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Studies of the Flocking Behaviour of Sanderlings,

Calidris alba

by

J. G. Roberts, B. A. (Oxon.)

**A thesis submitted for the degree of
Doctor of Philosophy**

Department of Biological Sciences

**University of Durham
1990**

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Abstract

The behaviour of sanderlings, *Calidris alba*, was studied at Teesmouth, N. E. England.

Flock sizes and within-flock spacing were related to factors such as substrate type, season, and prey distribution.

Sightings of individually-identifiable colour-ringed birds showed that turnover was high. Individuals varied in their vagility and in the way in which they allocated their time between feeding sites. There was a high degree of consistency between winters in the distributions of individual birds.

When individual sighting frequencies were taken into account, associations between individual sanderlings, in terms of both flock membership and of occurrences at the same sites on the same days, were non-significantly different from those expected by chance. Previously used methods for detecting non-random associations gave inadequate null models. Each individual appeared to make a decision about where to feed independently of the decisions made by any other particular individuals.

A number of aspects of the dynamics of flocks were examined, including flock cohesion; how flocks built up and broke down; whether birds tended to move to the largest or smallest, the nearest or furthest flocks; the effects of disturbance on flock dynamics; and the relationship between group size and the distance flown between flocks.

The responses of sanderlings to experimental disturbances tended to support the hypothesis that responses should be varied according to the costs and benefits of different courses of action rather than the hypothesis that birds should take flight as soon as a predator is sighted.

Birds often break off from performing an activity in order to raise their heads (scan). Preening birds had shorter inter-scan intervals than feeding birds. Flock size and spacing explained only a small proportion of the variance in vigilance. Vigilance was greater in autumn than in winter. There was some evidence for both feeding and preening birds avoiding very short inter-scan intervals but not for the avoidance of long intervals. Sequences of inter-scan interval durations of preening birds were non-random.

To my family.

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No part of this thesis has previously been submitted for a degree in this or any other university. The work described is my own except where duly acknowledged.

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Chapter I

General Introduction

This thesis is about the behaviour of individual birds and how that behaviour relates to the presence and behaviour of conspecifics.

There are a number of levels at which such relationships might occur, ranging from the degree of site-faithfulness (the tendency to return to the same site in successive years); through the degree of itinerancy and the extent of regular movements around the home range; to the degree to which individuals aggregate and the nature of the spacing between birds in such aggregations. At each level there is considerable behavioural variation both within and between species. Such variation invites functional explanation.

Wilson (1975, p. 585) defined a group as a “set of organisms, belonging to the same species, that remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics.” This theme of the potential importance of other individuals recurs throughout this thesis.

Finding food and avoiding predators are likely to be as important determinants of flocking behaviour as they are of any other aspect of behaviour. By joining flocks, birds may reduce their risk of being taken by predators and/or may increase their food intake. Barnard and Thompson (1985) review the ways in which these effects may come about. Other reviews of flocking behaviour include Bertram (1978), Clark and Mangel (1986) and Pulliam and Caraco (1984). An influential hypothesis is that birds should group together with other individuals since individual risk is less in flocks where a predator takes only one (Hamilton, 1971). Page and Whitacre (1975) showed that the chance of an individual wading bird being taken by a predator was greater when the bird was alone than when it was in a flock. Observations of birds forming larger flocks and abandoning territories in the presence of a predator (Caraco *et al.*, 1980a; Myers, 1984; Whitfield, 1988) also provide evidence for this hypothesis.

The most successful theory concerning the variation in flocking behaviour among waders (Goss-Custard, 1970) proposes that there is a trade-off between anti-predatory advantages of being in flocks and foraging disadvantages. While different waders may achieve similar benefits, there may be differences in susceptibility to foraging interference which determine the degree of aggregation. This thesis is not about the effects of flocking on foraging success (e.g. Goss-Custard, 1970, 1980). Nor is it about the optimal sizes of foraging groups (e.g. Pulliam and Caraco, 1984). Instead, much of it is concerned with some of those aspects of flocking behaviour which have received less attention.

The species studied was the sanderling, *Calidris alba*, a small (20 cm) wading bird (or shorebird) which breeds in the high arctic and winters along the coastlines of both the northern and southern hemispheres (Cramp and Simmons, 1983).

Waders are good subjects for behavioural and ecological research. This suitability lies both in the relative ease with which they can often be studied and in their intrinsic interest. The latter arises from the considerable inter- and intra-specific variation shown, which raises the question of how functional explanations can be provided. The advantages of sanderlings in particular as a study species for my research included the following: (1) a large number of birds had been colour-ringed so as to be individually-identifiable; (2) several years of observations had been made and so something of their behaviour and ecology was known, together with the histories of particular individuals (Brearey, 1982; Gudmundsson, 1985; Cooper, 1988); and (3) sanderlings were regularly found at the same sites and could be observed easily as they utilized an open habitat.

