAY)			EGG VOLUME (cm^3) ± 1 S.E.			HATCHLING WEIGHT (g) ± 1 S.E.		
YEAR	SAME FEMALES (n=11)		[1]OVERALL POPULATION	SAME FEMALES (n=13)		[1]OVERALL POPULATION	SAME FEMALES (n=9)		[1]OVERALL POPULATION
1986	8.82±1.28		9.71±1.29 (n=28)	47.86±0.91		47.65±0.47 (n=34)	39.40±0.78		39.20±0.42 (n=27)
	NS			NS			NS		
1987	7.00±1.35	PAIRED-t = 2.39*	8.57±0.95 (n=35)	47.82±0.90	PAIRED-t = 1.75NS	47.76±0.46 (n=40)	39.99±0.63	PAIRED-t = 2.68*	40.24±0.40 (n=33)
	NS			NS			NS		
1988	5.36±0.78		8.35±1.00 (n=40)	48.70±0.72		48.55±0.43 (n=45)	40.47±0.69		40.02±0.44 (n=36)

NS $p>0.05$ *$p<0.05$

Notes: 1. data from re-laid clutches are excluded.
Differences between years for each parameter in the overall population are not significant (i e. for laying dates, Kruskal-Wallis Test; X^2 = 1.31, d.f. = 2, $p>0.10$; for egg volumes, F = 1.37; d.f. = 2, 116; $p>0.10$; and for hatchling weights, F = 1.46; d.f. = 2, 93; $p>0.10$. Note, a Kruskal-Wallis Test is used for laying dates since the distribution of laying dates for the overall population was skewed).

6.3 DISCUSSION

6.3.1 Laying Date and Fledging Success

In two of the three years of this study late broods invariably failed, resulting in abrupt seasonal declines in fledging success. Almost all females known to have previous breeding experience laid their first clutches within a period of approximately ten days, during which laying date had no apparent effect on chick survival. Thus the failure of late broods was associated with the possibility that many may have been the products of inexperienced females (re-laid clutches being a relatively rare occurrence). Seasonal declines in fledging success occur in many temperate bird species (e.g. Perrins 1970, Birkhead et al. 1983, Coulson and Thomas 1984, Newton and Marquiss 1984) and they are often associated with the fact that inexperienced breeders lay later and may be less able to breed successfully (e.g. Coulson 1966, Baillie and Milne 1982, Newton and Marquiss 1984).

During this study fledging success also varied between study sites and there was a tendency for it to be poorer on those sites where laying was latest. The variation in fledging success between study sites is considered in detail in chapter 9, but at this stage it should be noted that in 1987 the seasonal decline in fledging success may have been due entirely to these associated differences between sites. However, in 1988 the seasonal decline in fledging success appeared to occur irrespective of inter-site variation (see 9.2.3).

The abrupt, rather than gradual, nature of the decline in fledging success suggested that neither a decreasing food supply, nor an increasing predation rate were the causal factors. Also, invertebrate sampling provided no evidence for a decline in chick food supply over the relevant period (8.2).

6.3.2 Relationships Between Egg volume, Hatchling Weight, and Chick Survival

In common with the results of this study, larger eggs have been shown to produce chicks which are either structurally larger and/or heavier at hatching in a wide variety of species (e.g. O'Connor 1979, Moss et al. 1981, Thompson et al. 1986, Rofstad and Jostein 1987, Galbraith 1988b). Since both measures of structural size in whimbrel hatchlings (ie. head plus bill length and tarsus plus toe length) increased with egg volume, the associated increase in hatchling body weight must have been due, at least in part, to the fact that heavier hatchlings were structurally larger than lighter ones. However, it is also possible that larger eggs produced chicks which retained greater yolk reserves on hatching. This has been found to occur in hooded crow, _Corvus corone cornix_, chicks (Rofstad and Jostein 1987) and studies of egg composition have demonstrated that absolute yolk content increases with egg size, although proportionately it may decrease (Ankney 1980, Galbraith 1988b). The considerably higher correlation obtained between egg volume and hatchling weight than with either of the other two measurements of hatchling size in whimbrel does not necessarily indicate that larger chicks also retained greater yolk reserves, since body weight at hatching could be more closely related to structural size than either of the other measurements taken (compare Galbraith 1988b).

Greater egg volume and/or hatchling weight have been associated with higher chick survival in several species (e.g. Nisbet 1978, Lundberg and Vaisanen 1979, Moss et al. 1981, Thomas 1983). In addition to the results of this study, within wader species this relationship occurred in lapwings Vanellus vanellus (Galbraith 1988b) but not in ringed plovers, Charadrius hiaticula (Pienkowski 1984b). As with early laying, larger egg size is often associated with increased female age or breeding experience (e.g. Gratto et al. 1983, Thomas 1983, Ollason and Dunnet 1986), though such an effect has not been consistently detected (Baillie and Milne 1982, Thompson et al. 1986).

Although egg volume in whimbrel did not increase significantly with the average age of females, hatchling weight may have. By studying the relationship within broods it was possible to control for any associated effects of age (or other unknown factors) on survival between broods. This revealed that a significant effect of hatchling weight on survival was apparent only up to seven days after hatching. Wader chicks are unable to thermoregulate on hatching (Chappel 1980) and must learn to feed themselves within the first few days of life. Mortality over this period is high (see 8.2.7) and the advantages of possessing any greater reserves at hatching can be expected to have the greatest effects on survival in the early stages of chick growth. A similar result, regarding the period over which egg volume influenced survival in lapwing chicks, was obtained by Galbraith (1988b).

The effect of hatchling weight on survival within broods was considerably less marked than between broods (at least in 1986 and 1987). This is not unexpected because broods which either failed or fledged all their chicks (ie. those most likely to have the lightest and heaviest chicks) were omitted from the within-brood analysis. Also, the extent of variability in hatchling weights within broods was small relative to that which occurred between broods (Table 6.3).

Therefore, during the early stages of chick-rearing hatchling weights did influence survival, and in some years this effect contributed significantly to differential survival rates between broods.

6.3.3 Variation in Laying Dates, Egg Volumes, and Hatchling Weights Between Females

Date of laying, egg volume and hatchling weight of individual females are controlled by a combination of inheritance and environmental conditions. For individual female whimbrel, egg volume and hatchling weight were highly correlated between years but laying date was not. This indicates a stronger influence of inheritance on egg volume and hatchling weight than on laying date, but such high consistency could also result if individual females experience relatively constant environmental conditions between years (e.g. if females were site faithful and spatial variation in territory quality was greater than year to year variation). Similar results regarding consistency in the egg volumes of individual females have been found for five other species of waders, but again no distinctions could be made between the respective roles of inheritance and environmental conditions (Vaisanen et al. 1972).

Studies on the heritability of egg size and laying date (ie. relating these traits between daughters and mothers) have shown relatively high heritability coefficients (ie. 60-70%) in the egg sizes of great tits (Parus major) and red grouse (Lagopus lagopus scoticus) but considerably lower coefficients (ie. 13-21%) for laying dates in great tits and sparrowhawks, Accipiter nisus (Ojanen et al. 1979, van Noordwijk et al. 1980, Moss and Watson 1982, Newton and Marquiss 1984). The results of these heritability studies on laying dates are supported by evidence from both experimental and field studies which have demonstrated that, through its effect on female body condition, increased food supply prior to laying can cause a considerable advance in the laying dates of individuals (Drent and Daan 1980, Newton and Marquiss 1981, 1984, Ewald and Rohwer 1982).

With regard to variation in egg volumes, these heritability studies have considered species in which clutch-size is variable, and also capable of responding to changes in environmental factors (Drent and Daan 1980, Newton and Marquiss 1981). In most wader species (including whimbrel) clutch-size is more or less fixed, and thus a greater environmental influence on egg volume might be predicted than in other species. However, little evidence exists for any relatively strong environmental influence on egg volume in waders. In a study of greenshanks (Tringa nebularia) mean fresh egg weights in the population were greater in years with higher spring soil temperatures and lower precipitation - though these climatic factors had a greater influence on the mean laying dates (Thompson et al. 1986). Also, positive correlations between egg volume and female body weight have been found in four wader species, indicating a possible effect of female body condition on egg size (Vaisanen et al. 1972, Galbraith 1988b). Such correlations though, could be due to a direct effect of female body size on egg size, and may be influenced by variations in the stage of incubation at which different females were trapped and weighed.

Thus, given the evidence which is available from other studies, the high correlations obtained between years for both the egg volumes and hatchling weights of individual female whimbrel suggests that environmental factors would have only a relatively minor influence on these parameters. A greater environmental influence on the laying dates of individuals would be expected.

7. USE OF RE-SEEDS AS FEEDING HABITAT BY ADULT WHIMBREL AND THE EFFECTS OF THIS ON BREEDING SUCCESS

7.1 INTRODUCTION

In addition to the loss of suitable nesting habitat for whimbrel, two other potential effects of re-seeding are; (i) that re-seeds may provide alternative feeding habitat for adults; and (ii) that re-seeds may provide alternative chick-rearing habitat.

This and the following chapter consider the extent to which whimbrel use re-seeds in these respects, the factors involved in causing such use, and any influence of this on breeding success. It was also necessary to consider the use of established pastures and mires by whimbrel, and thus to some extent both chapters are concerned with overall habitat-use.

Studies on habitat-use and food supply of adults were concentrated on the pre-laying stage of the breeding season; a period of approximately 11 days for females, and 14 days for males. Feeding conditions for adults during the pre-laying period have been shown to have important consequences for breeding success in a variety of bird species (e.g. Drent and Daan 1980, Newton and Marquiss 1981, 1984, Monaghan et al. 1989).

Note, the invertebrate sampling described in both chapters (ie. soil coring in this chapter and suction trapping in chapter 8) was carried out by Ruth Chambers, who has allowed me access to the raw data for the purposes of this thesis.

7.2 METHODS

7.2.1 Habitat-Use During the Pre-laying Period

During the pre-laying periods of 1987 and 1988 all five study sites were searched as described in 5.1.1 to record the presence of colour ringed adults. These searches included areas of re-seed and established pasture which were adjacent to heathland nesting areas. The locations of all colour ringed birds observed during these searches were plotted onto 1:3500 scale maps and, once a bird was known to have arrived, its presence or absence from the study site was recorded on all subsequent searches.

Time budget studies were carried out on pairs in which at least one adult was marked. All time budget observations were carried out from a hide or vehicle. During each, a single bird was observed for 10 to 60 minutes (average period = 20mins.). Activity and habitat occupied were continuously monitored over this period using a telescope and tape recorder.

7.2.2 Diet

Faecal samples from adult whimbrel were collected during the pre-laying and incubation periods of 1986 and 1987. Samples were collected when birds were observed to defaecate or during the course of nest-trapping adults. There was no evidence, either from faecal analysis or observations, to indicate that feeding habits changed between pre-laying and incubation. Therefore faeces from both periods were combined to to provide a larger sample size.

On collection, faeces were stored in 70% alcohol and later examined in the laboratory. Under a binocular microscope each faeces was broken up and the invertebrate fragments present in the sample (e.g. mandibles, wing parts, heads) were identified to the level of order or family, using methods similar to those described by Moreby (1988). A reference collection of invertebrates from study sites was used to assist with the identification of these fragments.

Faecal analysis was only used to provide a qualitative description of diet, and no attempt was made to quantify the occurrence of the different prey items. This was due to the potential biases involved in this method; in particular, the possibility that invertebrate groups which contain many hard parts (e.g. Coleoptera) will be over represented in the faeces, compared to those groups which contain few hard parts - e.g. adult Diptera (see Green 1984). To some extent such biases can be overcome by feeding captive birds with known numbers of animals from each invertebrate group, and then calculating conversion factors from the subsequent occurrence of particular fragments in the faeces of these birds (Davies 1977, Green 1984, Galbraith 1989). However, such methods may be extremely time consuming, and for certain invertebrate groups it is unlikely that reliable conversion factors can be obtained (e.g. for lumbricids, which are identified in faeces from the presence of their setae, structures which are highly variable in number between different individuals - Edwards and Lofty 1977).

During periods of feeding in the time budget observations, whenever possible the number of successful feeding attempts in a given time period (>60s) was recorded. For each successful attempt it was recorded whether the prey item had been obtained from on, or above, the ground surface, or by probing below the ground surface.

7.2.3 Food Supply

Sampling of soil invertebrates was carried out from the 1-25 May, 1988 (ie. to coincide with the main pre-laying period of whimbrel). Soil cores ($94cm^2$ in area and 10cm deep) were taken in heathland on each site, in mires on sites 1 and 5, and in a range of the re-seeds and established pastures on each site. Depending on area, between 15 and 25 cores were taken in each heathland site, 10 in each mire, and 15 in each re-seed and established pasture. Within each site or field sampling points were located by stratified random methods (Greig-Smith 1957).

Cores were hand sorted in the field and all macro-invertebrates (ie. >c.3mm in length) were extracted. Macro-invertebrates were identified to their major taxonomic groups and samples were dried to a constant weight at 105°C.

7.3 RESULTS

7.3.1 Occurrence on Habitats

During searches of study sites in the pre-laying period, 55 of the 62 pairs in which at least one adult was colour ringed were not consistently present on the habitat in which they subsequently nested (ie. heathland for 51 pairs and mires or surface re-seeds for the remaining four pairs). Of these 55 pairs, 27 were observed in ploughed or harrowed re-seeds, or established pastures during pre-laying, and it is likely that all 55 pairs used these habitats over this period, given that:-

(i) Four pairs were observed in these habitats at distances of more than 1km from their subsequent nest-sites. It is likely that other pairs used areas equally distant from subsequent nest-sites and since searches were usually limited to study sites, such pairs were unlikely to have been observed. (Note, the available area of these habitats was too extensive to allow effective searches to be made outside of study sites).

(ii) Little use appeared to be made of other available habitats (ie. no sightings were obtained of birds on the coast and they were only occasionally observed on the banks of lochs).

Approximately 65% (n=208) of all sightings of these 55 pairs were on the nesting habitat, and 31% were in ploughed or harrowed re-seeds, or established pastures. However, these figures over estimate the amount of time spent on the nesting habitat, since the efficiency of locating pairs was considerably lower in the improved habitats (for the reasons given above). When present on the nesting habitat, these pairs usually remained within an area which probably corresponded to their nesting territory (ie. excluding aerial displays and flying chases with other whimbrel, 86% of sightings were within 200m, and 92% within 300m, of their subsequent nest-site; n=135).

The remaining seven pairs, in which at least one bird was marked, were consistently found on the habitat in which they subsequently nested. One of these pairs nested on a harrowed re-seed, whilst the others nested on heathland at site 1 (four pairs), site 3, and site 4. Each of these pairs were sighted on at least three separate days during the pre-laying period, and five pairs were subject to periods of continuous observations during time budget studies. All sightings of these pairs (n=38) were within 300m, and 74% were within 200m, of their subsequent nest-sites.

7.3.2 Feeding Habitats

Ploughed or harrowed re-seeds and established pastures provided the main feeding habitats for adult whimbrel prior to laying (Fig. 7.1), apart from those pairs which remained on heathland throughout pre-laying.

Both birds from a pair usually remained within close proximity of each other throughout pre-laying. Thus both sexes were sighted in either ploughed or harrowed re-seeds, or established pastures on an equal proportion of occasions. Within these improved habitats females spent a significantly greater proportion of their time feeding than did males (Fig. 7.2). This did not influence the results shown in Fig. 7.1 since the magnitude of the difference between the sexes was relatively small. Also, the proportion of the time budget observations which were carried out on females did not differ between the two habitat categories (ie. 40% of those in heathland or mire, and 53% of those in the improved habitats).

The few sightings of pairs in surface re-seeds were almost entirely limited to those birds which nested within this habitat. Although no time budget observations were carried out on birds within surface re-seeds there was no evidence to indicate that these re-seeds were used as feeding sites to any greater extent than heathland.

Figure 7.1. The proportion of time in different habitats which was spent feeding by adult whimbrel during the pre-laying period. Data includes observations only on individuals using both habitat categories during this period.

$t=14.46$, d.f.$=29$, $p<0.001$ (arc-sine transformed data).

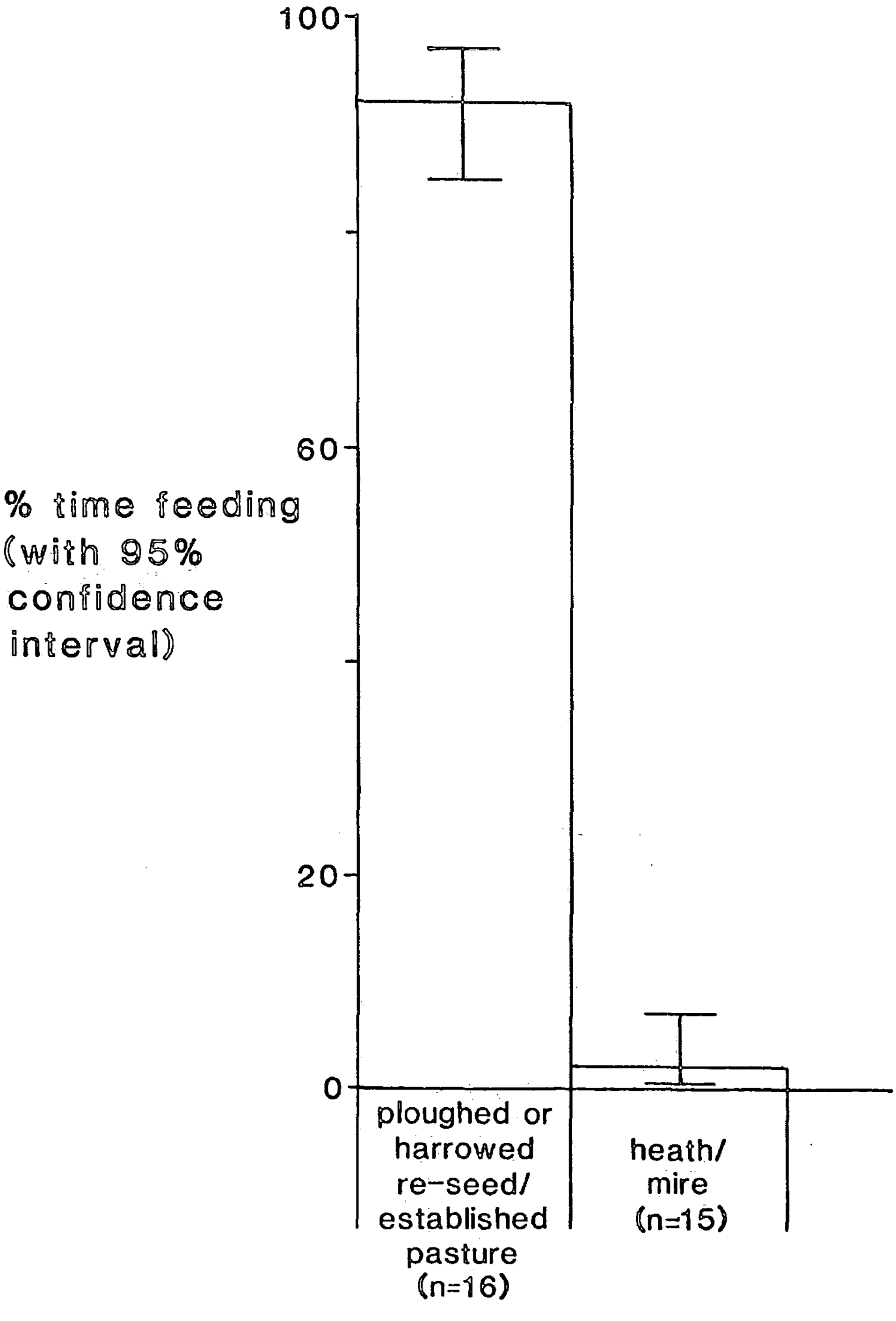

100
60
20
0
% time feeding (with 95% confidence interval)
ploughed or harrowed re-seed/ established pasture (n=16)
heath/ mire (n=15)

Figure 7.2. The proportion of time in ploughed or harrowed re-seeds and established pastures which was spent feeding by male and female whimbrel during the pre-laying period.

$t=2.21$, d.f.$=13$, $p<0.05$ (arc-sine transformed data).

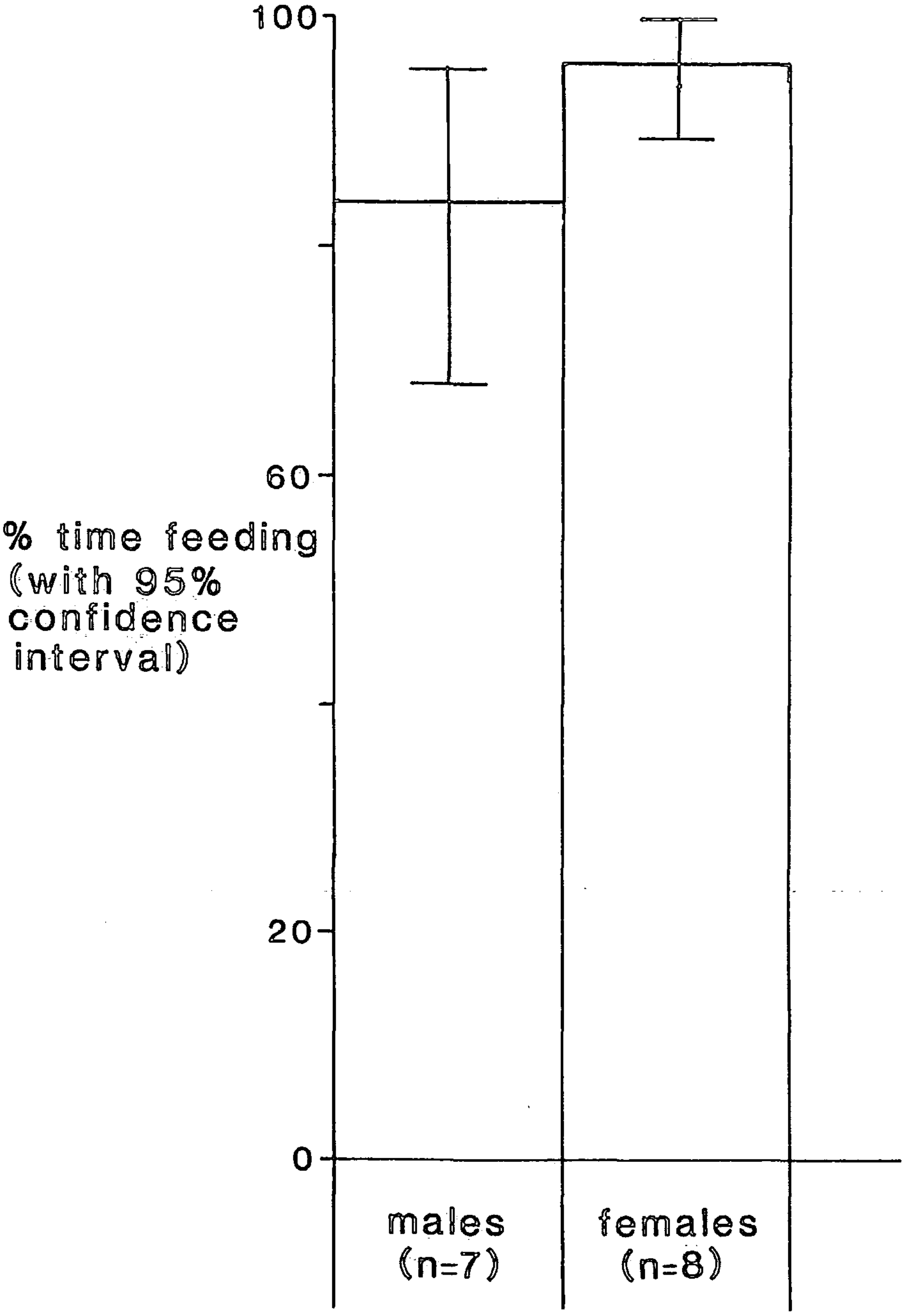
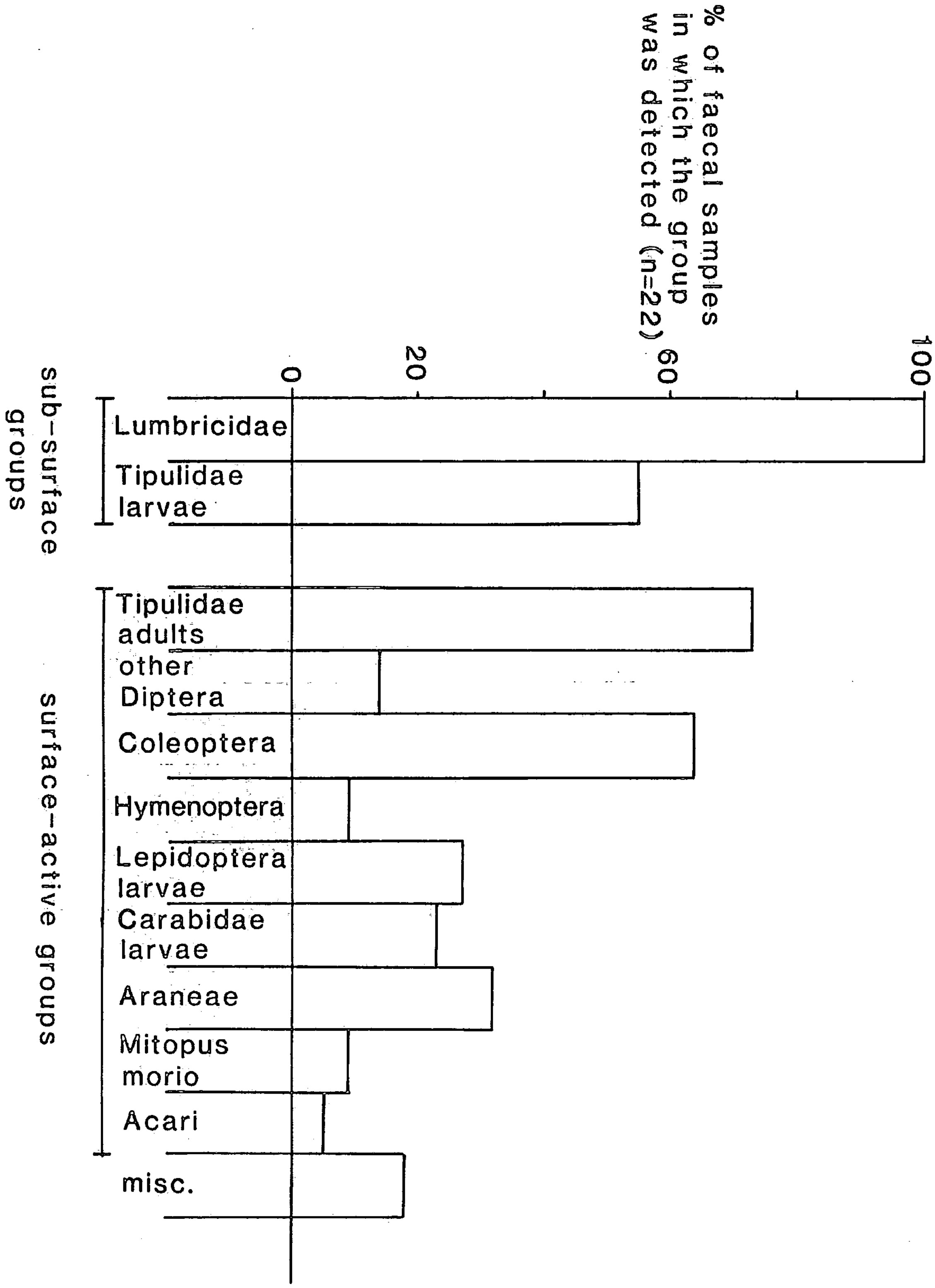

100
60
20
0
% time feeding (with 95% confidence interval)
males (n=7)
females (n=8)

Figure 7.3. Occurrence of different invertebrate groups in the faeces of adult whimbrel during the pre-laying and incubation periods.


% of faecal samples in which the group was detected (n=22)
0
20
60
100
sub-surface groups
Lumbricidae
Tipulidae larvae
surface-active groups
Tipulidae adults
other Diptera
Coleoptera
Hymenoptera
Lepidoptera larvae
Carabidae larvae
Araneae
Mitopus morio
Acari
misc.

7.3.3 Diet

Earthworms (ie. Lumbricidae) occurred in all faecal samples and larval tipulids - the other sub-surface group present - in 55% of samples (Fig. 7.3). Nine groups of surface-active invertebrates (ie. those groups collected by suction trapping - see 8.1.4 and Appendix 4) were identified. Of these, adult tipulids and Coleoptera were present in over 60% of samples but all other groups occurred in less than 40%.

Of 339 successful feeding attempts recorded from 152 minutes of observation, 65% involved prey items taken by probing below the ground surface (ie. earthworms and tipulid larvae - see 7.3.4). Typical dry weights for individual tipulid larvae and earthworms (in pasture) were 8-10mg and 35-50mg respectively. Studies of surface-active invertebrates in different habitats (see 8.1.4) demonstrated that dry weights of individuals of these invertebrate were rarely more than 5mg, and usually less than 1mg. Thus the two sub-surface invertebrate groups accounted for 65% of prey items by number but probably more than 90% by biomass.

Although more faecal samples contained earthworm remains (ie. setae) than larval tipulid remains (ie. mandibles and spiracular discs) earthworms were not necessarily more widespread in their occurrence in the diet. This is because of the large number of setae per earthworm, and because the time between the ingestion and voiding of setae may be greater than for other invertebrate fragments (Galbraith 1989).

7.3.4 Food Supply in Relation to Habitat

In terms of biomass, earthworms and larval tipulids together accounted for more than 95% of all macro-invertebrates found in each heathland site, mire, or improved field sampled.

Data on the biomass of earthworms in the different habitats are summarised in Fig. 7.4. Inherent soil conditions on sites contributed to variation in earthworm biomass, as is evident from the significant differences in biomass on the different heathland sites (Table 7.1). Significant differences in earthworm biomass also occurred within most other habitat categories. To control for such differences, between-habitat comparisons were only made within the same study site.

All three types of improved habitat usually held a greater biomass of earthworms than heathland, though differences were not significant on sites 1 and 3 (Fig. 7.4 and Table 7.2). The magnitude of these differences tended to be greatest on sites 2 and 5, where earthworm biomass on heathland was lowest. Both mires sampled did not differ significantly from heathland with respect to earthworm biomass.

Comparing the three types of improved habitats, earthworm biomass was usually greater on established pastures than on surface re-seeds. No differences in biomass occurred between ploughed or harrowed re-seeds and established pastures on site 4, but on site 2 biomass was significantly greater in the established pasture. Both types of re-seed were present together only at site 2 where earthworm biomass did not differ significantly between these two habitats.

Within particular habitat types the biomass of tipulid larvae in

Table 7.1. Kruskal-Wallis tests for variability in earthworm biomass amongst different study sites

HABITAT	NO. OF DIFFERENT SITES/FIELDS	KRUSKAL-WALLIS, X^2	d.f.	TOTAL NO. OF CASES
HEATHLAND	5	32.6***	4	95
MIRE	2	1.4NS	1	20
SURFACE RE-SEED	4	8.0*	3	60
PLOUGHED/HARROWED RE-SEED	4	22.5***	3	60
ESTABLISHED PASTURE	6	17.2**	5	90

NS $p>0.10$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

Notes: comparisons are based on the data shown in Fig. 7.4.
A Kruskal-Wallis test is used due to the large numbers of samples in which no earthworms were found, thus causing the data to be highly skewed in their distribution.

Figure 7.4. The biomass of earthworms in different habitats within each study site.

Kruskal-Wallis tests of variability amongst habitats:-

Site 1. $X^2=0.6$, d.f.=2, $p>0.10$

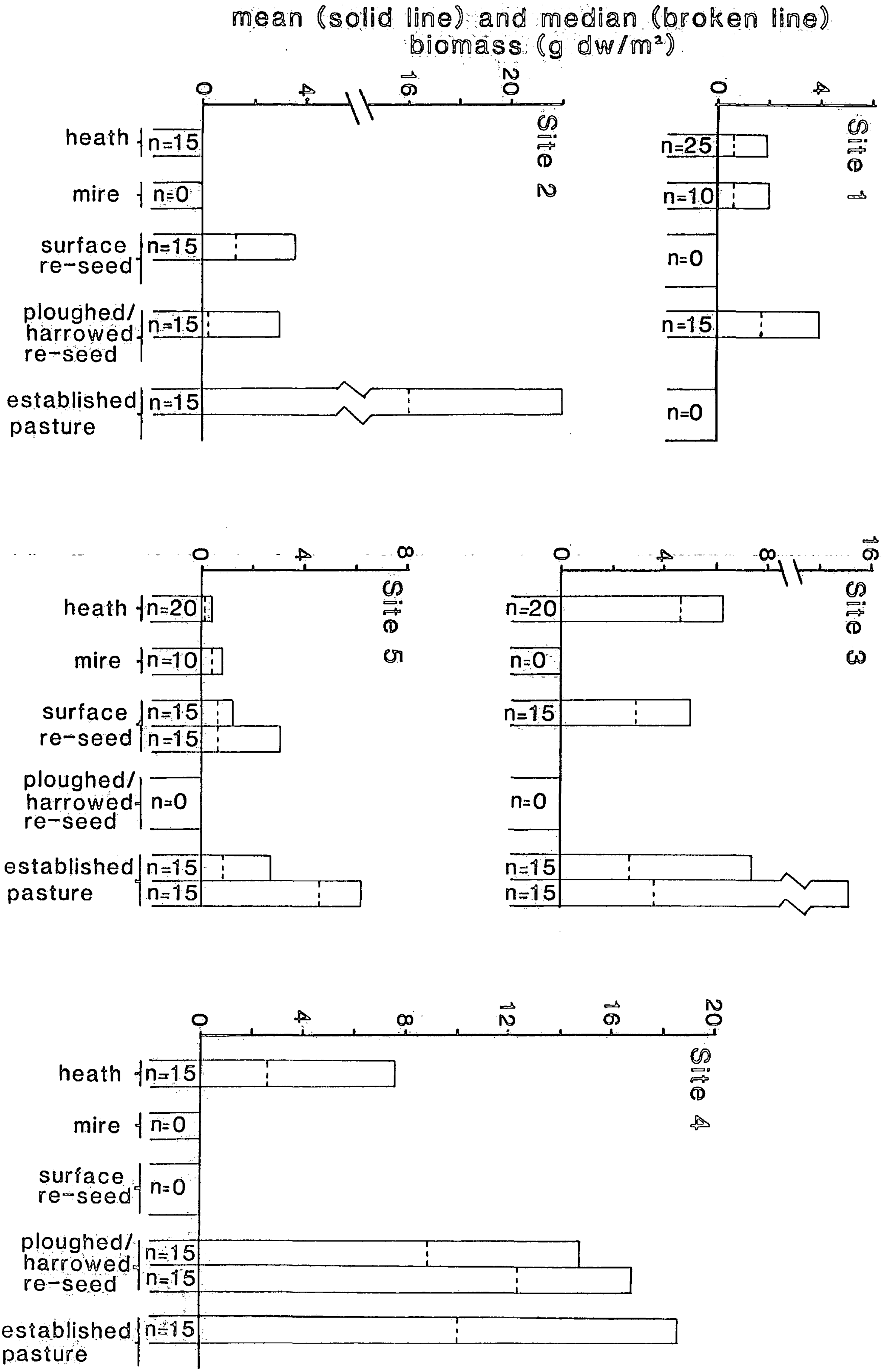
Site 2. $X^2=25.9$, d.f.=3, $p<0.001$

Site 3. $X^2=1.3$, d.f.=3, $p>0.10$

Site 4. $X^2=8.4$, d.f.=3, $p<0.05$

Site 5. $X^2=30.3$, d.f.=5, $p<0.001$

(Note, details of comparisons for each pair of habitats on sites 2, 4, and 5 are given in Table 7.2).



mean (solid line) and median (broken line)
biomass (g dw/m²)
Site 2
0
4
16
20
heath n=15
mire n=0
surface re-seed n=15
ploughed/ harrowed re-seed n=15
established pasture n=15
Site 1
0
4
n=25
n=10
n=0
n=15
n=0
Site 5
0
4
8
heath n=20
mire n=10
surface re-seed n=15
n=15
ploughed/ harrowed re-seed n=0
established pasture n=15
n=15
Site 3
0
4
8
16
n=20
n=0
n=15
n=0
n=15
n=15
Site 4
0
4
8
12
16
20
heath n=15
mire n=0
surface re-seed n=0
ploughed/ harrowed re-seed n=15
n=15
established pasture n=15

Table 7.2. Pairs of habitats within study sites 2, 4, and 5 in which the biomass of earthworms differed significantly (see Fig. 7.4.)

			Z-VALUES (CALCULATED FROM THE MANN-WHITNEY TEST)			
SITE	HABITAT (n)	HEATHLAND (n)	MIRE (n=10)	SURFACE RE-SEED (n=15)	PLOUGHED/ HARROWED RE-SEED (n=15)	PLOUGHED PASTURE (n=15)
2.	SURFACE RE-SEED (15)	3.96(15)***	-	-	NS	2.48**
	PLOUGHED/HARROWED RE-SEED (15)	3.20(15)**	-		-	2.70**
	ESTABLISHED PASTURE (15)	4.21(15)***	-			-
4.	PLOUGHED/HARROWED RE-SEED (15)	2.18(15)*	-	-	NS	NS
	PLOUGHED/HARROWED RE-SEED (15)	2.39(15)*	-	-		NS
	ESTABLISHED PASTURE (15)	2.35(15)*	-	-		-
5.	SURFACE RE-SEED (15)	2.31(20)*	NS	NS	-	2.72** NS
	SURFACE RE-SEED (15)	2.33(20)*	NS		-	3.74*** NS
	ESTABLISHED PASTURE (15)	4.86(20)***	3.42***		-	2.85**
	ESTABLISHED PASTURE (15)	2.24(20)*	NS		-	

NS $p>0.05$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

Table 7.3. Kruskal-Wallis tests of variability in larval tipulid biomass amongst different sites

HABITAT	NO. OF DIFFERENT SITES/FIELDS	KRUSKAL-WALLIS, X^2	d.f.	TOTAL NO. OF CASES
HEATHLAND	5	3.6 NS	4	95
MIRE	2	2.1 NS	1	20
SURFACE RE-SEED	4	3.9 NS	3	60
PLOUGHED/HARROWED RE-SEED	4	2.0 NS	3	60
ESTABLISHED PASTURE	6	18.3**	5	90

NS $p>0.05$ **$p<0.01$

Note: a Kruskal-Wallis test is used due to the large numbers of samples in which no tipulid larvae were found, thus causing the data to be highly skewed in their distribution.

Figure 7.5. The biomass of tipulid larvae in different habitats. Data from different study sites are clumped for all habitats except established pastures (see Table 7.3). Details of the significance of differences between habitats are given in Table 6.4.

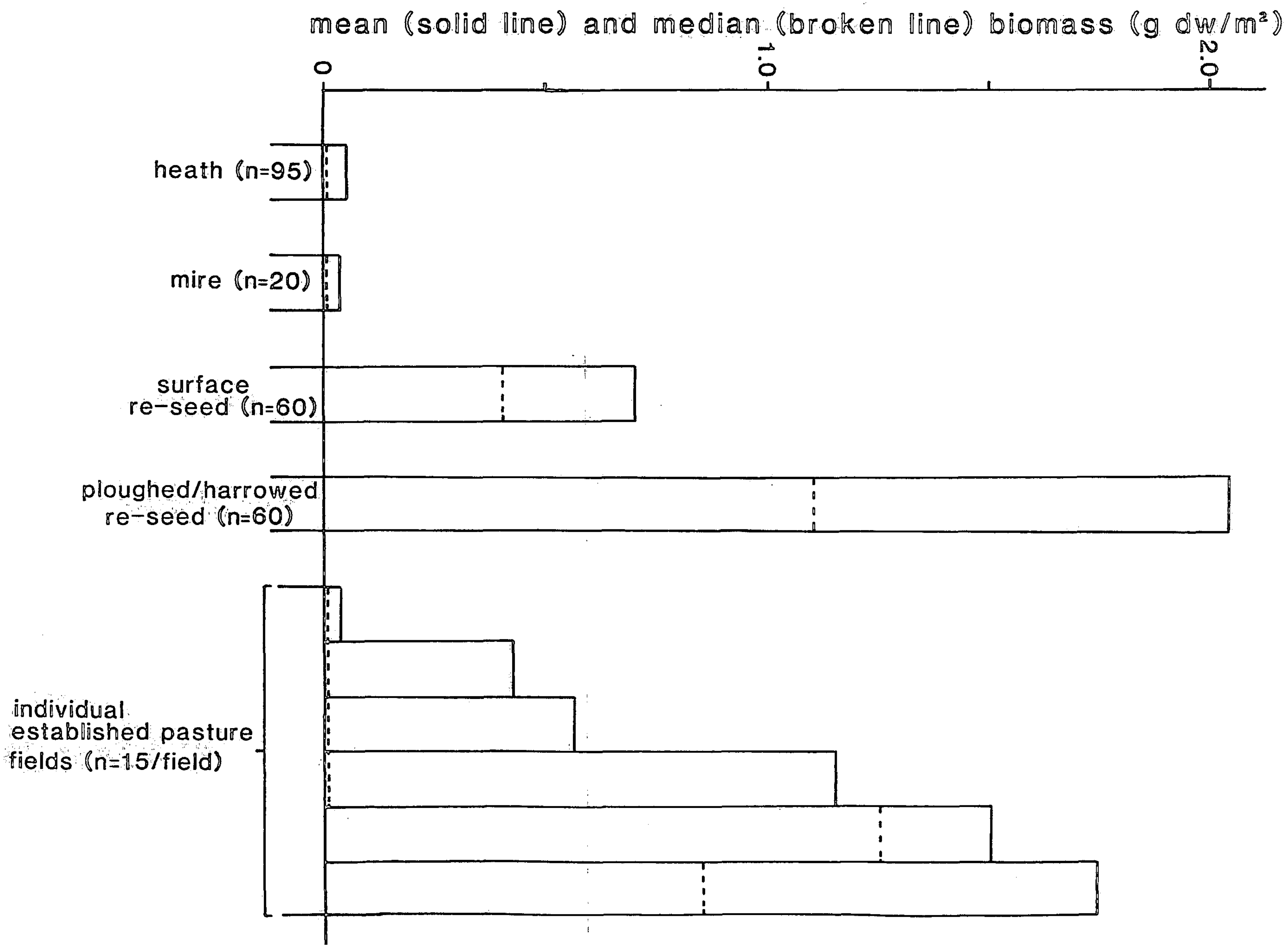

mean (solid line) and median (broken line) biomass (g dw/m²)
0
1.0
2.0
heath (n=95)
mire (n=20)
surface re-seed (n=60)
ploughed/harrowed re-seed (n=60)
individual established pasture fields (n=15/field)

Table 7.4. Mann-Whitney tests of significance for comparisons of tipulid larvae biomass in different habitats (see Fig. 7.5)

HABITAT		Z-VALUES (CALCULATED FROM THE MANN-WHITNEY TEST) HEATHLAND (n=95)	MIRE (n=20)	SURFACE RE-SEED (n=60)	PLOUGHED/HARROWED RE-SEED (n=60)
MIRE		NS	-	3.28***	4.47***
SURFACE RE-SEED		6.01***		-	2.75**
PLOUGHED/HARROWED RE-SEED		7.94***			-
INDIVIDUAL ESTABLISHED PASTURE FIELDS (n=15/FIELD)	1.	NS	NS	3.02**	3.98***
	2.	2.10*	NS	NS	2.80**
	3.	2.18*	NS	NS	2.39*
	4.	3.57***	NS	NS	NS
	5.	5.93***	3.74**	NS	NS
	6.	5.86***	3.74**	NS	NS

NS $p>0.05$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

the different sites differed significantly only for established pastures (Table 7.3). Except for established pastures, comparisons between habitats were made using the combined data from the different sites.