In Chapter 2 I introduce the species and the study site and go on to describe the spacing behaviour of sanderlings.

In Chapter 3 I update Cooper's (1988) study of sanderling distributions and movements around Teesmouth. Quantitative analyses of sightings of colour-ringed birds are presented in order to describe the range of behaviour shown by different individuals. This chapter also provides the background for the work on associations between individual sanderlings in Chapter 4.

The study of associations is basic to the investigation of social organization in

gregarious species. Many birds are gregarious, at least to some extent, and there is a large literature concerning the selective advantages of flocking and the reasons for the occurrence of flocks of particular sizes (e.g. Pulliam and Caraco, 1984). But this literature is mainly concerned with the advantages of being in a group *per se* and not with advantages to particular individuals of being in particular groups. There are a number of studies of associations among mammals but fewer of associations among birds (see references in Chapter 4). Therefore, for most species it is not known how flock membership changes through time and whether birds move independently between flocks or in groups. The aim of the study presented in chapter 4 was to describe the levels of association between individual sanderlings and explain these in terms of ecological factors, comparing the situation at Teesmouth with that found by Myers (1983) in California.

Few studies have taken a mechanistic approach to the question of how observed flock sizes are arrived at (Krebs, 1974; Barnard and Thompson, 1985; Caraco, 1979a, b, 1980; Caraco and Pulliam, 1980). In Chapter 5 I examine a number of aspects of flock dynamics in order to find the level of flock cohesion and to describe how flocks build up and break down.

In Chapter 6 I investigate the dependence of behaviour in response to disturbance on a number of factors including the presence and behaviour of other birds. It is usually assumed that birds take flight as soon as a predator is sighted and so flight responses have been taken as indicating vigilance levels (e.g. Barnard and Thompson, 1985). Hypotheses based on this assumption are tested against those based on the assumption that responses should be varied according to the costs and benefits of different courses of action (Ydenberg and Dill, 1986).

Chapter 7 is also concerned with the question of how behaviour depends on the presence and behaviour of others but this time with regard to vigilance behaviour. Many species of birds and mammals typically feed with their heads down, raising them occasionally to scan the environment, probably to detect predators but perhaps also for other reasons. This vigilance behaviour is particularly suited to quantitative analysis.

Finally, Chapter 8 provides a general discussion.

Throughout the thesis statistical analyses were carried out using SPSS-X (SPSS Inc., 1988). Siegel (1956) was referred to for non-parametric tests and Sokal and Rohlf (1981) for parametric tests.

Chapter II

The Study Species and the Study Site

2.1 The Study Species

Sanderlings breed in the high arctic and winter along the coasts of both northern and southern hemispheres. The number of sanderlings wintering in Europe was estimated as 14,300 by Prater and Davis (1978), of which 10,300 wintered around the coasts of Britain. The beaches around the Tees estuary support one of the main British wintering populations (Prater, 1981). The Birds of Estuaries Enquiry reported maximum counts of 210, 490, 476, 800 and 200 for the winters of 1983–84 to 1987–88 respectively (Salmon and Moser, 1984, 1985; Salmon *et al.*, 1987a, b, 1988), while Cooper (1988) reported peaks of 800–900 in the winters of 1981–82 to 1983–84.

There is some doubt over the location of the breeding quarters of the sanderlings wintering at Teesmouth. However, the observation of about twenty birds which were colour-ringed at Teesmouth and are known to have wintered there passing through Iceland in May 1988 (G. A. Gudmundsson, pers. comm.) suggests that a substantial proportion of the wintering population breeds in Greenland or further west.

Cooper (1988) and Evans and Pienkowski (1984) describe the typical seasonal movements of sanderlings at Teesmouth. Different individuals arrive at different times of year and stay for different lengths of time. Adult birds start to return from the breeding grounds in the latter part of July. Numbers continue to build up through August and September with juveniles arriving from late August. Passage of birds during August to early November results in fluctuations in numbers. Some birds arrive at Teesmouth in October and early November, having moulted elsewhere, notably at the Wash, while others move on at the same time after moulting at Teesmouth. Up to 800 moulting birds have been recorded in August and

September (Evans *et al.*, 1980). Spring passage occurs in April and May and few remain by late May and early June.

2.2 The Study Site

Figure 2.1 shows the coastline of N. E. England along which observations of colour-ringed sanderlings were made by a number of observers before my study period (see Chapter 3). The coastline comprises several long sandy beaches interspersed with rocky outcrops and cliffs. Both sandy and rocky beaches were utilised by sanderlings.