The biomass of tipulid larvae in both unimproved habitats was significantly less than in any of the three types of improved habitat (Fig. 7.5 and Table 7.4). Within the three improved habitats biomass was consistently greatest in ploughed or harrowed re-seeds, the differences being significant with surface re-seeds and three of the six established pasture fields.

7.3.5 Use of Individual Fields as Feeding Sites in Relation to the Biomass of Earthworms and Tipulid Larvae

Each established pasture and ploughed or harrowed re-seed field which was sampled for soil invertebrates was assigned to one of three categories according to the extent of its use as a feeding site prior to laying. These categories of use were defined as:-

(i) None:- fields in which no marked whimbrel were observed during the pre-laying periods of either 1987 or 1988.

(ii) Irregular:- fields in which at least one marked whimbrel was observed during the pre-laying periods of either 1987 and/or 1988, but which were not used consistently by any marked birds.

(iii) Consistent:- fields in which at least one marked pair invariably occurred during the pre-laying periods of both 1987 and 1988, except when the pair were on their nesting territory. Of the two fields included in this category, one was consistently used by one marked pair, and the other by two marked pairs. Each of these pairs were sighted within the relevant field on three to six separate occasions during each pre-laying period. In addition both fields were used less consistently by other marked pairs.

Both fields which were used consistently were ploughed or harrowed re-seeds, as were two of the irregularly used fieds.

Since all fields sampled for soil invertebrates were within approximately 300m of the subsequent nest-site of at least one marked pair in both years, these differences in use were not due to differences in their proximity to nesting areas.

Use of fields as feeding sites increased with the biomass of tipulid larvae in those fields (Fig. 7.6). Biomass in fields not used was significantly lower than in fields from either of the other categories, though the difference between fields used consistently and used irregularly was not significant. There was no apparent association between the use of fields as feeding sites and earthworm biomass (Fig. 7.7). Fields not used held as high a biomass of earthworms as those fields which were used consistently.

Surface re-seeds were excluded from the above comparisons since there was no evidence that they provided important feeding habitat. None of the surface re-seeds sampled held a higher biomass of tipulid larvae than any of the fields which were irregularly used.

Figure 7.6. The use of individual ploughed or harrowed re-seed and established pasture fields in relation to larval tipulid biomass. Note, definitions for each category of use are given in the text. (n=15 samples/field).

Differences between categories:-

consistent vs. irregular; z=1.45, p>0.10

consistent vs. none; z=4.33, p<0.001

irregular vs. none; z=4.29, p<0.001

(Note, z-values are calculated from the Mann-Whitney test).

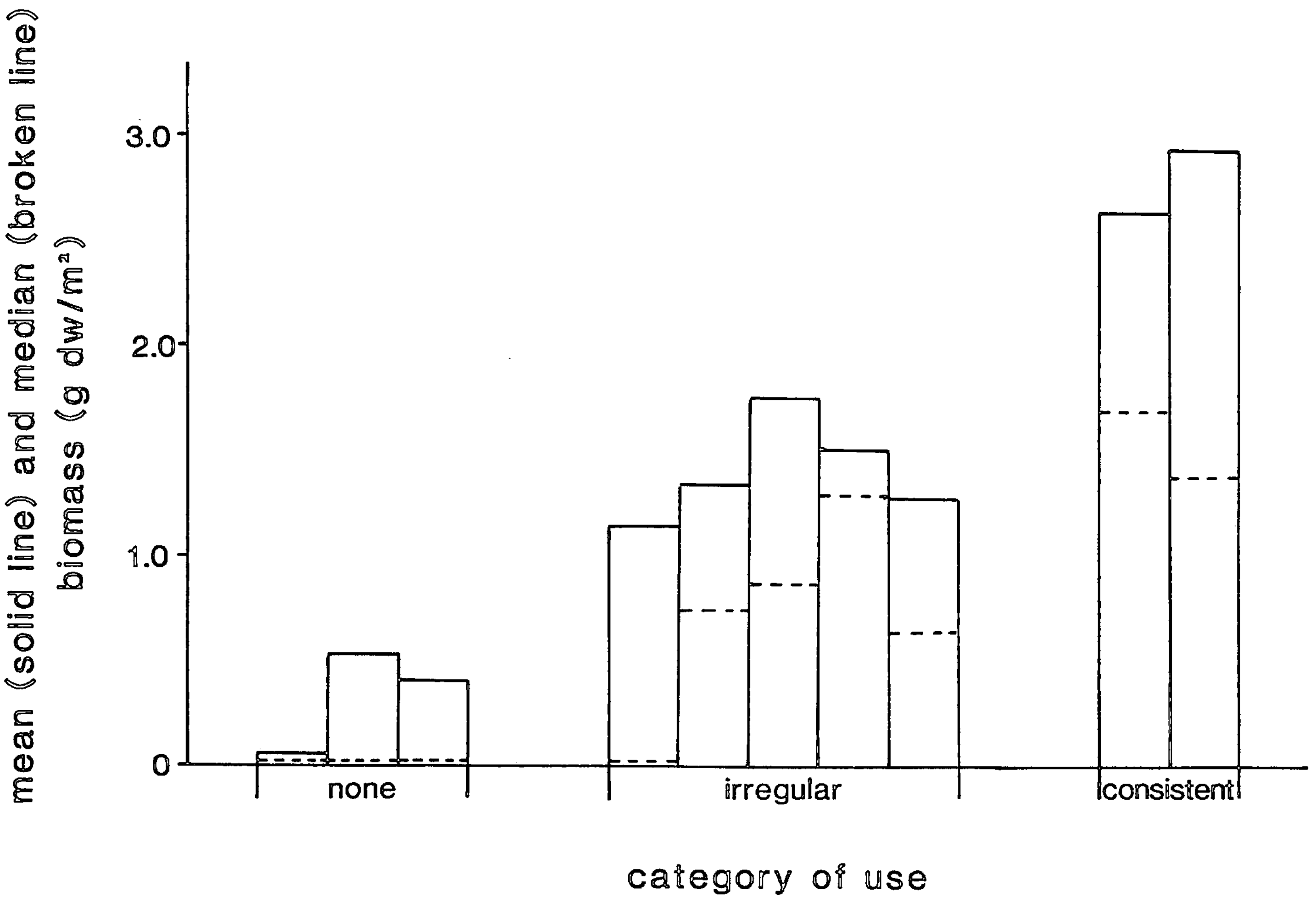
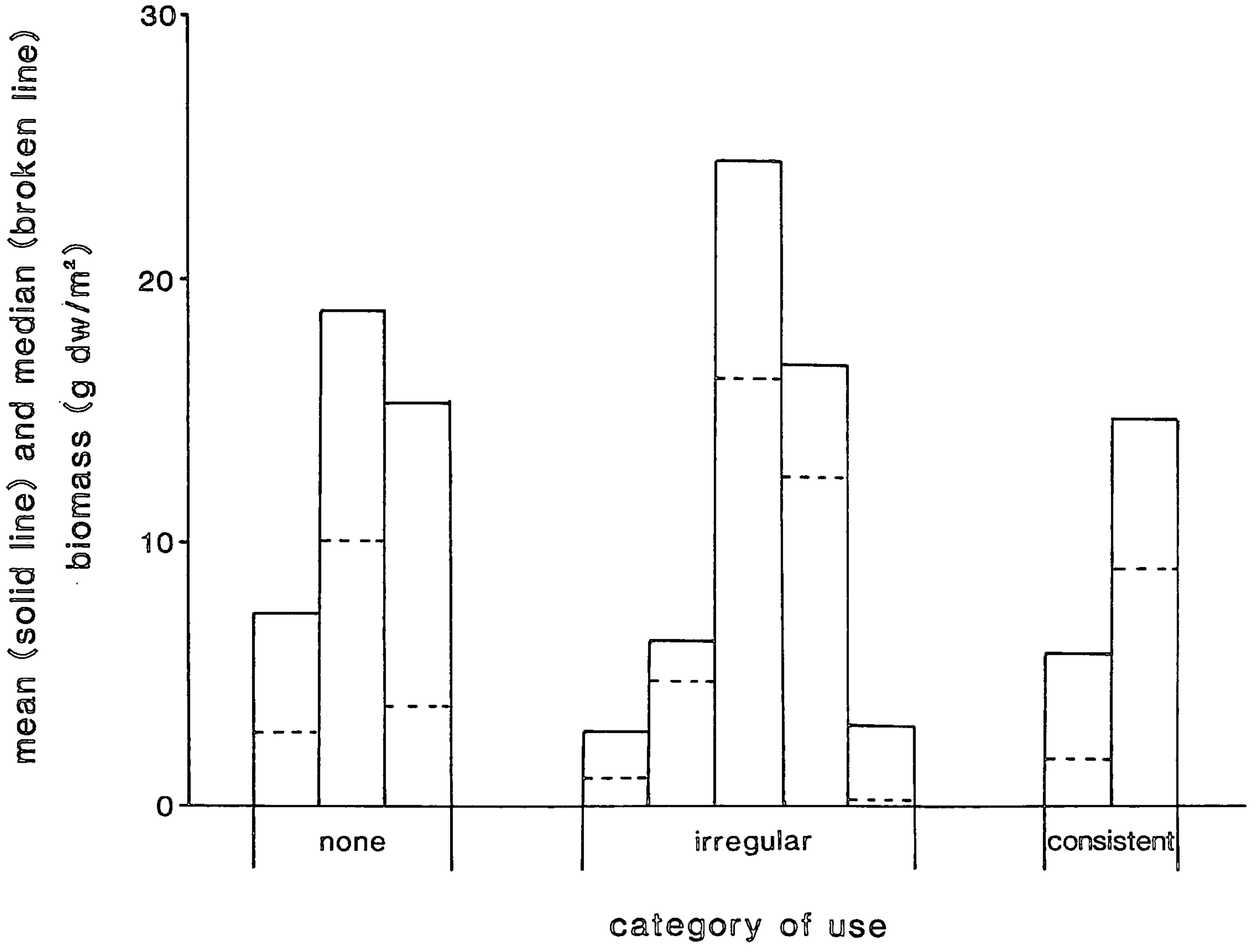

mean (solid line) and median (broken line)
biomass (g dw/m²)
3.0
2.0
1.0
0
none
irregular
consistent
category of use

Figure 7.7. The use of individual ploughed or harrowed re-seed and established pasture fields in relation to earthworm biomass. Note, definitions of each category of use are given in the text. (n=15 samples/field).


mean (solid line) and median (broken line)
biomass (g dw/m²)
30
20
10
0
none
irregular
consistent
category of use

7.4 DISCUSSION

7.4.1 Habitat-Use in Relation to Food Supply

The six pairs of whimbrel consistently found on heathland during pre-laying were present on study sites where the biomass of earthworms on heathland was relatively high for this habitat. Four of these pairs were on site 1 and they fed mainly on "lawns" of short (ie. 2-4cm) sedges and grasses which were interspersed amongst areas of more typical heath on this site (Grant 1988). The short vegetation of these "lawns" may have allowed easier detection and capture of earthworms than on other areas of heath where the vegetation is taller and denser.

For the majority of pairs (ie. >90%) established pastures and ploughed or harrowed re-seeds provided the main feeding habitats prior to laying. Fields belonging to these habitat categories held the greatest biomass of both major prey items.

Overall, biomasses of earthworms were considerably greater than those of tipulid larvae - e.g. the highest biomasses recorded in any field were 22.1g dw/m^2 for earthworms and 2.9g dw/m^2 for tipulid larvae. The main factor contributing to this difference was the greater weights of individual earthworms (see 7.3.3). Thus to a feeding bird the value of an individual earthworm was on average four to five times that of a tipulid larva (note, measurements of calorific content revealed no differences between these two invertebrate groups; ie. 4.95±0.17Kcal/g dw for tipulid larvae, and 4.77±0.16Kcal/g dw for earthworms - values are means with 1 S.E., n=5 in both cases).

Despite this, preference for individual fields as feeding sites was related to the biomass of tipulid larvae but not to that of earthworms. This may be due to differences in the availability of the two invertebrate groups to feeding whimbrel. All tipulid larvae were found within the top 3 to 4cm of soil cores, whilst earthworms were present throughout the depth of the core (ie. 10cm). Their closer proximity to the surface may mean that tipulid larvae are easier to detect and capture than earthworms. Further, tipulid larvae will remain close to the surface (and hence available to whimbrel) at all times, but the depth at which earthworms occur will vary in response to changes in environmental conditions (e.g. in dry conditions earthworms may burrow deeper and aestivate - Edwards and Lofty 1977). Evidence for a relationship between feeding rates and the depth of prey in the soil has been found for golden plovers (*Pluvialis apricaria*) and lapwings feeding on earthworms (Barnard and Thompson 1985).

Within the two main feeding habitats the biomass of tipulid larvae was greatest in ploughed or harrowed re-seeds. Assuming that birds show preferences for those food sources which maximise their energy intake (Krebs 1978, Barnard and Thompson 1985) it is therefore likely that re-seeding has improved the feeding conditions for adult whimbrel prior to laying.

Two factors could cause such benefits from re-seeding to be temporary. First, in terms of its productivity as a grassland, ploughed or harrowed re-seeds usually peak at three to four years of age (various crofters - pers. comm.). Thereafter productivity (and hence the food supply of tipulid larvae) declines unless further fertilisation and/or seeding is carried out. Also, high densities of tipulid larvae can cause a considerable reduction in grass productivity and pesticides are sometimes applied to control tipulid populations in re-seeds.

7.4.2 Possible Benefits to Breeding Success

Improvements in food supply prior to laying could allow female whimbrel to either lay earlier and/or lay larger eggs (increases in clutch-size being unlikely - 6.2.1). Following the results discussed in the previous chapter any influence on egg volume is likely to be relatively minor, and a greater effect on laying date is expected.

A seasonal decline in fledging success was apparent only in those pairs which laid relatively late (ie. at least ten days after the first clutch for that year). Such pairs comprised less than 25% of the study population in each year and there was evidence to suggest that most included inexperienced females (6.2.1). It is possible that inexperienced females would fail to rear chicks irrespective of their laying date, and late laying by such females may be associated with factors other than food supply (e.g. first time breeders may require a longer period to obtain a mate and territory).

Therefore, it is unlikely that improved feeding conditions for female whimbrel prior to laying would result in any major benefits to fledging success through effects on laying date, or egg volume. However, it is possible that improved feeding conditions for adults would have benefits which could not be assessed in the present study. For example, re-seeds were also used as feeding habitat by adults during the incubation period. This may have allowed adults to maintain better body condition throughout the incubation and chick-rearing periods, and hence, possibly have benefited breeding success (e.g. via improved attendance of chicks) and/or adult survival (see Nur 1984).

8. HABITAT-USE AT CHICK-REARING, WITH PARTICULAR REFERENCE TO THE USE OF RE-SEEDS AND THE EFFECTS OF THIS ON CHICK SURVIVAL

8.1 METHODS

8.1.1 Chick Survival and Brood Movements

Chick survival was determined by the methods described in 6.1.3. At each re-location of a brood the habitat(s) occupied by the chicks was also recorded and the locations of chicks were plotted onto 1:3500 scale maps using grid markers and other landmarks (e.g. fence lines) as reference points.

For each brood location on these maps the maximum distances from the nest-site and from the previous location were measured. The ranges used by successful broods were defined by drawing a polygon around the outermost locations for the brood (including the nest-site, each brood range was based on a minimum of eight re-locations in 1987 and 1988, and at least six re-locations in 1986).

8.1.2 Habitat Selection

Habitat selection was studied by comparing the observed number of locations at which broods were re-sighted in different habitats with the expected number based on the relative areas of each habitat available (ie. as in 4.1.1). The area of each habitat available to a brood was assessed by two different methods, as follows:-

(i) By measuring the area of each habitat within a circle centred on the brood's nest and with a radius equal to the maximum distance that the brood was recorded from the nest.

(ii) By measuring the area of each habitat within the observed range used by the brood (see 8.1.1).

Analyses of habitat selection were limited to broods which fledged chicks because both movements and habitat-use were influenced by brood age.

8.1.3 Chick Diet

Faeces were obtained from a few chicks which were occasionally caught during brood studies. Faecal samples were stored and analysed as for 7.2.2. Due to the biases involved in this method (discussed in 7.2.2), and because of the small sample size which was available, no attempt was made to quantify the occurrence of different prey items in the diet.

8.1.4 Chick Food Supply in Different Habitats

Surface-active invertebrates (see Appendix 4) were sampled in 1988 using a Dietrick Vacuum suction trap (see Southwood 1978 for description). To increase the suction pressure of this trap (and hence the extraction rates of invertebrates) a nozzle of relatively small diameter (ie. 17cm) was used.

Sampling was carried out on each heathland site, two mires, and a range of the re-seeds and established pastures on study sites. Each site, or improved field, was sampled once during the early to mid. chick-rearing period (ie. 21 June -4 July) and again during late chick-rearing (ie. 8-20 July). At both sampling periods, 10 to 25 samples were taken from each heathland site (sample size increasing with heathland area), 15 from each mire, and 10 or 15 from each improved field (10 samples being taken in those fields less than 4ha in area). Samples were taken from 0.25mx0.25m quadrats located at grid markers on heathland at study sites 1, 2, 3, and 5, and by a transect method at site 4 (no grid markers being present on this site). Transect methods of sampling were also used in mire sites and improved fields. Transects were located at equal distances across each site or field, and five samples were taken at equal distances along each transect. This sampling procedure was used, rather than a random method, in order to keep the time spent in each area, and hence the disturbance to broods, to a minimum. No sampling was carried out during periods of rain or high winds, and all samples were taken between 0800 and 1700 hours.

On collection, invertebrates from each sample were stored in 75% alcohol and later sorted into the main invertebrate orders or families (excluding Collembola and Acari). The numbers of each invertebrate group in each sample were recorded and samples were then dried to constant weight at 105° C.

Sampling invertebrates by suction trapping had two potential biases. Any species which were only active nocturnally were probably under represented in samples; and differences in vegetation structure between habitats may have influenced extraction rates in different habitats. In particular, it was evident during sampling that a proportion of the invertebrates which occurred under cover of dense _C. vulgaris_ on heathland were not collected. However, it is unlikely that invertebrates in such locations would have been detected by, and hence available to, feeding chicks. The biases involved in making relative estimates of surface-active invertebrate biomass by the only other feasible method of sampling - ie. pitfall trapping - were considered to be more serious than those involved in suction trapping (see Mitchell 1963; Greenslade 1964; and Desender and Maelfait 1986).

8.2 RESULTS

8.2.1 Brood Movements and Habitat-Use

Throughout chick-rearing, nesting territories were usually maintained and little overlap occurred in the ranges used by different broods (e.g. see Fig. 8.1). Prior to fledging, or failure, all broods in all three years of study (n=69) remained within 800m, and 93% within 400m, of their nest-site. The extent of movement from the nest-site tended to increase with brood age (Table 8.1). This tendency was not due to a progressive movement away from the nest-site since distances moved between consecutive re-locations were also greater in older broods.

In each year, 35-60% of the broods studied remained entirely on heathland up to fledging (or failure). Mires were used by 25%, re-seeds by 33%, and established pastures by 11% of all broods studied at some stage before fledging. Maximum distances moved from nest-sites and the size of brood ranges did not differ significantly according to the types of habitats used (Tables 8.2 and 8.3). Distance from the nest-site to an alternative habitat was important in determining whether or not a brood used that habitat. Few broods used habitats which were more than 200m from the nest (Table 8.4).

Figure 8.1. The ranges used by all broods in the east half of study site 1 in 1988. (Notes; (i) ranges are based on 7-8 sightings after hatching of the five successful broods and on 3-4 sightings after hatching of the two broods which failed; and (ii) coverage of broods was incomplete on the west side of this study site).

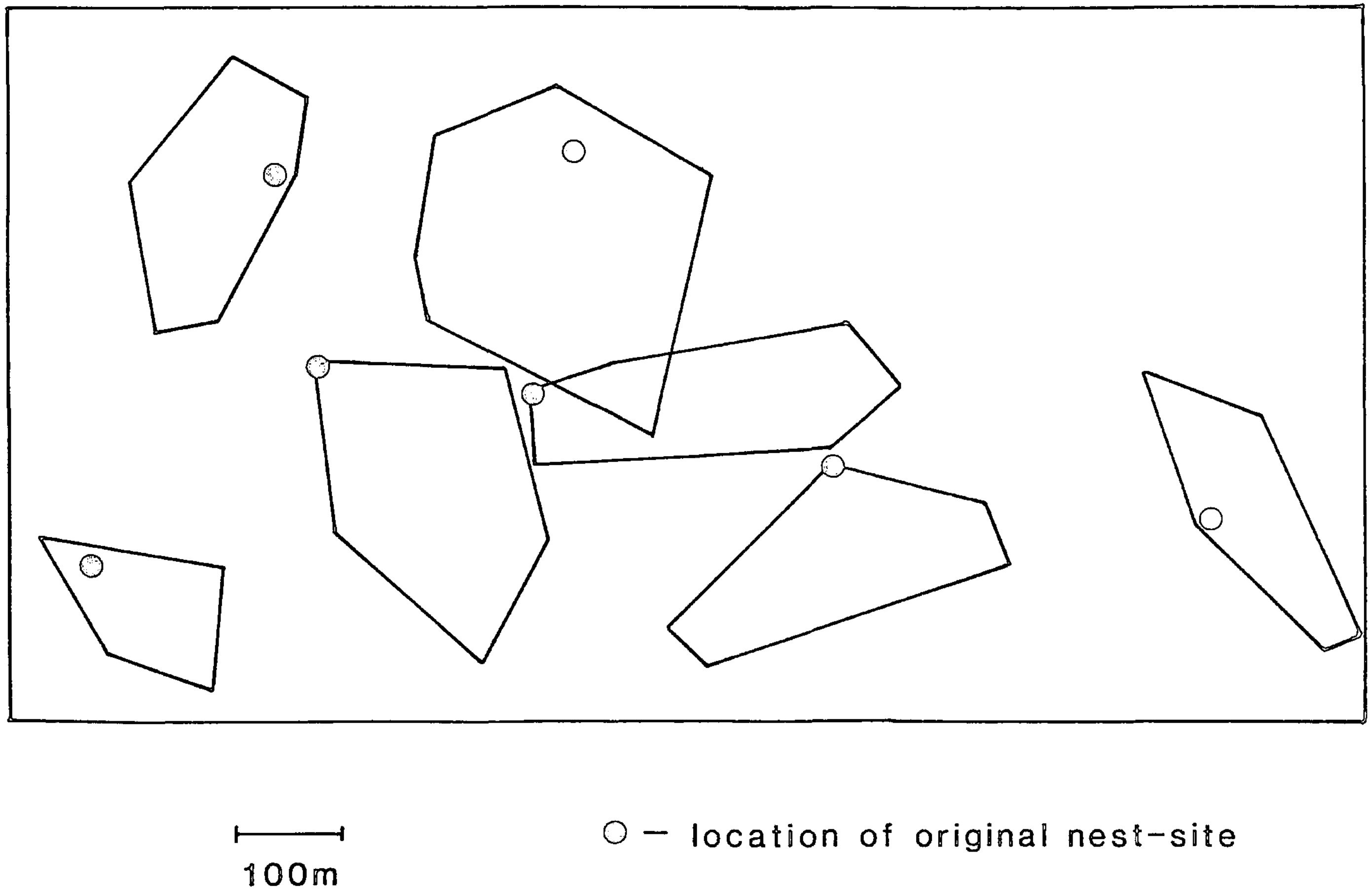

100m
○ – location of original nest-site

Table 8.1. Long distance movements from nest-sites by successful whimbrel broods, in relation to brood age

	BROOD AGE (DAYS)			
	$\leqslant 14$	>14	$\leqslant 20$	>20
NO. (%) OF BROODS FIRST SIGHTED AT >300m FROM THE NEST	4(11)	13(35)	-	-
	$X^2 = 5.0^*$ d.f. = 1			
NO. (%) OF BROODS FIRST SIGHTED AT >400m FROM THE NEST	-	-	0(0)	5(13)
			$X^2 = 3.4$NS d.f. = 1	

NS $p>0.05$ *$p<0.05$

Note: %'s based on observations of 37 broods

Table 8.2. Maximum distances moved (mean ± 1 S.E.; m) from nest-sites by successful whimbrel broods in relation to habitat-use

YEAR	HABITATS USED			
	HEATHLAND ONLY		OTHER HABITATS	
1986	254±41 (n=7)		359±77 (n=7)	
1987	283±31 (n=5)	F = 0.46NS d.f. = 2, 14	368±86 (n=5)	F = 1.01NS d.f. = 2, 17
1988	229±32 (n=5)		259±25 (n=8)	
OVERALL	255±21 (n=17)		321±36 (n=20)	

t = 1.59, d.f. = 29.96, NS

NS p>0.10

Note: t-value calculated using a separate variance estimate.

Table 8.3. Brood ranges (mean ± 1 S.E.; ha) of successful whimbrel broods in relation to habitat-use

	HABITATS USED			
YEAR	HEATHLAND ONLY		OTHER HABITATS	
1986	4.9±1.6 (n=7)		4.7±1.2 (n=7)	
1987	5.2±1.1 (n=5)	F = 0.55NS d.f. = 2, 14	8.5±2.2 (n=5)	F = 1.01NS d.f. = 2, 17
1988	3.3±0.7 (n=5)		3.9±0.6 (n=8)	
OVERALL	4.6±0.8 (n=17)		5.3±0.8 (n=20)	
	t = 0.65, d.f. = 35, NS			

NS p>0.10

Table 8.4. The influence of distance from nest-sites on the use of mires re-seeds, and established pastures by whimbrel broods

	DISTANCE (MEAN ± 1 S.E.; m) FROM NEST TO RELEVANT HABITAT					
	1986		1987		1988	
MIRE USED	177±64 (n=5)	t = 1.94NS d.f. = 11	73±23 (n=5)	[1]t = 4.38** d.f. = 8.32	156±44 (n=6)	t = 2.04NS d.f. = 16
MIRE NOT USED	373±69 (n=8)		403±72 (n=8)		332±56 (n=12)	
IMPROVED HABITAT USED	188±58 (n=7)	t = 1.82NS d.f. = 14	91±27 (n=8)	[1]t = 5.61*** d.f. = 5.90	90±18 (n=9)	[1]t = 4.64*** d.f. = 8.73
IMPROVED HABITAT NOT USED	377±80 (n=9)		616±90 (n=6)		500±86 (n=9)	

NS $p>0.05$ ***$p<0.001$

Notes: [1]indicates t-values calculated using a separate variance estimate. Any broods which nested on the non-heathland habitat used are omitted from the analysis, as are any broods which failed and remained on heathland.

8.2.2 Habitat Selection

Broods did not use habitats in proportion to their availability, as assessed by assuming that broods could move equal distances from the nest in any direction (Table 8.5). Using the methods of Neu et al. (1974, and as in 4.2.1) significant preferences were shown for re-seeds and mires, but established pastures and heathland were avoided to a significant extent. Despite the apparent avoidance of heathland (but see below), 65% of all locations of successful broods were within this habitat, due to it being the most extensive habitat on study sites. Since 83% of the locations of successful broods in re-seeds were in those which had been ploughed or harrowed, preferences were shown primarily for these habitats rather than for surface re-seeds.

For broods using other habitats in addition to heathland within the observed brood range, re-seeds were significantly preferred and established pastures significantly avoided, as in the previous analysis (Table 8.6). However, the observed use of heathland and mires did not differ significantly from that predicted by the availability of these habitats. The biases involved in both methods of analysing habitat selection are considered in 8.3.1.

8.2.3 Chick Diet

Due to the small sample size available (ie. 7) and the inherent biases involved in faecal analysis (discussed in 7.3.1) only limited information was obtained on chick diet. Faecal samples were obtained from chicks of various ages which were present on different habitats.

Surface-active invertebrates formed the major component of

Table 8.5. Locations of sightings of successful whimbrel broods in relation to habitat availability within potential brood ranges

HABITAT	TOTAL AREA WITHIN POTENTIAL BROOD RANGE (ha)	PROPORTION OF TOTAL AREA (P)	TOTAL NO. OF SIGHTINGS IN HABITAT	EXPECTED NO. OF SIGHTINGS IN HABITAT+	PROPORTION OF SIGHTINGS IN EACH HABITAT	95% CONFIDENCE INTERVAL FOR THE PROPORTION OF SIGHTINGS
HEATHLAND	850	0.74	178	202	0.65	0.58-0.72
MIRE	81	0.07	36	19	0.13	0.08-0.18
RE-SEED	110	0.10	47	27	0.17	0.11-0.23
ESTABLISHED PASTURE	109	0.09	12	19	0.04	0.01-0.07
TOTAL	1150		273	273		

The difference between the observed and expected number of sightings is significant: $X^2 = 39.6$; d.f. = 3; $p<0.001$.

Notes: +calculated by multiplying P for each habitat by the total number of sightings (i.e. 273).
Data for all types of re-seed are combined due to small expected values for surface re-seeds.

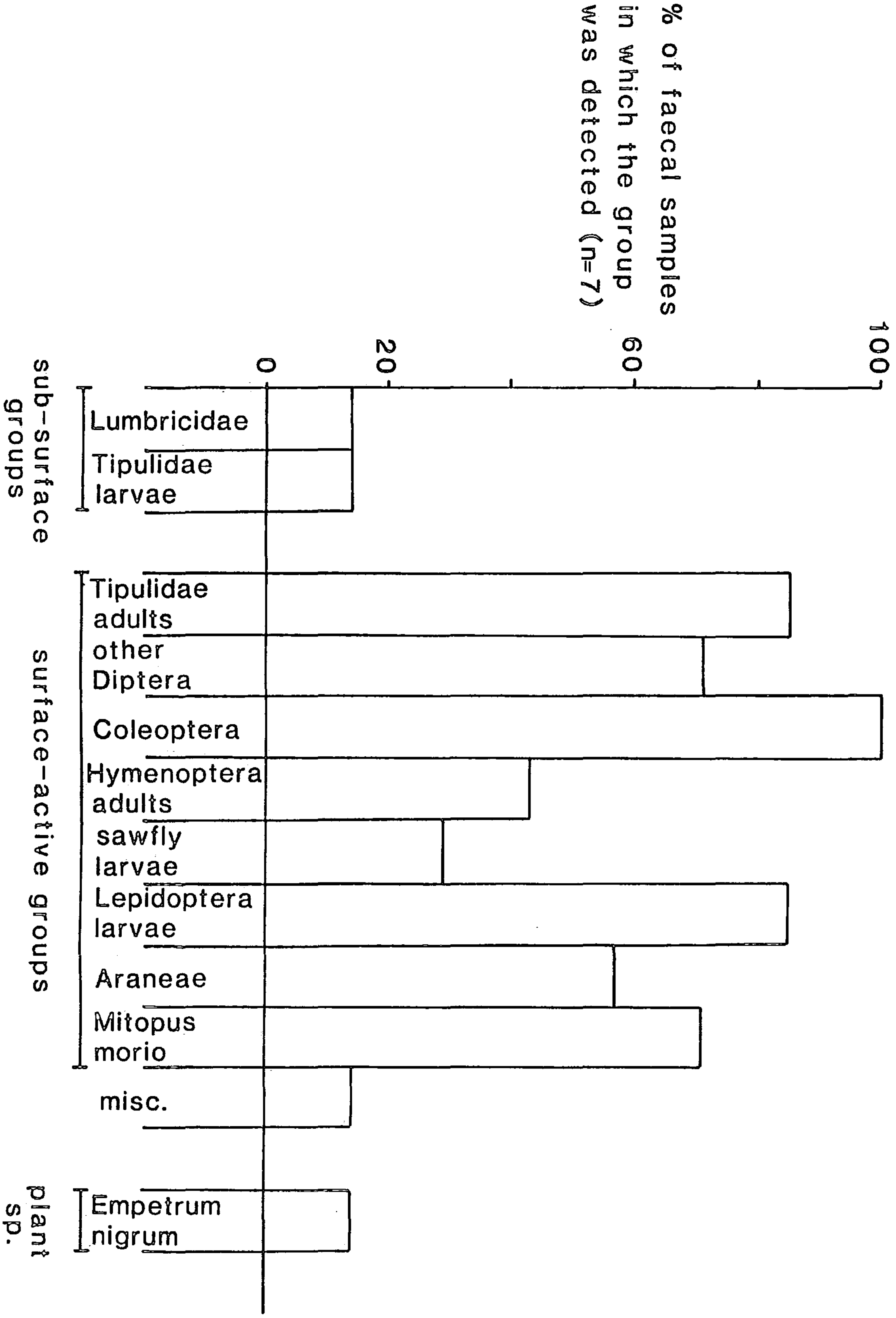
Table 8.6. Locations of sightings of successful whimbrel broods which used both heathland and other habitats in relation to habitat availability within observed brood ranges

HABITAT	TOTAL AREA WITHIN POTENTIAL BROOD RANGE (ha)	PROPORTION OF TOTAL AREA (P)	TOTAL NO. OF SIGHTINGS IN HABITAT	EXPECTED NO. OF SIGHTINGS IN HABITAT+	PROPORTION OF SIGHTINGS IN EACH HABITAT	95% CONFIDENCE INTERVAL FOR THE PROPORTION OF SIGHTINGS
HEATHLAND	52	0.49	72	82	0.43	0.33-0.52
MIRE	22	0.21	36	35	0.22	0.14-0.30
RE-SEED	18	0.17	47	28	0.28	0.19-0.37
ESTABLISHED PASTURE	14	0.13	12	22	0.07	0.02-0.12
TOTAL	106		167	167		

The difference between the observed and expected number of sightings is significant; $X^2 = 18.7$; d.f. = 3; $p<0.001$

Notes: +calculated by multiplying P for each habitat by the total number of sightings (i.e. 167)
Data for all types of re-seed are combined due to small expected values for surface re-seeds.

Figure 8.2. Occurrence of different food items in the faeces of whimbrel chicks.


% of faecal samples in which the group was detected (n=7)
0
20
60
100
sub-surface groups
Lumbricidae
Tipulidae larvae
surface-active groups
Tipulidae adults
other Diptera
Coleoptera
Hymenoptera adults
sawfly larvae
Lepidoptera larvae
Araneae
Mitopus morio
misc.
plant sp.
Empetrum nigrum

faecal samples (Fig. 8.2) and during brood studies chicks were never observed probing below the ground surface. Almost all invertebrate groups found in the faeces were medium to large sized invertebrates. All adult Diptera found were from the families Tipulidae, Cordilurinae, and either Muscidae and/or Calliphoridae, whilst the Araneae in faeces were comprised of the Thomisidae and Lycosidae families. Amongst the Coleoptera, however, smaller prey items were taken and over 50% of individuals identified belonged to the family Curculionidae.

Empetrum nigrum was not an important food source for chicks. It was abundant only at site 5 and the berries did not begin to ripen until the end of the chick-rearing period. Fragments of other plant material (e.g. grass leaves and seeds) and pieces of grit were also found in the faeces.

8.2.4 Chick Food Supply in Different Habitats

Data on surface-active invertebrate biomass were examined in two ways. First, in terms of the biomass of the invertebrate families or orders which were known to occur in the chicks' diet (subsequently referred to as food-item biomass), and secondly in terms of the biomass of all invertebrate species found in samples (subsequently referred to as total-item biomass). (The various invertebrate orders obtained in samples are listed in Appendix 4).

Data from both sampling periods (ie. early and late chick-rearing) were combined since food-item biomass did not differ significantly between these periods at more than one, and total-item biomass at two, of the 22 sites or fields which were sampled.

Considerable variation in both food-item and total-item biomass occurred between different study sites or fields within a habitat-type (Table 8.7). Limiting the comparison between habitats to those occurring within the same study site produced significant differences in food-item biomass only at sites 4 and 5 (Fig. 8.3). At site 4 this was due to one established pasture field in which food-item biomass was particularly high. At site 5 food-item biomass in the mire was significantly greater than in the other habitats, and biomass in heathland was significantly greater than in certain improved fields (Table 8.8). Total-item biomass differed significantly between habitats on all study sites except site 3 (Fig. 8.4). Improved habitats and mires generally held a greater biomass of all surface-active invertebrates than heathland (Fig. 8.4 and Table 8.9). There was no consistent trend in the differences between re-seeds and established pastures.

8.2.5 Habitat-Use and Food Supply

In the following analysis the potential range of a brood is considered to be the area determined by a circle centred on the nest, with a radius equal to the maximum distance that the brood was recorded from the nest. Neither food-item biomass nor total-item biomass differed significantly between those improved fields or mires which were used by broods in 1988 and those improved fields which were not used but were within the potential range of at least one brood (Table 8.10). There was no significant trend for broods to use fields or mires in which either food-item biomass or total-item biomass were greater than in fields or mires within their potential

Table 8.7. Kruskal-Wallis tests of variability in the biomass of; (i) all surface-active invertebrates; and (ii) only those that were taken by whimbrel chicks, amongst different sites

HABITAT	BIOMASS OF	NO. DIFFERENT SITES/FIELDS	KRUSKAL-WALLIS, X^2	d.f.	TOTAL NO. OF CASES
HEATHLAND	(i) TOTAL-ITEMS	5	13.8**	4	178
	(ii) CHICK FOODS		16.4**		
MIRE	(i) TOTAL-ITEMS	2	8.9**	1	60
	(ii) CHICK FOODS		8.4**		
SURFACE RE-SEEDS	(i) TOTAL-ITEMS	4	9.4*	3	110
	(ii) CHICK FOODS		6.5NS		
PLOUGHED/HARROWED RE-SEEDS	(i) TOTAL-ITEMS	4	52.5***	3	110
	(ii) CHICK FOODS		2.2NS		
ESTABLISHED PASTURE	(i) TOTAL-ITEMS	7	38.4***	6	140
	(ii) CHICK FOODS		21.7***		

NS $p>0.05$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

Notes: comparisons are based on the data shown in Figs. 8.3. and 8.4. A Kruskal-Wallis test is used due to the large number of samples which contained few invertebrates, thus causing the data to be skewed in their distribution.

Figure 8.3. The biomass of surface-active invertebrate groups known to be taken by whimbrel chicks, on different habitats within each study site.

Kruskal-Wallis tests of variability amongst habitats:-

Site 1. $X^2=3.8$, d.f.=2, $p>0.10$

Site 2. $X^2=2.0$, d.f.=4, $p>0.10$

Site 3. $X^2=1.3$, d.f.=3, $p>0.10$

Site 4. $X^2=16.4$, d.f.=3, $p<0.001$

Site 5. $X^2=32.7$, d.f.=5, $p<0.001$

(Note, details of comparisons for each pair of habitats on sites 4 and 5 are given in Table 8.8).

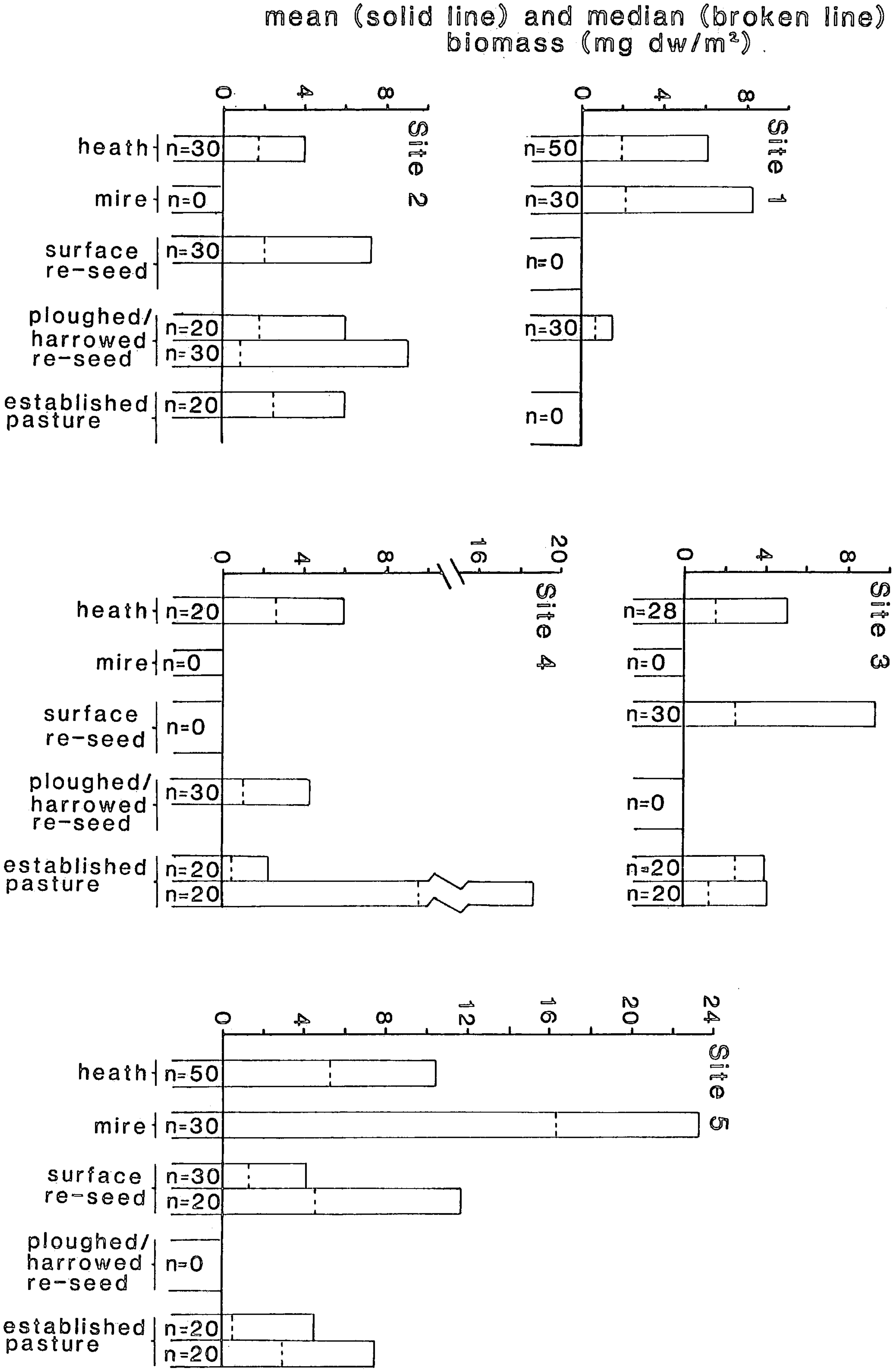

mean (solid line) and median (broken line)
biomass (mg dw/m²)
Site 2
Site 1
Site 4
Site 3
Site 5
0
4
8
12
16
20
24
heath
mire
surface re-seed
ploughed/ harrowed re-seed
established pasture
n=30
n=0
n=30
n=20
n=30
n=20
n=50
n=30
n=0
n=30
n=0
n=20
n=0
n=0
n=30
n=20
n=20
n=28
n=0
n=30
n=0
n=20
n=20
n=50
n=30
n=30
n=20
n=0
n=20
n=20

Table 8.8. Pairs of habitats within a study site in which the biomass of surface-active invertebrate groups known to be taken by whimbrel chicks differed significantly (see Fig. 7.3.)