Figure 2.2 shows my main study site in more detail. Coatham Rocks and Redcar Rocks are outcrops of calcareous sandstone. At Redcar Rocks these outcrops run in parallel ridges, typically 0.5–1.0m high, approximately perpendicular to the line of the shore. The rocks are encrusted with molluscs, particularly the blue mussel, *Mytilus edulis*, and have a patchy cover of *Enteromorpha*. Between these ridges are flatter rocky areas, areas with a shallow covering of sand, areas of deeper sand, and inlets in which deposits of wrack (detached sea-weed) collect.

Sanderlings are typically thought of as birds of sandy beaches (e.g. Cramp and Simmons, 1983) and it is unclear how widespread is the habit of feeding on rocky areas.

2.3 Feeding Methods

Sanderlings feed by (1) pecking on rocky substrates; (2) pecking on sandy substrates; (3) probing in sand; (4) stitch-feeding in sand; and (5) water-column feeding (Brearey, 1982). When pecking, the bill penetrates the substrate little or not at all, whereas it does penetrate the substrate when probing or stitch-feeding. Probing birds tend to make less frequent and more pronounced feeding movements than do pecking birds. Stitching birds make numerous probes in rapid succession while moving forwards, interspersing these feeding movements with short runs.

Sanderlings feed visually and by using touch and chemoreception (e.g. Gerritsen and van Heezik, 1985; Gerritsen and Meiboom, 1986). Foraging profitability is affected by the density, size and depth of their prey and by substrate penetrability