		Z-VALUES (CALCULATED FROM THE MANN-WHITNEY TEST)				
SITE	HABITAT (n)	HEATHLAND (n)	MIRE(n=30)	SURFACE RE-SEED (n)	PLOUGHED/HARROWED RE-SEED (n)	ESTABLISHED PASTURE (n)
4.	ESTABLISHED PASTURE (20)	2.28(20)*	-	-	3.17***	3.65***
5.	MIRE (30)	2.36(50)*	-		-	
	SURFACE RE-SEED (30)	3.50(50)***	4.07***	2.49(20)**	-	
	SURFACE RE-SEED (20)	NS	1.90*		-	2.71**
	ESTABLISHED PASTURE (20)	3.80(50)***	3.79***		-	NS
	ESTABLISHED PASTURE (20)	NS	2.44**	NS	-	

NS $p>0.05$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

Note: n = no. of samples taken from each habitat, or individual improved field, at each study site.

Figure 8.4. The biomass of all surface-active invertebrate groups on different habitats within each study site.

Kruskal-Wallis tests of variability amongst habitats:-

Site 1. $X^2=25.0$, d.f.=2, $p<0.001$

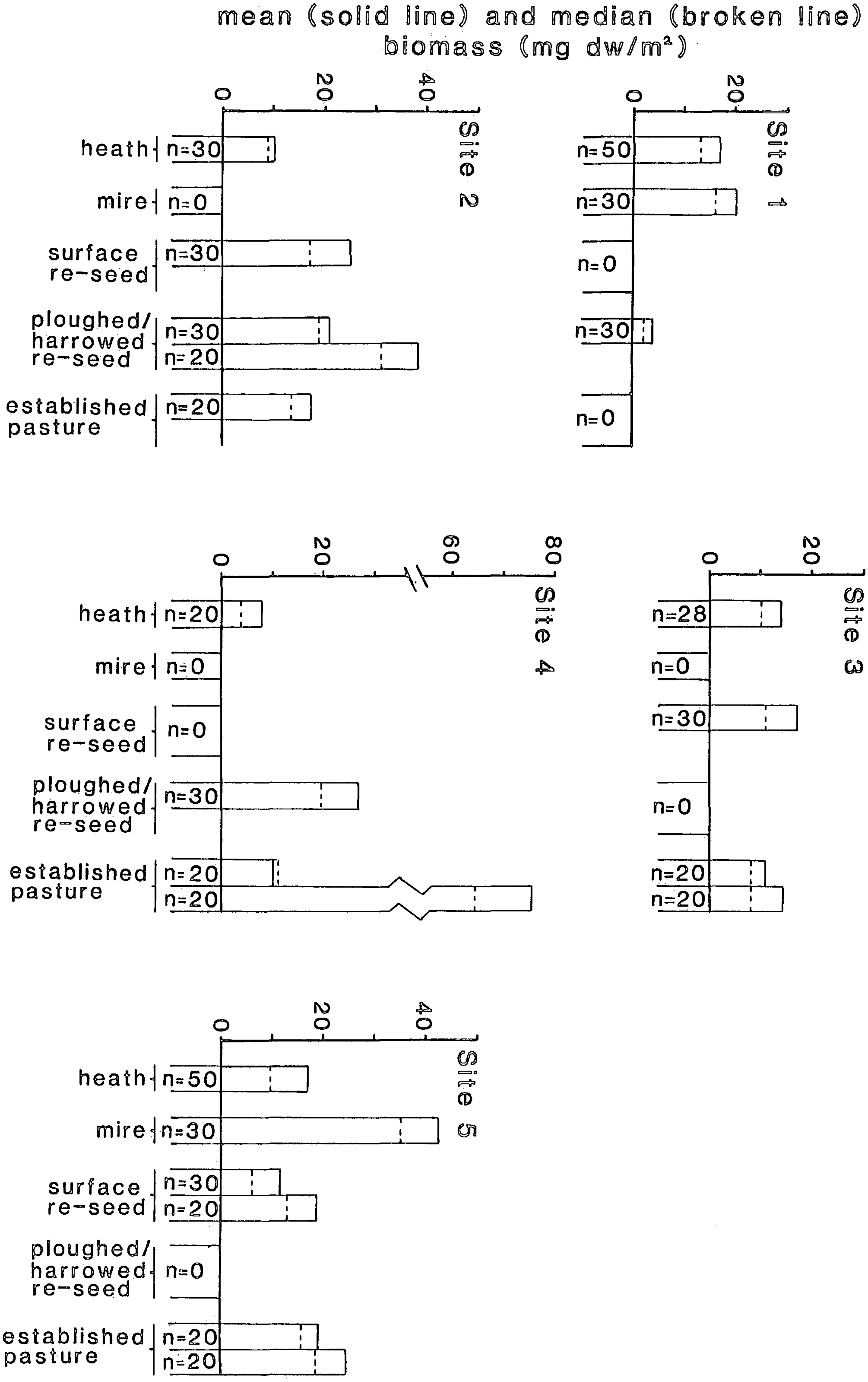
Site 2. $X^2=30.1$, d.f.=4, $p<0.001$

Site 3. $X^2=0.6$, d.f.=3, $p>0.10$

Site 4. $X^2=38.5$, d.f.=3, $p<0.001$

Site 5. $X^2=28.5$, d.f.=5, $p<0.001$

(Note, details of comparisons for each pair of habitats on sites 1, 2, 4, and 5 are given in Table 8.9).



mean (solid line) and median (broken line)
biomass (mg dw/m²)
Site 1
Site 2
Site 3
Site 4
Site 5
0
20
40
60
80
heath
mire
surface re-seed
ploughed/ harrowed re-seed
established pasture
n=50
n=30
n=0
n=28
n=20

Table 8.9. Pairs of habitats within a study site in which the biomass of all surface-active invertebrate groups differed significantly (see Fig. 8.4.)

Z-VALUES (CALCULATED FROM THE MANN-WHITNEY TEST)

SITE	HABITAT	HEATHLAND (n)	MIRE (n=30)	SURFACE RE-SEED (n)	PLOUGHED/HARROWED RE-SEED (n)	ESTABLISHED PASTURE (n=20)
1.	PLOUGHED/HARROWED RE-SEED (30)	5.13(50)***	3.39***	-	-	-
2.	SURFACE RE-SEED (30)	2.55(30)**	-	-		NS
	PLOUGHED/HARROWED RE-SEED (20)	5.13(30)**	-	2.59(30)**	2.97(30)**	3.46***
	PLOUGHED/HARROWED RE-SEED (30)	3.21(30)**	-	NS		NS
4.	PLOUGHED/HARROWED RE-SEED (30)	3.62(20)***	-	-	-	
	ESTABLISHED PASTURE (20)	NS	-	-	2.74(30)**	4.57***
	ESTABLISHED PASTURE (20)	4.77(20)***	-	-	3.56(30)**	
5.	MIRE (30)	3.61(50)***	-		-	
	SURFACE RE-SEED (30)	2.29(50)*	4.29***	2.11(20)*	-	
	SURFACE RE-SEED (20)	NS	2.78**		-	
	ESTABLISHED PASTURE (20)	NS	2.61**	2.62(30)** NS	-	
	ESTABLISHED PASTURE (20)	NS	NS	2.91(30)** NS	-	

NS $p>0.05$ *$p<0.05$ **$p<0.01$ ***$p<0.001$

Note: n = no. of samples taken from each habitat, or individual improved field, at each study site.

Table 8.10. Differences in the biomass of surface-active invertebrates between those improved fields or mires which were used by whimbrel broods in 1988 and those which were not used despite being within potential brood ranges

	BIOMASS (MEAN ± 1 S.E.; mg dw/m^2)			
	FOODS OF WHIMBREL CHICKS		ALL SURFACE-ACTIVE GROUPS	
FIELDS/MIRES USED (n=8)	2.66±0.61	t=1.16NS d.f. = 10	7.89±1.80	t=1.44NS d.f. = 10
FIELDS/MIRES NOT USED (n=4)	1.16±0.40		3.92±1.29	

NS p>0.10

Table 8.11. Use of habitats by whimbrel broods in relation to the biomass of surface-active invertebrates

	% BROODS USING HABITAT WITH GREATEST BIOMASS OF:-	
	(i) FOODS OF WHIMBREL CHICKS	(ii) ALL SURFACE-ACTIVE GROUPS
1. FIELD/MIRE USED vs. FIELD/MIRE NOT USED BUT WITHIN BROOD'S POTENTIAL RANGE (n=9 BROODS)	67% NS	78% NS
2. HEATHLAND IN WHICH NESTED vs. FIELD MIRE USED (n=10 BROODS)	80% NS	90%*
3. HEATHLAND IN WHICH NESTED vs. FIELD/MIRE NOT USED BUT WITHIN BROOD'S POTENTIAL RANGE (n=7 BROODS)	43% NS	29% NS

NS $p>0.05$ *$p<0.05$

Note: significance values calculated using the Sign Test.

range which were not used (Table 8.11). A significant proportion of broods used fields or mires in which total-item (but not food-item) biomass was greater than on the heathland used for nesting. However, this result provided little evidence for an association between habitat-use and invertebrate biomass since fields or mires which were not used also tended to have a greater total-biomass than heathland (though the tendency was not significant in this case).

8.2.6 Habitat-Use and Vegetation Structure

With respect to vegetation structure, by early chick-rearing, re-seeds and established pastures could be classed into the following two categories:-

(i) Fields which had been grazed so that a short grass sward was produced.

(ii) Fields which had been left largely ungrazed (usually to be cut as hay) so that the vegetation had become tall and dense (often reaching a height of 30 to 40cm - see Fig. 8.5).

Both categories of field were used by broods and there were no differences in the stage of chick-rearing at which broods first entered such fields (Table 8.12). Broods also moved into mires at a similar stage of chick-rearing. By then the vegetation in mires, as in ungrazed fields, was usually taller and denser than on heathland.

8.2.7 Chick Survival

The relationship between chick age and survival was similar in each year of the study, with over 80% of all chick mortality occurring between hatching and 14 days (Fig. 8.6). Survival of chicks to fledging did not differ according to whether or not broods used re-seeds, or to whether or not broods used habitats other than heathland (Table 8.13).

Figure 8.5. Photographs illustrating the differences in the vegetation structure between; a) a ploughed or harrowed re-seed which had been grazed from mid. May to early June; and b) a ploughed or harrowed re-seed which was used as a hayfield, and had been left ungrazed from mid. May to early June. (Notes; (i) the canes in the photographs are 60cm high and are marked at 5cm intervals; and (ii) both photographs were taken during the early chick-rearing period of 1987).

a)

b)

Table 8.12. First use of improved fields and mires by whimbrel broods in relation to the age of chicks

HABITAT/FIELD TYPE	DAYS SINCE HATCHING; ± 1 S.E.	
GRAZED FIELD	12.4±2.9 (n=14)	F = 0.17NS d.f. = 2, 39
UNGRAZED FIELD	14.1±2.7 (n=14)	
MIRE	11.4±2.4 (n=14)	

NS p>0.10

Note: vegetation in ungrazed fields and mires was tall and dense.

Figure 8.6. The survival of chicks from hatching to fledging in each year of study. Survival rates differed significantly between the four periods of each survival curve:-

1986. $X^2=17.5$, d.f.=3, $p<0.001$

1987. $X^2=11.6$, d.f.=3, $p<0.01$

1988. $X^2=20.0$, d.f.=3, $p<0.001$

(Note, there was a slight tendency for broods which failed to be over represented in the sample for which details on survival throughout chick-rearing were obtained).

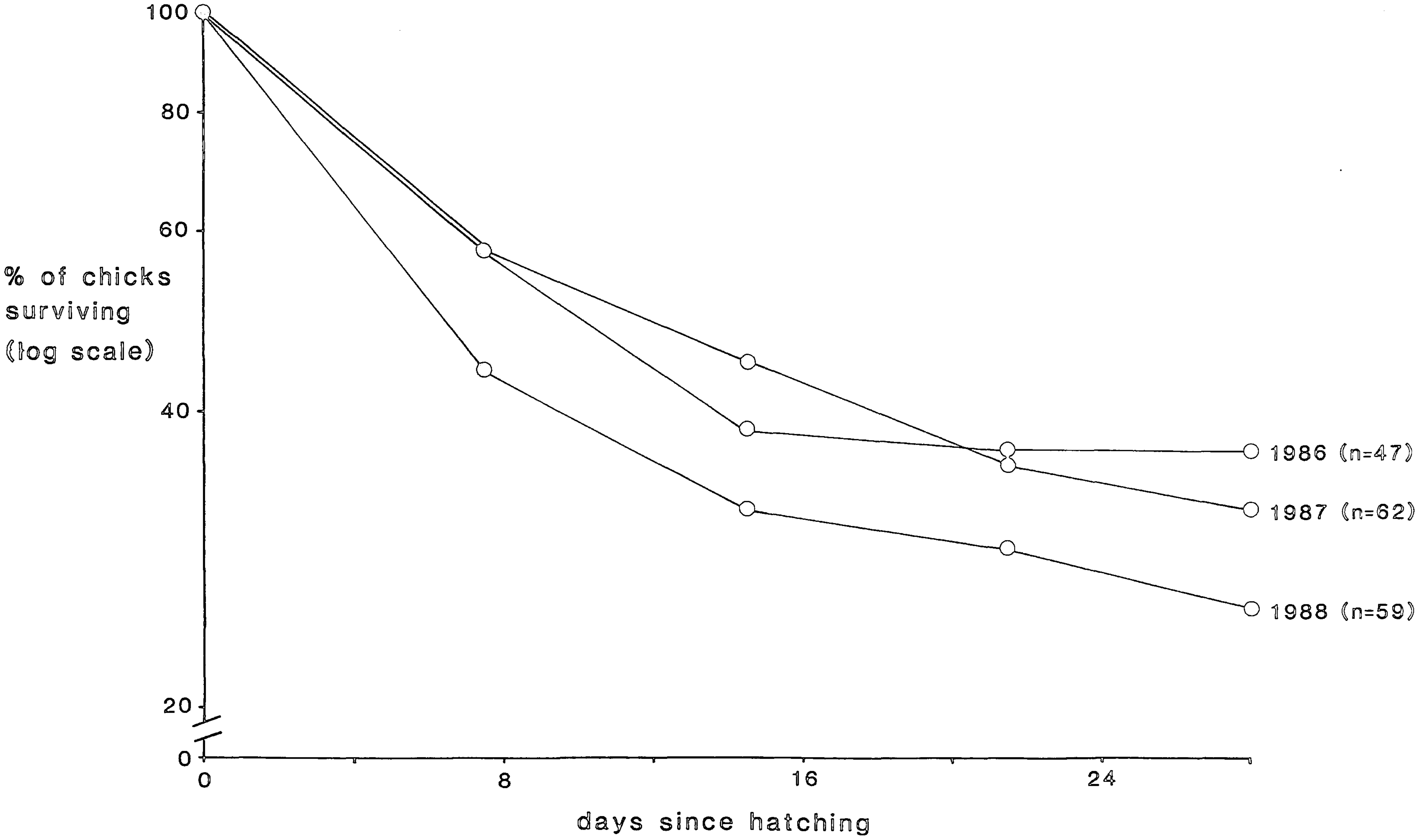

% of chicks
surviving
(log scale)
100
80
60
40
20
0
0
8
16
24
days since hatching
1986 (n=47)
1987 (n=62)
1988 (n=59)

Table 8.13. Chick survival between hatching and fledging in relation to habitat-use by broods

HABITATS	% SURVIVAL 1986	 1987	 1988	ALL YEARS COMBINED	
RE-SEEDS NOT USED	35 (n=48)	36 (n=44)	31 (n=62)	34 (n=154)	X^2 = 0.62NS d.f. = 1
RE-SEEDS USED	36 (n=14)	18 (n=33)	34 (n=29)	28 (n=76)	
HEATHLAND ONLY	37 (n=35)	41 (n=32)	33 (n=39)	37 (n=106)	X^2 = 1.90NS d.f. = 1
OTHER HABITATS USED	33 (n=27)	20 (n=45)	31 (n=52)	27 (n=124)	

NS p >0.10

Notes: n = no. of chicks.
Differences in each year are not significant

8.3 DICUSSION

8.3.1 Habitat Selection

The two methods used to assess habitat availability for broods (and therefore habitat selection) were subject to different biases. Since exclusive territories were usually maintained an equal area of land in any direction of the nest-site would not have been available to most broods (as was assumed by calculating the areas of each habitat within a circle centred on the nest and with a radius equal to the maximum distance that the brood was recorded from the nest). Thus areas of habitat which were not available to some broods would have been included in this analysis. The second method of analysing habitat selection was limited to those broods which used other habitats in addition to heathland, since broods remaining on heathland may not have had access to these other habitats. By limiting the analysis to the areas of each habitat which were within the observed ranges of these broods, areas of habitat which were avoided may have been omitted.

Despite the different biases, both methods of analysis indicated that whimbrel broods selected re-seeds and avoided established pastures. Whilst there was some evidence for an avoidance of heathland by broods, in terms of overall use this was still the most important habitat at chick-rearing. Further, since broods did not generally move off heathland until the chicks were at least ten days old, this habitat may be of particular importance in the early (and most vulnerable) stages of a chick's life.

8.3.2 Factors Determining Habitat-Use

Chicks may have benefited by moving from heathland into other habitats if this either decreased the risk of predation and/or increased their food supply.

In mires and ungrazed fields the height and density of vegetation was greater than in heathland, and so cover from predators for chicks was potentially greater than on heathland. However, broods did not usually move into these habitats until after the period of most mortality. Broods also used grazed fields which provided no extra cover for chicks, and where chicks were less well camouflaged than on heathland. Therefore, movement from heathland into other habitats was not associated with decreasing the risk of predation on chicks.

In several species of precocial birds selection for particular habitats has been associated with an increased food supply for chicks (e.g. for various gamebird species - Green 1984, Hill 1985, and Erikstad 1985; and for lapwings - Galbraith 1988a). In this study there were no consistent differences between habitats in the biomass of those invertebrate groups known to be taken by chicks, and the most notable aspect of these comparisons was the considerable variability between the different sites or fields within a habitat-type. It is possible that other invertebrate groups were taken by chicks but were not identified by faecal analysis (due to the small sample size and the possibility that faeces would contain no recognisable fragments of invertebrates which possess few hard parts - e.g. adult Trichoptera). In terms of all surface-active invertebrates, biomass was greater in re-seeds than in heathland but biomass was also greater in established pastures than in heathland, and established pastures were avoided by broods.

There was no significant trend for broods to use those particular fields or mires in which invertebrate biomass was greatest. However, these comparisons only considered whether or not a field or mire had been used by a brood, and too little data were available to consider actual selection for particular fields or mires. Further, studies of diet were not sufficiently detailed to determine whether certain prey items were of particular importance to whimbrel chicks. Therefore, these results do not conclusively demonstrate the lack of a relationship between food supply and selection for particular fields or mires.

During pre-laying and incubation, re-seeds often provided particularly suitable feeding areas for adult whimbrel due to the abundance of tipulid larvae which appeared to be the preferred prey of adults (7.3.5). <u>Tipula paludosa</u> was usually the largest and most abundant species in re-seeds, comprising 62% (n=103) of adult tipulids caught in pitfall traps in three different re-seeds from late April to mid. August, 1986. The main emergence period of this species began in late July so that tipulid larvae (or pupae) were still abundant in re-seeds during chick-rearing. It is possible that adults led their broods into re-seeds in order to improve their own food supply (and possibly to reduce overlap with chick diet), whilst enabling them to remain within close proximity of their chicks (which is presumably important for the purposes of protecting the chicks against predators).

Irrespective of which factors caused selection for re-seeds during chick-rearing, any benefits to be gained from this were not reflected in improved chick survival and were not sufficient to cause a large scale movement of broods off heathland and into re-seeds (as appears to occur in the Faeroes, where whimbrel have been recorded moving over 1.5km from heathland into improved land - Williamson 1946). This was also true for other non heathland habitats which were used by broods.

9. PRODUCTIVITY AND THE INFLUENCE OF BREEDING SITE

9.1 METHODS

Nests were located as described in 4.1.2, and the breeding success of pairs determined as described in 6.1.

Estimates of chick survival and fledging success were made for only 70-75% of the broods on study sites in each year. To estimate the productivity of the whole study population (ie. the mean number of chicks fledged per pair) it was necessary to extrapolate to those broods for which fledging success was not measured.

In both later years of the study, the territories of those broods for which fledging success was not determined were visited 28-30 days after hatching. Whether or not broods had fledged chicks was assessed by the presence and behaviour of the adults. This was possible since broods usually remained within 400m of the nest-site (8.2.1), and because the behaviour of adults with chicks was conspicuous and characteristic (ie. adults with chicks would fly distances of up to 400m to scold approaching intruders). For five of the nine broods which were assessed by this method to have been successful, confirmation was obtained by sightings of fledglings.

In 1987 and 1988 this method was used to determine the number of pairs which fledged chicks in all five study sites. The average fledging success per pair in these years was then estimated by assuming that chicks in the successful broods for which fledging success was not known had survived at the same rate as chicks in successful broods for which the fledging success had been determined.

In 1986 the total number of pairs which fledged chicks was not known. Average fledging success in this year was estimated by assuming that the survival rate of all chicks hatched was equivalent to that for the sample of chicks which had been studied.

In 1986 the broods which were studied to fledging were selected to represent a proportion from each study site. Results from that year indicated that fledging success varied between study sites and so in later years the broods studied were selected to provide comparisons between those sites considered likely to show most variation in fledging success. Thus in 1987 and 1988, 67% of broods on site 1, and all broods on sites 2, 4, and 5 (excluding the latest brood in 1988) were studied.

9.2 RESULTS

9.2.1 Overall Productivity

Differences between the estimated average fledging success per pair in each year could not be tested statistically due to the approximate methods of calculation. However, the estimated fledging success was similar in each year, and none of the parameters on which this estimate was based differed significantly between years (Table 9.1).

Mortality rates during chick-rearing were higher than those of eggs between laying and hatching. Of all eggs found (n=449), 28% failed prior to hatching, whilst mortality of chicks between hatching and fledging accounted for an estimated 49% of all the eggs which were found. (Note, the figure for egg losses is probably a slight

Table 9.1. Overall productivity of whimbrel, 1986-88 (data from all study sites combined)

	[1]CLUTCH-SIZE PER PAIR MEAN ± 1 S.E.		[1]HATCHING SUCCESS PER PAIR MEAN ± 1 S.E.		% OF HATCHED CHICKS FLEDGING FROM STUDY BROODS		% OF PAIRS FLEDGING AT LEAST ONE CHICK		[2]ESTIMATED MEAN FLEDGING SUCCESS PER PAIR
1986	3.49±0.14 (n=35)		2.57±0.25 (n=35)		35.5 (n=62)		-		0.91 (n=35)
[4]1987	3.75±0.08 (n=40)	[3]X^2=1.3NS d.f. = 2	2.58±0.24 (n=41)	[3]X^2=0.4NS d.f. = 2	29.1 (n=79)	X^2=0.9NS d.f. = 2	43.9 (n=41)	X^2=0.1NS d.f. = 1	0.90 (n=41)
[4]1988	3.70±0.10 (n=45)		2.89±0.20 (n=45)		31.9 (n=91)		38.6 (n=44)		0.75 (n=44)

NS $p>0.10$

Notes:

1. figures exclude the failed first clutches of any pairs which re-laid
2. see text for methods of estimating this figure (S.E. not attached due to approximate nature of the estimate)
3. these X^2 values are calculated from the Kruskal-Wallis test, due to the large proportion of clutches and broods of 4.
4. sample sizes for the number of pairs differs within both 1987 and 1988, since in 1987 one clutch was observed being predated before it had been found (and therefore the clutch-size was unknown), and in 1988 the fate of the latest brood could not be determined due to termination of the study.

underestimate since some clutches of less than four eggs may have suffered partial predation prior to their location).

Predation of eggs was the main cause of failure between laying and hatching, accounting for 45% of known egg losses at this stage (n=126). Successful predation on nests was observed on only one occasion, and in this case both hooded crows and arctic skuas (*Stercorarius parasiticus*) were involved. Several unsuccessful predation attempts by arctic skuas were also observed. Addling and embryo death accounted for 23% and 12% of egg failures respectively, whilst other smaller losses were due to trampling, desertion, and predation of a breeding adult (probably by a great skua, *Catharacta skua skua*).

Causes of chick mortality could not usually be ascertained. Predation of chicks by arctic skuas was observed twice and by herring gulls (*Larus argentatus*) once. Attempted predation by arctic skuas was also observed on several occasions. All such attempts were made on chicks which were less than ten days old. Other likely causes of chick mortality, particularly for young chicks, included chilling and starvation.

9.2.2 Inter-Site Differences in Productivity

Since breeding success data were most complete in 1987 and 1988, comparisons of productivity on different study sites are limited to those two years.

Neither clutch-size nor hatching success differed significantly between study sites in either year (Table 9.2). However, there were marked differences between study sites in the average fledging success per pair (estimated for site 1 as in 9.1) and this was primarily due to differences in chick survival (Table 9.3). On the four sites in which chick survival was studied, survival was highest in both years on sites 4 and 1 and lowest on sites 2 and 5 (though none of the differences between sites 1 and 2 were significant). Four of the five broods on site 3 successfully reared chicks in 1987, but in 1988 all seven broods on this site appeared to have failed (no adults being present by the expected fledging dates).

9.2.3 Possible Causes of Differential Productivity Between Study Sites

(i) Nesting Densities. Although density was highest on one of the two sites (ie. site 1) in which fledging success was consistently high, it was lowest on site 4 where fledging success was also high (see 4.2.4). Also, within study sites, there were no significant correlations between nearest neighbour distance and either fledging success or chick survival (ie. magnitude of $r<0.35$, $p>0.10$, for each site in each year of the study).

(ii) Associated Differences in Hatchling Weights, Laying Dates, and Breeding Experience. Both average chick weight at hatching and dates of laying were correlated with chick survival and/or fledging success in certain years of this study (6.2).

Mean hatchling weights did not differ significantly between study sites in either year (ie. in 1987; $F=0.64$, d.f.=4, 28, $p>0.10$; and in 1988; $F=1.24$, d.f.=4, 34, $p>0.10$). Thus, differences in chick survival between study sites were not due to associated differences in hatchling weights.

Table 9.2. Clutch size and hatching success of whimbrel on five study sites

	CLUTCH SIZE PER PAIR; MEAN ± 1 S.E.				HATCHING SUCCESS PER PAIR; MEAN ± 1 S.E.			
SITE	1987		1988		1987		1988	
1.	3.93±0.07 (n=14)		3.77±0.17 (n=13)		2.71±0.40 (n=14)		3.38±0.33 (n=13)	
2.	3.83±0.17 (n=6)		3.14±0.40 (n=7)		2.00±0.77 (n=6)		2.57±0.61 (n=7)	
3.	3.67±0.33 (n=6)	$X^2=6.9$NS d.f. = 4	3.75±0.16 (n=8)	$X^2=5.7$NS d.f. = 4	2.83±0.65 (n=6)	$X^2=0.9$NS d.f. = 4	2.75±0.45 (n=8)	$X^2=3.7$NS d.f. = 4
4.	3.67±0.33 (n=3)		3.50±0.29 (n=4)		3.00±0.00 (n=3)		2.75±0.95 (n=4)	
[1]5.	3.54±0.21 (n=11)		3.67±0.17 (n=13)		2.50±0.48 (n=12)		2.46±0.40 (n=13)	

NS p>0.10

Notes: 1. sample sizes in 1987 differ since one clutch was observed being predated before it had been found (and therefore clutch-size, but not hatching success, was unknown).

All X^2 values are calculated from the Kruskal-Wallis test, due to the large proportion of clutches and broods of 4.

Data excludes any failed first clutches of pairs which re-laid.

Table 9.3. Survival of chicks from hatching to fledging and productivity of whimbrel on four study sites, 1987-88

SITE	% OF HATCHED CHICKS FLEDGING FROM STUDY BROODS			[1]MEAN FLEDGING SUCCESS PER PAIR; ± 1 S.E. (FOR SITES 2, 4)		
	1987	1988	TOTAL	1987	1988	TOTAL
1.	53.6 (n=28)	36.4 (n=33)	44.3 (n=61)	1.36 (n=14)	1.15 (n=13)	1.26 (n=27)
2.	16.7 (n=12)	27.8 (n=18)	23.3 (n=30)	0.33±0.33 (n=6)	0.71±0.36 (n=7)	0.54±0.24 (n=13)
4.	55.5 (n=9)	63.6 (n=11)	60.0 (n=20)	1.67±0.88 (n=3)	1.75±0.85 (n=4)	1.71±0.56 (n=7)
5.	3.3 (n=30)	17.2 (n=29)	10.2 (n=59)	0.08±0.08 (n=12)	0.42±0.23 (n=12)	0.25±0.12 (n=24)

Notes: 1. since chick survival was determined for only a proportion of the broods on site 1, fledging success is estimated approximately and no S.E. is attached (see text for method of estimation).

Differences in chick survival are significant; between sites 1 and 5 in 1987 (i.e. $X^2 = 15.9$, d.f. = 1, $p<0.001$) and for both years combined (i.e. $X^2 = 15.8$, d.f. = 1, $p<0.001$); between sites 2 and 4 for both years combined (i.e. $X^2 = 5.4$, d.f. = 1, $p<0.05$); and between sites 4 and 5 in 1987 (i.e. $X^2 = 10.8$, d.f. = 1, $p<0.01$), 1988 (i.e. $X^2 = 6.1$, d.f. = 1, $p<0.05$), and both years combined (i.e. $X^2 = 18.3$, d.f. = 1, $p<0.001$).
For sites 2,4 and 5, differences in fledging success are significant between sites 4 and 5 for both years combined (i.e. $Z = 2.94$, $p<0.01$; note, Z-value is calculated from the Mann-Whitney test).

In both 1987 and 1988, seasonal declines in chick survival were abrupt rather than gradual and all clutches laid more than 11 days after the first clutch in each year failed to produce fledglings (6.2.1). Approximately 70% of such late clutches occurred on site 5 where chick survival was poorest (Table 9.4). Limiting comparisons of chick survival to clutches which were laid within 11 days of the first clutch for that year demonstrated that inter-site differences were still apparent, at least in 1987 (Table 9.5). Since all clutches laid later than 11 days after the first clutch in 1987 occurred on site 5, the relationship between chick survival and laying date in 1987 may have been due to the associated inter-site variation in chick survival. This did not appear to be the case in 1988 when late broods on sites 1 and 2 also failed, and when inter-site variation amongst the earlier broods was not significant. Limiting these comparisons of chick survival to clutches laid within 11 days of first laying is somewhat arbitrary. However, analyses of covariance also demonstrated that differences between study sites contributed significantly to variation in chick survival and fledging success, irrespective of laying date (Table 9.6).

Evidence presented in chapter 6 indicated that female breeding experience may also have been involved in causing the relationship between fledging success and laying date (ie. such that females with previous breeding experience tended to lay earlier, and may have been able to rear chicks more successfully, than inexperienced females). Since late clutches were most frequent on site 5, differences in the proportions of experienced females on study sites was another possible cause of inter-site variation in productivity. However,

Table 9.4. Occurrence of late clutches on different study sites, 1987-88. (Late clutches are defined as those laid more than 11 days after the first clutch for that year)

	% OF CLUTCHES LAID LATE ON EACH SITE				
	1.	2.	3.	4.	5.
1987:	0.0 (n=12)	0.0 (n=5)	0.0 (n=5)	0.0 (n=3)	55.5 (n=9)
1988:	7.7 (n=13)	42.9 (n=7)	0.0 (n=7)	0.0 (n=4)	41.7 (n=12)
TOTAL:	4.0 (n=25)	25.0 (n=12)	0.0 (n=13)	0.0 (n=7)	47.6 (n=21)

comparing sites 1 to 4 with site 5, for both years combined; $X^2 = 14.5$, d.f. = 1, $p<0.001$.

Note: re-laid clutches are included.

Table 9.5. Survival of chicks from hatching to fledging on different study sites: comparison of early and late broods

% OF HATCHED CHICKS FLEDGING FROM STUDY BROODS

SITE	1987 EARLY BROODS	1987 LATE BROODS	1988 EARLY BROODS	1988 LATE BROODS
1.	53.6 (n=28)		41.4 (n=29)	0.0 (n=4)
2.	16.7 (n=12)		41.7 (n=12)	0.0 (n=6)
4.	55.5 (n=9)		63.6 (n=11)	
5.	6.2 (n=16)	0.0 (n=14)	25.0 (n=20)	0.0 (n=9)

Note: early broods are from clutches laid within 11 days of the first clutch for that year.

Differences in chick survival from early broods are significant in 1987, between sites 1 and 5 ($X^2 = 7.9$, d.f. = 1, $P<0.01$) and sites 4 and 5 ($X^2 = 5.2$, d.f. = 1, $p<0.05$), but not in 1988 (i.e. $X^2 = 5.4$, d.f. = 3, $P>0.10$).
Within sites none of the differences in survival between early and late broods are significant.

Table 9.6. Analyses of covariance for (i) chick survival, and (ii) fledging success in relation to study site, incorporating laying date as the covariate

	YEAR	NO. OF CLUTCHES/ BROODS	F-VALUE	d.f.
(i) CHICK SURVIVAL	1987	24	2.24NS	3, 19
	1988	27	2.41NS	3, 22
	BOTH COMBINED	51	4.29**	3, 46
(ii) FLEDGING SUCCESS	1987	26	3.07*	3, 21
	1988	31	0.90NS	3, 26
	BOTH COMBINED	57	3.32*	3, 52

NS $p>0.05$ *$p<0.05$ **$p<0.01$

Notes: only data from study sites 1, 2, 4 and 5 are used.
Chick survival data were arc-sine transformed for this analysis.

Table 9.7. Survival of chicks from hatching to fledging and productivity on different study sites for whimbrel pairs in which the female was known to have previous breeding experience

SITE	% OF HATCHED CHICKS FLEDGING FROM STUDY BROODS	[1]MEAN FLEDGING SUCCESS PER PAIR; ± 1 S.E. (FOR SITES 2, 4, 5)
1.	35.5 (n=40)	1.06 (n=17)
2.	10.0 (n=10)	0.33±0.33 (n=3)
4.	52.9 (n=17)	1.80±0.66 (n=5)
5.	14.8 (n=27)	0.40±0.27 (n=10)

Notes: 1. since chick survival was determined for only a proportion of the broods on site 1, fledging success has been estimated approximately and no S.E. is attached (see text for method of estimation for site 1).
Data for 1987 and 1988 are combined.

Differences in chick survival are significant between sites 4 and 5 (i.e. $X^2 = 5.6$, d.f. = 1, $p<0.05$). For sites 2, 4 and 5 the differences in fledging success are not significant.

differences in both chick survival and fledging success persisted when comparisons were limited to those pairs in which the females were known to have bred in a previous year (Table 9.7).

A similar analysis carried out on pairs in which males were known to have bred in a previous year produced the same result.

(iii) Chick Food Supply. Although broods used habitats other than heathland, movements off heathland did not usually occur until after the main period of chick mortality (8.2). Thus, if chick food supply was involved in causing differences in productivity between study sites, variation in the food supply on heathland was likely to be most important.

Data on surface-active invertebrate biomasses (as determined by D-vac. suction trapping) were presented in 8.2.4 (see Figs. 8.3 and 8.4). The biomass of surface-active invertebrate groups which were known to be taken by whimbrel chicks was significantly higher on heathland at site 5 than at all other sites. Biomasses of these invertebrate groups did not differ significantly between heathland on the other study sites. In terms of all surface-active invertebrate groups collected, biomass was greatest on heathland at sites 1 and 5. Heathland on both of these sites held significantly greater biomasses of all surface-active invertebrate groups than on sites 2 and 4.

Therefore, no associations were apparent between the invertebrate biomass on heathland at each study site and the differences between those sites in chick survival.

(iv) Predation. Differences in the extent of predation between study sites could only be determined prior to hatching. As assessed by the proportion of nests which suffered any predation, predation rates were lowest on site 1 and highest on site 4. However, only sites 1 and 5 differed significantly in this respect (Table 9.8).

Table 9.8. Nest predation in relation to study site. (Data from 1986-88 combined)

SITE	1	2	3	4	5
% OF NESTS LOSING $\geq$ 1 EGG TO PREDATORS	9.8 (n=41)	26.3 (n=19)	20.0 (n=20)	40.0 (n=10)	33.3 (n=30)

The difference between sites 1 and 5 is significant; $X^2 = 5.1$, d.f. = 1, $p<0.05$.

Note: no differences between study sites in any single year, or within a study site in different years, were significant.

9.3 DISCUSSION

9.3.1 Factors Determining Differential Productivity on Study Sites

Much of the variation in productivity between study sites could not be attributed to associated differences in factors known to be correlated with productivity (e.g. laying dates). This suggests that differences in site attributes which directly influenced chick survival and/or in the abilities of the adults on these sites to successfully rear chicks were involved in causing differential productivity.

Similar variations in productivity between different breeding sites, or habitats, have been demonstrated in a wide range of species (e.g. for other waders - Galbraith 1988a, 1988c, and Jackson 1988; for raptors - Newton et al. 1979, Watson et al. 1987; and for passerines - Krebs 1971, Alatalo et al. 1985). Although these studies have been unable to discriminate between the effects of site quality and bird quality, some have found associated differences in factors which probably determine either site quality (e.g. food supply - Watson et al. 1987) and/or bird quality (e.g. age - Krebs 1971).

In the present study little evidence could be found to identify any factors which were associated with the variation in productivity between sites, and which may have determined either, the quality of the sites, or of the birds on these sites. Differential predation rates may have been involved, but these could only be measured for nests, rather than chicks, and significant differences were limited to sites 1 and 5. Also, if important, the ultimate causes of such differences in predation rates were not apparent. Both the species and densities of potential predators tended to be similar on all study sites, and there were no apparent differences in the extent to which heathland on different sites provided cover for nests, or chicks.

In terms of chick food supply, the biomass of surface-active invertebrates was greatest on site 5, where chick survival was poorest. However, as discussed previously (see 8.3.2), the limited information obtained on chick diet did not allow the relative importance of the different prey items to be assessed. Thus, the evidence for the lack of an association between food supply and chick survival on different study sites is not conclusive.

9.3.2 Productivity in Relation to Adult Survival

Minimum estimates of adult survival were determined in 5.2.2. These estimates did not differ between years or sexes, and overall at least 89% of adults colour ringed by the end of one breeding season, survived to the following breeding season.

Based on this survival rate, each breeding adult must, on average, produce 0.11 recruits into the breeding population each year, to maintain a stable population. This represents 25% of the average number of chicks fledged per adult per year during this study. If it is assumed that; (i) most whimbrel first breed when they are three years old (in Manitoba two breeding adults, ringed as chicks, were trapped three years later - Skeel 1983; and other waders of a similar size to whimbrel generally breed for the first time at two or three years - Evans and Pienkowski 1984); and (ii) the annual survival rate between one and three years is the same as for breeding adults (as in several other wader species - Evans and Pienkowski 1984); then approximately 35% of fledglings must survive to the end of their first year of life to achieve the required recruitment rate.

A 35% survival rate is lower than most other estimates of juvenile survival for wader species, which usually range from 40-60% and which probably underestimate survival (Evans and Pienkowski 1984). It is therefore likely that more than 35% of fledged whimbrel survive their first year, and this result is consistent with the current increases in the whimbrel population in Shetland (Richardson 1989). However, caution should be exercised in extrapolating from the estimates of productivity obtained in this study to those for the whole Shetland population. Productivity on different study sites varied to such an extent that on some sites it was insufficient to balance adult mortality (ie. site 5 and possibly site 2). The sites used in this study may not be a representative sample of other breeding areas for whimbrel in Shetland, particularly since all study sites were located on the Northern Isles and none on Mainland Shetland.

10. GENERAL DISCUSSION

10.1 THE EFFECTS OF AGRICULTURAL IMPROVEMENTS ON BREEDING WADER POPULATIONS

The effects of recent changes in agricultural practices have been documented for several wader species in Britain. For example, throughout much of the lowlands of England and Wales the occurrence of breeding snipe (Gallinago gallinago) and redshank (Tringa totanus) on grasslands is now largely restricted to a few localities where grassland management tends to be less intensive than in most regions (Smith 1983). Also, lapwing populations on arable farmland have undergone a considerable decline over the past 25 years (O'Connor and Shrubb 1986). Causal factors for this decline include a loss of nesting habitat as the extent of autumn sown cereals has increased and reduced breeding success of pairs nesting in spring cereals. Autumn cereals are avoided due to their tall, dense vegetation at the start of the breeding season (O'Connor and Shrubb 1986, Shrubb 1988), whilst birds nesting in spring cereals rely for suitable chick-rearing habitat on adjacent pastures which are being ploughed and cultivated to an increasing extent (Galbraith 1988a). Within upland areas, improvements of marginal grasslands have been shown to result in reduced nesting densities of snipe, redshank, lapwing, and curlew, Numenius arquata, (Baines 1988).

These studies indicate that recent changes in agricultural practice have had detrimental effects on breeding wader populations. This was also the case in the present study, since re-seeding (at least when carried out with prior ploughing or harrowing) resulted in a loss of suitable nesting habitat for whimbrel. Although whimbrel did use these re-seeds for other purposes (see chapters 7 and 8) there was little evidence to suggest that such use of re-seeds was likely to have had any major influences on productivity. If nesting pairs are displaced following habitat change, a loss of suitable nesting habitat will have a detrimental effect on a population only if the availability of such habitat is a limiting factor. For the lapwing, this may not be the case, since its recent decline on arable areas has coincided with an increase on sheep-rearing areas (O'Connor and Shrubb 1986). It is therefore possible that land-use changes have influenced the distribution, rather than the size, of British lapwing populations.

10.2 HABITAT AVAILABILITY ON THE BREEDING GROUNDS

The presence of large expanses of heathland in Shetland on which no whimbrel nest, and the current expansion of the population, both suggest that habitat availability does not limit breeding whimbrel in Shetland. However, not all heathland may be suitable for nesting whimbrel. As mentioned previously (4.3.3) birds apparently prefer heathland overlying serpentine rock, whilst they avoid heathland with steep gradients (Richardson 1989).

The presence of other species nesting on an area of heathland may also influence whether or not that particular area can support breeding whimbrel. On Fetlar there are only two extensive areas of heathland on which whimbrel do not nest. Both areas support large colonies of great skuas, a species which may prey upon adult whimbrel (Witherby et al. 1944, pers. obs.) and, if nesting in close proximity, would be a potentially serious predator of recent fledglings. (Heavy predation by great skuas on the fledglings of other species, notably arctic skuas, does occur in Shetland - Furness 1987, pers. obs.). An apparent avoidance by whimbrel of heathland on which great skuas nest has been noted elsewhere in Shetland (Richardson 1989). By contrast, whimbrel in Shetland rarely nest on heathland from which arctic skuas are absent (Richardson 1989). High nesting densities of arctic skua (ie. 15-30 pairs/100ha) occurred on all five sites used in the present study. Mutual defence of the nesting area against potential predators (e.g. hooded crows, large gulls, and great skuas) may provide benefits to whimbrel nesting close to arctic skuas, which outweigh the losses to the skuas of some whimbrel eggs and chicks.

Further evidence for variation in the quality of different heathland sites for nesting whimbrel was obtained during the present study, since sites differed in both nesting densities and productivity (4.2.4 and 9.2.2). Causes of such inter-site variation could not be determined but the relationships between site occupation, nesting density and productivity conform, to some extent at least, with theories which attempt to relate variation in site quality with territoriality and the density dependent regulation of populations (Brown 1969, Fretwell 1972).

These theories predict that the highest quality habitats should be colonised first (see also Patterson 1985). According to the Ideal Despotic Distribution hypothesis, by maintaining territories, colonisers impose a limit to the density within the habitat. Once this limit is attained, further colonisers will be forced to occupy habitats of progressively lower quality, in which the potential nesting density and breeding output of individuals are relatively low (e.g. for great tits - Krebs 1971). Eventually further colonisers may have to refrain from breeding altogether as all suitable habitats become fully occupied (e.g. for red grouse - Watson 1967, and carrion crows, Corvus corone, - Patterson 1980).

In the present study, nesting densities were highest on site 1, which was one of the two sites on which productivity was relatively high. The timing of occupation (as assessed by arrival dates of colour ringed adults) did not differ between sites within any year, but for species (such as whimbrel) in which adults are highly site faithful between years, it is likely that it is the timing of the initial occupation by first time colonisers which is important in this respect. Site 1 was the only site on which the number of nesting pairs did not increase over the study period. This may indicate that the carrying capacity for site 1 had been reached, but that other sites were still in the process of being colonised. Also, during the current expansion of the whimbrel population in Shetland, the serpentine heathlands of Unst and Fetlar (ie. areas of similar habitat and with similar nesting densities of whimbrel to site 1) were probably some of the first sites to be colonised (Venables and Venables 1955, Berry and Johnston 1980).

Site 4 does not fit with the proposed hypothesis since breeding success was also high on this site, despite the low nesting densities. However, the area of heathland on this site was relatively small and rather fragmented by improved land and mires, and this may have influenced densities. Also, only three to four pairs nested on this site and thus it may not be an important exception.

Therefore, optimal breeding habitat for whimbrel in Shetland may be a limiting factor, and it is possible that a proportion of the population is now breeding on heathland on which nesting densities and productivity will remain relatively low. Clearly such a conclusion must be tentative without either, a longer term study to confirm the causes and consistency of the observed variations between study sites, or an experimental study which involves the removal of territorial pairs on the apparently preferred habitats.

Amongst other wader species there is no conclusive evidence that the availability of suitable breeding habitat limits populations (Evans and Pienkowski 1984). Although experimental removals of territorial dunlin (Calidris alpina) in Alaska (Holmes 1970) and oystercatchers (Haematopus ostralegus) on Skokholm Island (Harris 1970) demonstrated that the removed birds were replaced by others which were capable of breeding, in neither study was the source of the replacement birds established. Thus, without the removal experiments, these replacement birds may have bred in equally suitable habitat elsewhere. However, as in the present study, circumstantial evidence suggesting that the availability of suitable breeding habitat is a limiting factor has been found in other populations. Lapwings breeding on three sites in upland rough grazing habitat, occupied the sites sequentially during the breeding season. Nesting densities and productivity were lowest on the last site to be occupied (Galbraith 1988c). Also, the occurrence of nonbreeding birds on the breeding grounds has been found for oystercatchers (Harris 1970, Briggs 1984) and temminck's stint, Calidris temminckii (Hilden 1979), indicating a possible surplus of potential breeders.

10.3 PREDICTING THE EFFECTS OF FURTHER RE-SEEDING

On the basis of the results obtained in the present study (chapter 4), re-seeding following ploughing or harrowing of heathland is considered to cause a loss of suitable nesting habitat for whimbrel. If, following such re-seeding, displacement of nesting pairs does not occur it is considered likely that nesting success would be reduced through increased trampling of nests by livestock, and possibly increased predation rates on nests. Ready access to heathland for young chicks may also be important since re-seeds were not generally used by broods in which the chicks were less than ten days old. In terms of mortality rates, this is the critical stage of the chick-rearing period (8.2).

Following the previous discussion (ie. 10.2), if displacement does occur it cannot be assumed that the displaced birds would obtain equally suitable breeding habitat elsewhere. Re-seeding a substantial proportion of the sites which appear to provide the most suitable habitat for whimbrel in Shetland (in particular the serpentine heathlands of Unst and Fetlar) could have a considerable effect on the overall production of fledglings from the population. This is particularly so since on certain other sites breeding output may not be sufficient to balance adult mortality (e.g. on site 5 in this study).

The results of this study demonstrated that the initial habitat changes following surface re-seeding were considerably less marked than those following re-seeding with prior ploughing or harrowing. Nesting pairs were not displaced, and these re-seeds retained the attributes which were important in the selection of nest-sites by whimbrel. However, nesting pairs are likely to suffer higher rates of nest losses from trampling due to the increased stocking densities in these re-seeds. Also, almost all surface re-seeds on study sites were relatively recent (ie. less than four years old by 1988), and greater habitat change may occur with time. Therefore, it is suggested that further monitoring of changes in habitat attributes, and the occurrence of nesting whimbrel, in these re-seeds is required.

SUMMARY

1. As in many other areas of Britain, the extent of agricultural improvements in the Shetland Isles have increased in recent years. One such improvement is the re-seeding of heathland. This allows crofters to increase stocking densities of livestock on the land, and entails applying lime, fertiliser, and high quality grass-seed mixtures to the heathland, either directly (ie. surface re-seeding), or after prior ploughing or harrowing of the heathland.

2. Shetland holds c.95% of the British breeding population of whimbrel, which probably numbers 450-500 pairs. Heathland is the major nesting habitat for this species in Shetland, and the main aim of the present study was to identify the effects of re-seeding heathland on the breeding ecology of whimbrel. Work was carried out on five study sites located on the islands of Unst and Fetlar.

3. Almost 90% of all whimbrel nests on study sites occurred on heathland. Ploughed or harrowed re-seeds and established pastures (ie. old improved grasslands) were avoided to a significant extent by whimbrel for nesting. However, surface re-seeds were not avoided, and whimbrel continued to nest in such habitat.

4. Re-seeding after ploughing or harrowing resulted in marked changes in the vegetation composition and structure of the habitat. Such re-seeds lacked habitat attributes important in the selection of nest-sites by whimbrel (ie. hummocks and *C. vulgaris*). Changes

following surface re-seeding were less marked and these re-seeds retained both attributes identified as important in nest-site selection (at least for the first few years after re-seeding).

5. Over the study period the numbers of breeding pairs increased on all study sites, except site 1. Nesting densities were consistently highest on site 1, which was located on serpentine heathland.

6. Approximately 90% of breeding adults nested within 200m of the previous year's nest-site, and most retained the same mate as previously. Return rates of adults to study sites were higher for males than females (ie. 87% and 70% respectively). Survival rates did not differ between the two sexes and almost 90% of adults marked by the end of one breeding season were sighted during the following season.

7. Abrupt seasonal declines in fledging success occurred in two of the three years of this study, and were due to the complete failure of late broods. Laying date was influenced by female age, and all pairs in which the female was known to have previous breeding experience laid their first clutches within a relatively short period (ie. 10 days). No seasonal decline in chick survival occurred from such clutches.

8. Chick weight at hatching was highly correlated with egg volume, at least partly because chicks from larger eggs were structurally larger, though they may also have retained greater yolk reserves on

hatching.

9. In two of the three years of this study mean hatchling weight in a brood was positively, and significantly, correlated with the proportion of chicks in the brood which survived to fledging.

10. To control for any associated factors (e.g. female age) which may have influenced the correlation between hatchling weight and chick survival between broods, the relationship was also studied within broods. Although there was relatively little variation in hatchling weights within broods, a significant positive effect of hatchling weight on survival was apparent up to seven days after hatching (ie. the period over which body reserves at hatching are most likely to influence survival).

11. The egg volumes and hatchling weights of individual female whimbrel were highly correlated between years, but the laying dates of individual females were not (at least for 1986-1987). When considered in conjunction with heritability studies on other bird species, these results indicate that changes in environmental conditions are likely to have a greater influence on laying dates than on egg volumes or hatchling weights.

12. No consistent relationships were found between laying date, egg volume, or hatchling weight, and either female body weight, or any of the five measurements of female body size which were taken.

13. During the pre-laying period most pairs (ie. >90%) fed mainly outside of the nesting territory, in ploughed or harrowed re-seeds and established pastures. These habitats held the greatest biomass of both of the main prey items for adult whimbrel at this stage - ie. earthworms and tipulid larvae.

14. Preferences for individual improved fields as feeding sites for adults during the pre-laying period were related to the biomass of tipulid larvae in those fields (such that fields with the highest biomass were used most consistently), but not to the biomass of earthworms. This was probably due to differences in the availability of these two prey items to feeding whimbrel.

16. Larval tipulid biomass was usually greater in ploughed or harrowed re-seeds than in established pastures. It is therefore likely that re-seeding improved feeding conditions for adults during the pre-laying period, though there were reasons to believe that such benefits may have been of a short term nature.

17. Improved feeding conditions for females prior to laying were unlikely to result in major benefits to fledging success, via effects on egg volumes or laying dates. Any influence on egg volume was likely to be relatively minor, whilst the relationship between fledging success and laying date was due entirely to the latest laying pairs (ie. <25% of all pairs) invariably failing. Such pairs possibly included inexperienced females and these may have failed to rear chicks irrespective of their laying date.

18. Improved feeding conditions for adults may have benefits which could not be assessed during this study (e.g. increased rates of adult survival).

19. During the chick-rearing period 93% of all broods remained within 400m of the nest-site, and adults continued to maintain exclusive territories, up to fledging. Broods which used habitats other than heathland had usually nested within 200m of that particular habitat.

20. The habitat selection of broods was assessed by two methods which were subject to different biases. By both methods re-seeds (mainly those which were ploughed or harrowed) were selected for, whilst established pastures were avoided.

21. Due to it being the most extensive habitat on study sites, 65% of all locations of successful broods were on heathland. Over 80% of all chick mortality occurred within 14 days of hatching, and since few broods moved off heathland until the chicks were at least ten days old, heathland may have been of particular importance during the most vulnerable stages of a chick's life.

22. No consistent differences were found between habitats in the biomass of surface-active invertebrate groups which were known to be taken by whimbrel chicks (as assessed by suction trapping). The biomass of all surface-active invertebrates was generally greater on re-seeds, established pastures, and mires than on heathland.

23. There was no significant tendency for broods to use those improved fields and mires in which invertebrate biomasses were greatest.

24. The use of habitats other than heathland was not associated with a decreased risk of predation on the chicks. Broods did not enter other habitats until after the period of most chick mortality, and they used improved fields in which cover and camouflage for chicks were less than on heathland, as well as fields in which cover for chicks was greater than on heathland.

25. Selection for re-seeds may have occurred to improve adult feeding conditions, whilst enabling the adults to remain within close proximity of their chicks.

26. Chick survival to fledging did not differ according to the habitat-use of broods.

27. The estimated fledging success for the overall study population in each year of study ranged from 0.75-0.91 fledglings per breeding pair.

28. Marked differences in fledging success occurred between the different study sites, and this was due primarily to differential rates of chick survival to fledging (ranging from 10% on site 5 to 60% on site 4). One of the two sites where fledging success was relatively high was site 1; ie. the site on which nesting densities

were highest.

29. Variation in productivity between study sites could not be attributed entirely to any associated differences in other factors which were known to be related to productivity (e.g. laying dates). However, little evidence was found to identify any attributes of the sites themselves which may have caused the observed variation in productivity.

30. It is estimated that the overall production of fledglings from study sites is sufficient to balance adult mortality, if at least 35% of fledglings survive to the end of their first year of life. Juvenile survival in waders is usually higher than 35%, and this result is consistent with the current increase in the whimbrel population in Shetland.

31. Based on the observed variation in nesting densities and productivity on study sites, it is hypothesised that, during the current expansion of the whimbrel population in Shetland, areas of heathland have been colonised sequentially in terms of their suitability as breeding habitat. Thus heathlands on which potential densities and productivity are highest have been occupied first, and the availability of optimal breeding habitat may be a limiting factor for the population.

32. The above hypothesis has important implications for assessing the effects of re-seeding heathland on breeding whimbrel since; (i)

it cannot be assumed that any birds displaced from nesting habitat would obtain equally suitable habitat elsewhere and; (ii) the extent of detrimental effects may vary according to the quality of the site which is re-seeded.

REFERENCES

ALATALO, R.V.; LUNDBERG, A.; & ULFSTRAND, S. 1985. Habitat selection in the pied flycatcher *Ficedula hypoleuca*. In M.L. Cody (ed.). Habitat selection in birds. pp.59-83. Academic Press.

ANKNEY, C.D. 1980. Egg weight, survival and growth of lesser snow goslings. J. Wildl. Manage. 44. 174-82.

BAILLIE, S.R. & MILNE, H. 1982. The influence of female age on breeding in the eider (*Somateria mollissima*). Bird Study 29. 55-66.

BAINES, D. 1988. The effects of improvement of upland, marginal grasslands on breeding waders (Charadriiformes) and invertebrates. Unpubl. Ph.D thesis. Uni. of Durham.

BARNARD, C.J. & THOMPSON, D.B.A. 1988. Gulls and plovers: the ecology and behaviour of mixed species feeding groups. Croom Helm.

BEINTEMA, A.J. & MUSKENS, G.J.D. 1987. Nesting success of birds breeding in Dutch agricultural grasslands. J. Appl. Ecol. 24. 743-58.

BERRY, R.J. & JOHNSTON, J.L. 1980. The natural history of Shetland. New Naturalist. Collins.

BIRKHEAD, M; BACON, P.J.; & WALTER, P. 1983. Factors affecting the breeding success of the mute swan *Cygnus olor*. J. Anim. Ecol. 52. 727-42.

BRIGGS, K. 1984. The breeding ecology of coastal and inland oystercatchers in north Lancashire. Bird Study 31. 141-7.

BROWN, J.L. 1969. The buffer effect and productivity in tit populations. Amer. Natur. 103. 347-54.

BULL, A.L.; MEAD, C.J.; & WILLIAMSON, K. 1976. Bird-life on a Norfolk farm in relation to agricultural changes. Bird Study 23. 163-82.

CHAPPEL, M.A. 1980. Thermal energetics of chicks of arctic shorebirds. Comparative Biochemistry & Physiology 65A. 311-17.

CLARK, P.J. & EVANS, F.C. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. Ecology 35. 445-53.

COOKE, A.S.; BELL, A.A.; & HAAS, M.B. 1982. Predatory birds, pesticides and pollution. Institute of Terrestrial Ecology. N.E.R.C.

COULSON, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the kittiwake gull _Rissa tridactyla_. J. Anim. Ecol. 35. 269-79.

COULSON, J.C. & THOMAS, C. 1985. Differences in the breeding performance of individual kittiwake gulls, Rissa tridactyla (L.). In R.M. Sibly & R.H. Smith (eds.). Behavioural ecology: ecological consequences of adaptive behaviour. pp.489-506. Blackwell Scientific Publications.

CRAMP, S. & SIMMONS, K.E.L. 1983. Handbook of the birds of Europe, the Middle East and North Africa. vol.III. Oxford Uni. Press.

DAVIES, N.B. 1977. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46. 37-57.

DEMENTIEV, G.P.; GLADKOR, N.A.; & SPANGENBERG, E.P. 1969. Birds of Soviet Union 3. Jerusalem. Israel program for scientific translation.

DESENDER, K. & MAELFAIT, J. 1986. Pitfall trapping within enclosures: a method for estimating the relationship between the abundance of coexisting carabid species (Coleoptera: Carabidae). Holarct. Ecol. 9. 245-50.

DRENT, R.H. & DAAN, S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68. Suppl. 225-52.

DRY, F.T. & ROBERTSON, J.S. 1982. Soil and land capability for agriculture. Orkney and Shetland. The Macaulay Institute for Soil Research.

EDWARDS, C.A. & LOFTY, J.R. 1977. Biology of earthworms (2nd edition). Chapman & Hall.

ERIKSTAD, K.E. 1985. Growth and survival of willow grouse chicks in relation to home range size, brood movements and habitat selection. Ornis Scand. 16. 181-90.

EVANS, P.R. & PIENKOWSKI, M.W. 1984. Population dynamics of shorebirds. In J. Burger & B.L. Olla (eds.). Shorebirds, breeding behaviour and populations. Behaviour of marine animals. vol. 5. pp.125-45. Plenum Press.

EWALD, P.W. & ROHWER, S. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in red-winged blackbirds Agelaius phoeniceus. J. Anim. Ecol. 51. 429-50.

FERNS, P.N.; GREEN,G.H.; & ROUND,P.D. 1979. Significance of the Somerset and Gwent Levels in Britain as feeding areas for migrant whimbrels, Numenius phaeopus. Biol. Conserv. 16. 7-22.

FISHER, P. & RICHARDSON, M.G. 1983. Whimbrel and wader distributions, Shetland, 1983. Unpubl. report to N.C.C.

FRETWELL, S.D. 1972. Populations in a seasonal environment. Princeton Uni. Press.

FURNESS, R.W. 1987. The skuas. Poyser.

FURNESS, R.W. & FURNESS, B.L. 1981. A technique for estimating the hatching dates of eggs of unknown laying date. Ibis 123. 98-102.

GALBRAITH, H. 1988a. Effects of agriculture on the breeding ecology of lapwings Vanellus vanellus. J. Appl. Ecol. 25. 487-504.

GALBRAITH, H. 1988b. Effects of egg size and composition on the size, quality and survival of lapwing Vanellus vanellus chicks. J. Zool., Lond. 214. 383-98.

GALBRAITH, H. 1988c. The effects of territorial behaviour on lapwing populations. Ornis Scand. 19. 134-8.

GALBRAITH, H. 1989. The diet of lapwing, Vanellus vanellus, chicks on Scottish farmland. Ibis 131. 80-5.

GALBRAITH, H.; FURNESS, R.W.; & FULLER, R.J. 1984. Habitats and distribution of waders breeding on Scottish agricultural land. Scott. Birds 13. 98-107.

GALBRAITH, H. & GREEN, R. 1985. The prediction of hatching dates of lapwing clutches. W.S.G. Bull. 43. 16-18.

GARDNER, B. 1983. The Common Agricultural Policy of the E.E.C. and and the environment. In Agriculture and bird life in Europe. Report to the 13th conference, 1981. I.C.B.P.

GRANT, M.C. 1988. Use of re-seeds and established pastures during the pre-laying period by whimbrel (Numenius phaeopus). Shetland Bird Report 1987.

GRATTO, C.L.; COOKE, F.; & MORRISON, R.I.G. 1983. Nesting success of yearling and older breeders in the semipalmated sandpiper, Calidris pusilla. Can. J. Zool. 61. 1133-7.

GRATTO, C.L.; MORRISON, R.I.G.; & COOKE, F. 1985. Philopatry, site tenacity and mate fidelity in the semipalmated sandpiper. Auk 102. 16-24.

GREEN, R.E. 1984. The feeding ecology and survival of partridge chicks (*Alectoris rufa* and *Perdix perdix*) on arable farmland in East Anglia. J. Appl. Ecol. 21. 817-30.

GREEN, R.E. 1988. Effects of environmental factors on the timing and success of breeding in common snipe *Gallinago gallinago* (Aves: Scolopacidae). J. Appl. Ecol. 25. 79-93.

GREENSLADE, P.J.M. 1964. Pitfall trapping as method of studying populations of Carabidae (Coleoptera). J. Anim. Ecol. 33. 301-10.

GREIG-SMITH, P. 1957. Quantitative plant ecology. Butterworths.

GUDMONDSSON, F. 1957. Natturufraedingurinn Islenzkir fuglar xv. Spoi *Numenius phaeopus*.

HARRIS, M.P. 1970. Territoriality limiting the size of the breeding population of the oystercatcher (*Haematopus ostralegus*) - a removal experiment. J. Anim. Ecol. 39. 707-13.

HERFST, M. & RICHARDSON, M.G. 1982. Whimbrel and wader distributions Unst, Shetland. Unpubl. report to N.C.C.

HILDEN, O. 1979. Territoriality and site tenacity of temminck's stint *Calidris temminckii*. Ornis Fenn. 56. 56-74.

HILL, D.A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. J. Appl. Ecol. 22. 645-54.

HOLMES, R.T. 1970. Differences in population density, territoriality and food supply of dunlin on Arctic and subarctic tundra. In A. Watson (ed.). Animal populations in relation to their food resources. pp.303-19. Blackwell.

HOWE, M.A. 1982. Social organisation in a population of eastern willets (Catoptrophorus semipalmatus). Auk 99. 88-102.

JACKSON, D.B. 1988. Habitat selection and breeding ecology of three species of waders on the Western Isles of Scotland. Unpubl. Ph.D thesis. Uni. of Durham.

JOURDAIN, F.C.F. 1962. Numenius phaeopus phaeopus, whimbrel. In A.C. Bent (ed.). Life histories of North American shorebirds. pp.136-40. Dover Publications.

KREBS, J.R. 1971. Territory and breeding density in the great tit, Parus major L. Ecology 52. 2-22.

KREBS, J.R. 1978. Optimal foraging: decision rules for predators. In J.R. Krebs & N.B. Davies (eds.). Behavioural ecology: an evolutionary approach. pp.23-63. Blackwell Scientific Publications.

LEWIS, A.M. 1976. Phytosociological studies in the Northern Isles of Shetland. Unpubl. Ph.D thesis. Uni. of Durham.

LUNDBERG, C. & VAISANEN, R.A. 1979. Selective correlation of egg size with chick mortality in the black headed gull (*Larus ridibundus*). Condor 81. 146-56.

MAYFIELD, H.F. 1961. Nesting success calculated from exposure. Wilson Bull. 73. 255-61.

MAYFIELD, H.F. 1975. Suggestions for calculating nest success. Wilson Bull. 87. 456-66.

MITCHELL, B. 1963. Ecology of two carabid beetles, *Bembidion lampros* (Herbst.) and *Trechus quadristriatus* (Schrank). J. Anim. Ecol. 32. 377-92.

MOLLER, A.P. 1983. Changes in Danish farmland habitats and their populations of breeding birds. Holarct. Ecol. 6. 95-100.

MONAGHAN, P.; UTTLEY, J.D.; BURNS, M.D.; THAINE, C.; & BLACKWOOD, J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns *Sterna paradisaea*. J. Anim. Ecol. 58. 261-74.

MOREBY, S.J. 1988. An aid to the identification of arthropod fragments in the faeces of gamebird chicks (Galliformes). Ibis 130. 519-26.

MOSS, R. & WATSON, A. 1982. Heritability of egg size, hatch weight, body weight and viability in red grouse (*Lagopus lagopus scoticus*). Auk 99. 683-6.

MOSS, R.; WATSON, A.; ROTHERY, P.; & GLENNIE, W.W. 1981. Clutch-size, hatch weight, and laying date in relation to early mortality in red grouse (Lagopus lagopus scoticus). Ibis 123. 450-62.

MYKURA, W. 1976. British regional geology. Orkney and Shetland. Institute of Geological Sciences. N.E.R.C.

NEU, C.W.; BYERS, C.R.; & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38. 541-5.

NEWTON, I. 1979. Population ecology of raptors. Poyser.

NEWTON, I. & MARQUISS, M. 1981. Effect of additional food on laying dates and clutch-sizes of sparrowhawks. Ornis Scand. 12. 224-9.

NEWTON, I. & MARQUISS, M. 1984. Seasonal trend in the breeding performance of sparrowhawks. J. Anim. Ecol. 53. 809-29.

NEWTON, I.; MARQUISS, M.; & MOSS, D. 1979. Habitat, female age, organo-chlorine compounds and breeding of European sparrowhawks. J. Appl. Ecol. 16. 777-93.

NEWTON, I.; MARQUISS, M.; & MOSS, D. 1981. Age and breeding in sparrowhawks. J. Anim. Ecol. 50. 839-53.

NISBET, I.C.T. 1978. Dependence of fledging success on egg size, parental performance and egg composition among common and roseate terns, Sterna hirundo and S. dougalli. Ibis 120. 207-15.

NOORDWIJK, A.J. van.; BALEN, J.H. van.; & SCHARLOO, W. 1980. Heritability of ecologically important traits in the great tit. Ardea 68. Suppl. 193-203.

NORUSIS, M.J. 1983. SPSSX introductory statistics guide. McGraw-Hill.

NUR, N. 1984. The consequences of brood size for breeding blue tits. 1. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53. 479-96.

O'CONNOR, R.J. 1979. Egg weights and brood reduction in the European swift (Apus apus). Condor 81. 133-45.

O'CONNOR, R.J. & SHRUBB, M. 1986. Farming and birds. Cambridge Uni. Press.

OJANEN, M.; ORELL, M.; & VAISANEN, R.A. 1979. Role of heredity in egg size variation in the great tit Parus major and the pied flycatcher Ficedula hypoleuca. Ornis Scand. 10. 22-8.

OLLASON, J.C. & DUNNET, G.M. 1986. Relative effects of parental performance and egg quality on breeding success of fulmars Fulmarus glacialis. Ibis 128. 290-6.

ORING, L.W. & LANK, D.B. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. In J. Burger & B.L. Olla (eds.). Shorebirds, breeding behaviour and populations. Behaviour of marine animals. vol. 5. pp.125-45. Plenum Press.

OSBOURNE, P. 1984. Bird numbers and habitat characteristics in farmland hedgerows. J. Appl. Ecol. 21. 63-82.

PATTERSON, I.J. 1965. Timing and spacing of broods in the black-headed gull *Larus ridibundus*. Ibis 107. 433-59.

PATTERSON, I.J. 1980. Territorial behaviour and the limitation of population density. Ardea 68. Suppl. 53-62.

PATTERSON, I.J. 1985. Limitation of breeding density through territorial behaviour: experiments with convict cichlids, *Cichlasoma nigrofasciatum*. In R.M. Sibly & R.H. Smith (eds.). Behavioural ecology: ecological consequences of adaptive behaviour. pp.393-405. Blackwell Scientific Publications.

PEACOCK, M.A.; BEVERIDGE, F.M.; & CAMBELL, L.H. 1985. Moorland bird survey in Shetland, 1985. Unpubl. report to R.S.P.B.

PERRINS, C.M. 1970. The timing of birds' breeding seasons. Ibis 112. 242-56.

PICOZZI, N. 1975. Crow predation on marked nests. J. Wildl. Manage. 39. 151-5.

PIENKOWSKI, M.W. 1984a. Breeding biology of ringed plovers, *Charadrius hiaticulata*, 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 hiaticulata, and its relationship to growth and survival to reproductive age. Ibis 126. 133-55.

PIERSMA, T. (compiler). 1986. Breeding waders in Europe: a review of population size estimates and a bibliography of information sources. W.S.G. Bull. 48. Suppl., 1-116.

PRATER, A.J.; MARCHANT, J.H.; & VUORINEN, J. 1977. Guide to the identification and ageing of Holarctic waders. B.T.O.

REDFERN, C.P.F. 1982. Lapwing nest-sites and chick mortality in relation to habitat. Bird Study 29. 201-8.

REDMOND, R.L. & JENNI, D.A. 1986. Population ecology of the long-billed curlew (Numenius americanus) in Western Idaho. Auk 103. 755-67.

RICHARDSON, M.G. 1989. The status, distribution and habitat preferences of whimbrel, Numenius p. phaeopus in Shetland - and Britain. Unpubl. report to N.C.C.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish Res. Board Can. Bull. no. 191.

ROSTAD, G. & JOSTEIN, S. 1987. Morphology of hatchling hooded crows and its relation to egg volume. Condor 89. 494-500.

ROYAL SOCIETY FOR THE PROTECTION OF BIRDS. 1984. Hill farming and birds. A survival plan. R.S.P.B.

SHARROCK, J.T.R. 1976. The atlas of the breeding birds in Britain and Ireland. Poyser.

SHRUBB, M. 1988. Report on the 1987 B.T.O. lapwing survey. B.T.O. News 156. 6-7.

SKEEL, M.A. 1976. Nesting strategies and other aspects of the breeding biology of the whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. Unpubl. MSc. thesis. Uni. of Toronto.

SKEEL, M.A. 1982. Sex determination of adult whimbrels. J. Field Ornithol. 53. 414-16.

SKEEL, M.A. 1983. Nesting success, density, philopatry, and nest-site selection of the whimbrel (*Numenius phaeopus*) in different habitats. Can. J. Zool. 61. 218-25.

SLINGSBY, D.R.; CARTER, S.; KING, R.J.; & JENNER, C. 1983. The serpentine vegetation of Fetlar and Haaf Gruney. Unpubl. report to N.C.C.

SMITH, K.W. 1983. The status and distribution of waders breeding on wet lowland grasslands in England and Wales. Bird Study 30. 177-92.

SOIKELLI, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4. 158-97.

SOIKELLI, M. 1970. Dispersal of dunlin *Calidris alpina* in relation to sites of birth and breeding. Ornis Fenn. 47. 1-9.

SOKAL, R.R. & ROHLF, F.J. 1981. Biometry (2nd edition). W.H. Freeman & Co.

SOUTHWOOD, T.R.E. 1978. Ecological methods. Chapman & Hall.

SPENCER, R. 1984. The ringer's manual (3rd edition). B.T.O.

THOMAS, C.S. 1983. The relationship between breeding experience, egg volume and reproductive success in the kittiwake *Rissa tridactyla*. Ibis 125. 567-74.

THOMPSON, D.B.A.; THOMPSON, P.S.; & NETHERSOLE-THOMPSON, D. 1986. Timing of breeding and breeding performance in a population of greenshanks (*Tringa nebularia*). J. Anim. Ecol. 55. 181-99.

TOLHURST, B.E. 1974. Development of the chick embryo in relation to the shell, yolk, albumen and extra-embryonic membranes. In B.M. Freeman & M.A. Vince. Development of the avian embryo. pp.277-91. Chapman & Hall.

VAISANEN, R.A.; HILDEN, O.; SOIKELLI, M.; & VUOLANTO, S. 1972. Egg dimension variation in five wader species: the role of heredity. Ornis Fenn. 49. 25-44.

VENABLES, L.S.V. & VENABLES, U.M. 1955. Birds and mammals of Shetland. Oliver & Boyd.

WATSON, A. 1967. Territory and population regulation in the red grouse. Nature 215. 1274-5.

WATSON, J.; LANGSLOW, D.R.; & RAE, S.R. 1987. The impact of land-use changes on golden eagles in the Scottish Highlands. N.C.C.

WILLIAMSON, K. 1946. Field-notes on the breeding biology of the whimbrel, *Numenius phaeopus phaeopus* (Linnaeus). The North Western Naturalist 21. 167-84.

WITHERBY, H.F.; JOURDAIN, F.C.R.; TICEHURST, N.F.; & TUCKER, B.W. 1944. The handbook of British birds. Lond.

APPENDIX 1: SEXING THE STUDY POPULATION

A1.1 INTRODUCTION

Whimbrels show no evident plumage dimorphism with respect to sex. Although females tend to be larger than males considerable size overlap occurs so that no single biometric measurement can be used to reliably sex a large proportion of birds (Prater et al. 1977). Using a discriminant function analysis (DFA), based on four biometric measurements (ie. wing length, bill length, tail length, and tarsometatarsus length) taken from whimbrel in the study population and a reference group of whimbrel museum skins of known sex, Skeel (1982) was able to sex 83% of the birds trapped and marked in her study.

If individually marked birds are present in a population it should be possible to sex some of these birds on the basis of behavioural observations.

A1.2 METHODS

A total of 97 adults nesting on study sites were nest trapped (under N.C.C. licence) during the incubation periods of 1986-88. Birds were caught using a "walk-in" trap with a funnelled entrance. To prevent breakage and chilling of eggs, during trapping the eggs were removed (being placed in an insulated container) and replaced with a "dummy" clutch. If after 30 minutes no adult had entered the trap the attempt was aborted and the trap removed and the clutch replaced. Each adult trapped was fitted with a numbered metal ring and a unique combination of four colour-rings which allowed individual recognition. Six biometric measurements were taken (ie. body weight, and the lengths of the, right wing, right tarsus plus toe, head plus bill, bill, and tail), following the methods described and recommended in Spencer (1984) and Prater et al. (1977). Linear measurements were recorded to the nearest 1.0mm and weight to the nearest 5.0g.

Behavioural observations were carried out on marked birds which returned to study sites during the pre-laying periods of 1987 and 1988 (see chapters 5 and 7). A sample of these birds were sexed from observations of copulation, pre-copulatory behaviour (ie. when the male pursues the female, moving his head rapidly back and forth as if pecking at the female's back - pers. obs.; Lofaldi, after Cramp and Simmons 1983), and the display flight song (described in detail by Skeel 1976, and carried out by the male only - see A1.3). This sample formed a reference group used to sex the remaining birds by DFA on the basis of their biometric measurements.

A1.3 RESULTS

A1.3.1 Birds Sexed by Behavioural Observations

Prior to the start of the study it was considered that, of the behaviours used to sex birds, those associated with copulation could be used conclusively to identify sex. However, whilst the display flight song had been attributed to the male (and is performed by the male in other Numenius species - Cramp and Simmons 1983) it was considered that confirmation was required, since no previous study had used individually marked adults.

16 different birds were observed performing the display flight

song and in all cases only one member of any pair did so. Four of these birds were conclusively sexed as males on the basis of copulatory behaviour, confirming that the display flight song was performed by males and not females.

A further six males were sexed on copulatory behaviours, providing a total of 22 pairs in which the sexes were known. In seven of these cases one adult was not trapped but due to mate changes in subsequent years, from these observations it was possible to identify the sexes of 45 marked adults (ie. 46% of all those trapped). Biometric information was incomplete for two of these birds so that the reference group for the DFA comprised 21 males and 22 females.

A1.3.2 Sexing by DFA

Body weight was the biometric measurement which had the greatest power to discriminate between the sexes, having a relatively high discriminant function coefficient (Table A1.1). The discriminant function coefficients for tarsus plus toe length and bill length were both close to zero and therefore of little use in discriminating between males and females.

Using a minimum probability level of 95% to accept classification as a particular sex, the DFA correctly sexed 65% (ie. 28) of the birds from the reference group. The remaining 15 were classed as of unknown sex, including four assigned to the wrong sex but with probabilities of <95%.

Of the 52 birds not sexed by behavioural observations, 63% (ie.33) were sexed with probabilities of ≥95%. In no cases were birds which had previously bred together classed as the same sex with probabilities of ⩾95%. However, to reduce the chances of misclassification it was determined not to accept as classified any known pairs in which both members were assigned to the same sex unless the probabilities were <75% for one and ⩾99% for the other (the bird with the lower probability being assigned to the opposite sex). Thus, two of the 33 birds sexed with probabilities of ⩾95% were regarded as being unclassified. A further 12 birds which were classified with probabilities of <95% were sexed on the basis of the fact that a previous mate was classified as the opposite sex with a probability of ⩾95%. This resulted in nine birds remaining unsexed, representing 9% of all birds caught during the study.

Using the data for all birds sexed (by behaviour and DFA), females were significantly larger for each of the six biometrics measured (Table A1.2). As would be expected from the results in Table A1.1, the extent of this difference is greatest for body weight.

Table A1.1. Separation of male and female whimbrel by discriminant function analysis

BIOMETRIC	STANDARDISED DISCRIMINANT FUNCTION COEFF.	UNSTANDARDISED DISCRIMINANT FUNCTION COEFF.
BODY WEIGHT	0.662	0.0294
WING LENGTH	0.233	0.0447
TARSUS & TOE LENGTH	0.099	0.0299
HEAD & BILL LENGTH	0.374	0.0764
BILL LENGTH	0.037	-0.0081
TAIL LENGTH	0.139	0.0255

Note: coefficients are calculated from the measurements of those birds sexed by behavioural observations.

Example of application:-

using the unstandardised coeffs.,

discriminant score = 0.0294 x wt + 0.0447 x wg + 0.0299 x t&t +0.0764 x h&b - 0.0081 x b + 0.0255 x t -39.0514.

If score < -1.152, bird is male with a probability of $> 95\%$

If score > 0.920, bird is female with a probability of $> 95\%$

Table A1.2. A comparison of six measurements of male and female whimbrel

BIOMETRIC	SEX	MEAN ± 1 S.E.	n	t-VALUE
BODY WEIGHT (g)	MALE	400.0±3.6	40	10.73***
	FEMALE	452.2±3.3	47	
WING LENGTH (mm)	MALE	257.8±0.9	39	8.56***
	FEMALE	267.4±0.7	47	
TARSUS & TOE LENGTH (mm)	MALE	110.1±0.5	40	6.69***
	FEMALE	115.0±0.5	48	
HEAD & BILL LENGTH (mm)	MALE	120.5±0.6	40	9.11***
	FEMALE	129.1±0.7	47	
BILL LENGTH (mm)	MALE	79.6±0.6	40	7.99***
	FEMALE	86.9±0.7	47	
TAIL LENGTH (mm)	MALE	98.7±0.8	40	6.32***
	FEMALE	105.7±0.7	48	

***$p<0.001$

Note: data includes all birds sexed by observation and DFA.

APPENDIX 2: DETERMINATION OF LAYING DATES

The majority of nests were found after incubation had started so that laying dates had to be estimated by back-dating from the hatching date. Since previous information on the laying and incubation periods of whimbrel was sparse and variable (e.g. Williamson 1946, Jourdain 1962, and Skeel 1976) the length of these periods had to be determined in the present study.

The date on which incubation began was ascertained for 23 clutches which subsequently hatched chicks. Incubation periods ranged from 25 to 28 days with a mean value of 26.02 days (±0.17;S.E.). The average period between the laying of successive eggs was found to be 1.25 days (±0.08;S.E.; n=28), whilst in four egg clutches (ie. the maximum and modal clutch-size - see 6.2.1), incubation started on the laying of the last egg in 46% of cases, the third egg in 50% of cases and the second egg in 4% of cases (n=24). Therefore, for three and four egg clutches not found during laying the date on which the first egg had been laid was assumed to be 29 days prior to the hatching date (ie. a 26 day incubation period plus three days between the laying of the first egg and the start of incubation). This date was taken to be 28 days prior to hatching for two egg clutches which hatched (n=5) and 27 days for single egg clutches which hatched (n=1). Due to the small number of one and two egg clutches, the possibility that these had originally been larger clutches which had lost eggs prior to being found was considered to be a minor source of error.

For clutches not found during laying and which failed to hatch, laying dates could not be estimated by back-dating. Since egg density decreases during incubation (Furness and Furness 1981) previous studies have used the regression of mean egg density (ie. mean egg weight/mean egg volume) against days to hatching for successful clutches, to predict the hatching dates of failed clutches on the basis of their mean egg densities at the time of their location (e.g. Galbraith and Green 1985).

However, from the data collected in the first year of this study the correlation coefficient obtained for this relationship was relatively low (ie. $r=0.52$, $n=28$, $p<0.01$). The difference between the actual hatching dates of clutches and those predicted from the regression equation could be up to 23 days (average=7.25 days) and therefore the equation was of little use in predicting the hatching dates of failed clutches. Since in both subsequent years 90% of all clutches were found, and therefore the eggs were measured, within six days of the start of incubation an accurate prediction of days to hatching from egg density could not be expected and the calculations were not carried out.

APPENDIX 3: EFFECTS OF STUDY METHODS ON NESTING SUCCESS

A3.1 MARKING AND VISITING NESTS

In studies of ground nesting birds it is possible that marking and visiting nests may lead to artificially high predation rates on nests (e.g. Picozzi 1975). As considered previously, nest markers could not have provided cues for predators to locate nests since the markers were in place prior to laying, and were at random distances and directions to nests (see 4.1.1).

Using data from 1987 and 1988 (ie. the years in which visiting for a proportion of nests could be considerably limited), predation rates on nests visited at least twice between the date of location (or clutch completion, if found during laying) and the start of chipping were no higher than for nests visited on at most one occasion during the same period (Table A3.1). Too few nests were not visited at all over this period to provide a useful comparison, and the period was taken to the start of chipping, rather than to hatching, since frequent visits were necessary at all nests after chipping began (see 6.1.1). That nest visits were particularly frequent after the start of chipping, and that over the whole study only five eggs were known to be predated between chipping and hatching also suggests that visiting nests did not increase predation rates.

A3.2 NEST TRAPPING ADULTS

In this study only one pair were ever known to desert a clutch during incubation (though on a few occasions pairs did desert the last egg to hatch, if the other eggs had already hatched and the chicks had left the nest). Desertion of this clutch occurred after trapping the second adult at this nest. However, trapping was not considered to be the ultimate cause of the desertion, since both adults from this nest were found to have serious leg injuries and both appeared to be in poor condition (ie. body weights, at 340g and 395g for the male and female respectively, were the lowest for any birds of that particular sex caught during this study). Therefore, it is considered likely that this nesting attempt would have failed irrespective of trapping.

It is possible that trapping may have had other effects on breeding success. For example, after trapping, a bird may become more likely to leave the nest when disturbed, therefore increasing the risk of predation. The possibility that such effects occurred was tested by comparing the success of nests on which birds were trapped with that of nests on which no birds were trapped, in 1987 and 1988. No differences were found between the two groups, either in overall egg losses from nests, or in losses from predation only (Table A3.2). Further, of the nests on which trapping was carried out in 1987 and 1988, only two suffered predation of eggs after the actual trapping of an adult (trapping usually being carried out in the late stages of incubation).

Eggs which failed due to addling or embryo death were collected (under N.C.C. licence) and examined to ascertain whether any embryo development had occurred, and, if so, the approximate stage of development which had been reached. (A series of photographs of embryo development in the eggs of domestic fowl, Gallus gallus, were used for comparison in estimating the stage of embryo development - see Tolhurst 1974). For those clutches on which adults had been trapped, and which contained eggs which had failed due to embryo death (n=5), there was only one in which it was likely that the embryos had died after trapping had occurred.

Table A3.1. The effects of nest visiting on the success of nests in 1987-88

	NESTS VISITED ON 0-1 OCCASIONS (n=35)	NESTS VISITED ON $\geqslant$2 OCCASIONS (n=52)
% NESTS IN WHICH $\geqslant$ 1 EGG FAILED TO HATCH	51.4	38.5
	X^2 = 1.0NS d.f. = 1	
% NESTS IN WHICH $\geqslant$ 1 EGG WAS PREDATED	22.8	11.5
	X^2 = 1.2NS d.f. = 1	

NS $p>0.10$

Note: the comparison is restricted to the period between locating a nest (or clutch completion, if the nest was found during laying), and the start of chipping.

Table A3.2. The effects of trapping adults on the success of nests in 1987-88

	NESTS AT WHICH ADULTS(S) TRAPPED (n=37)	CONTROL NESTS (i.e. NO TRAPPING) (n=52)	
% NESTS IN WHICH $\geqslant$ 1 EGG FAILED TO HATCH	62.5	40.4	$X^2 = 1.1$NS d.f. = 1
% NESTS IN WHICH $\geqslant$ 1 EGG PREDATED	13.5	23.1	$X^2 = 0.69$NS d.f. = 1

NS $p>0.10$

APPENDIX 4: A list of the invertebrate orders which occurred in suction trap samples and which were subsequently classed as surface-active invertebrates in this study.

Isopoda

Diplopoda

Chilopoda

Opiliones

Araneae

Acari

Collembola

Plecoptera

Dermaptera

Hemiptera

Adult Lepidoptera

Larval Lepidoptera

Trichoptera

Adult Diptera

Adult Hymenoptera

Larval Hymenoptera (sawfly larvae only)

Adult Coleoptera

Larval Coleoptera

APPENDIX 5: Grid references of study sites (given to the approximate centre of each site).

Site 1 : 622927

Site 2 : 617915

Site 3 : 653903

Site 4 : 666906

Site 5 : 624139