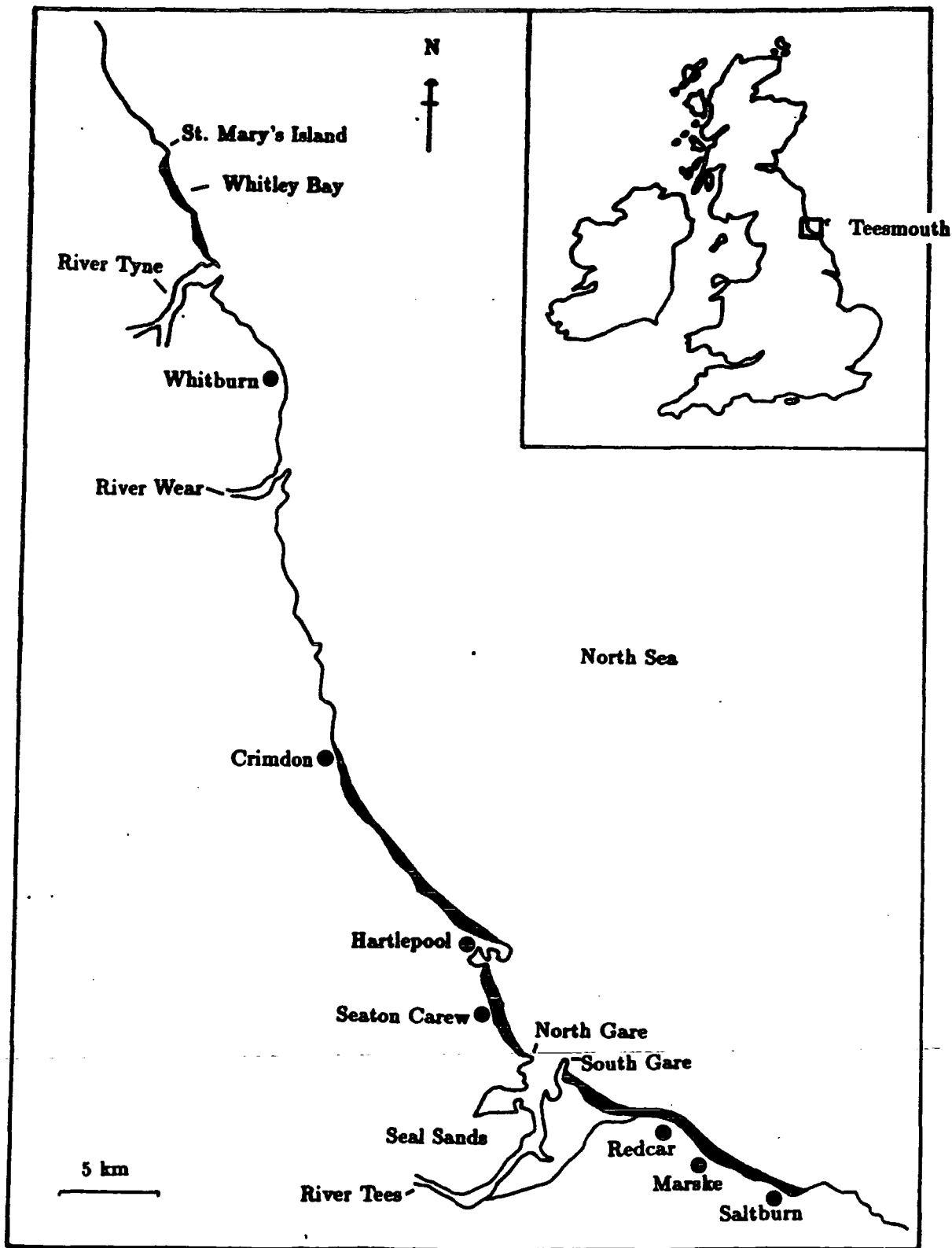


Figure 2.1 — Areas Searched for Sanderlings before 1986

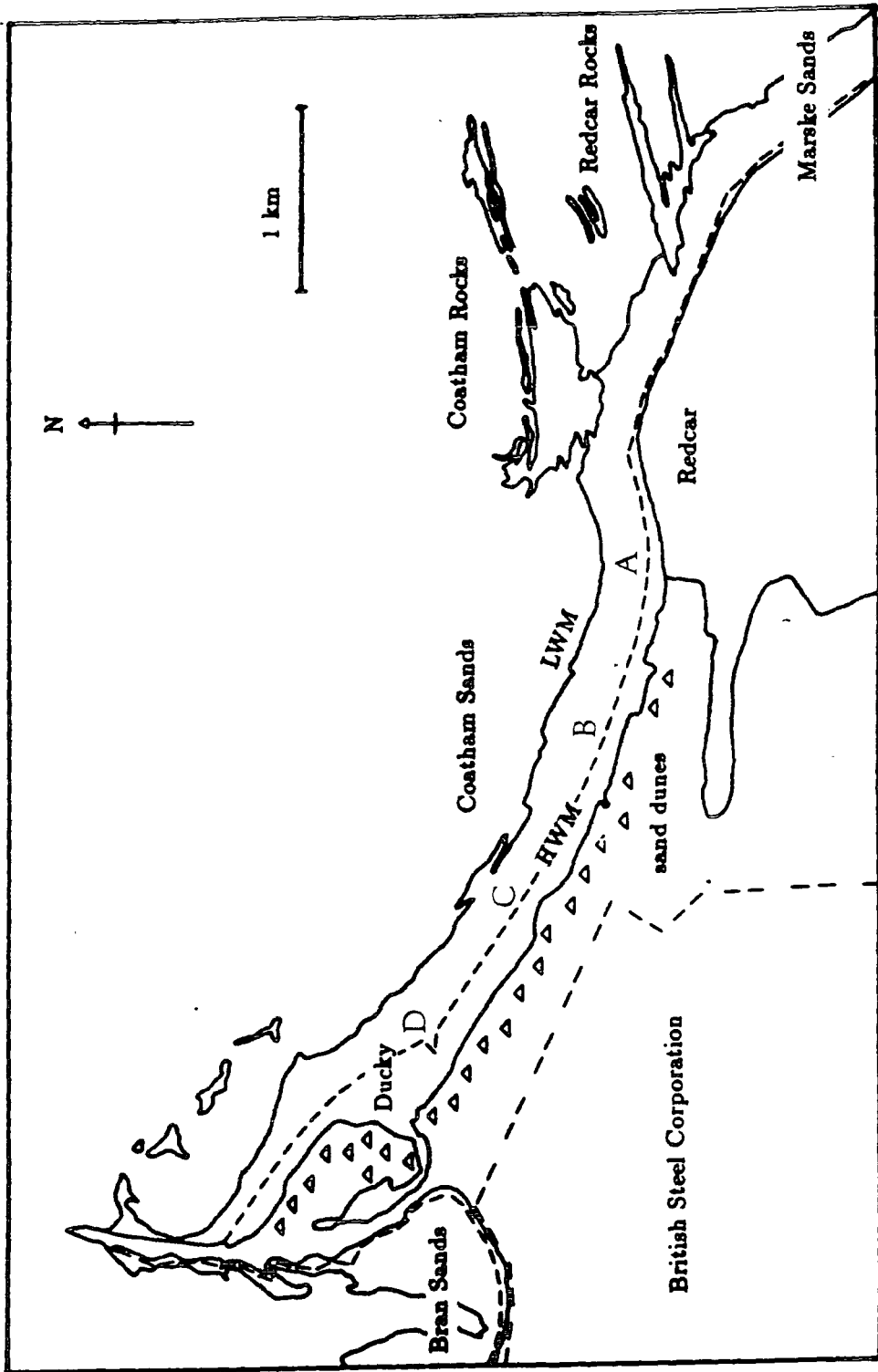


Figure 2.2 — The Study Site

(Myers *et al.*, 1980). Burger *et al.* (1977) found that sanderlings tended to feed on water-covered sandy areas.

2.4 Prey

At Teesmouth sanderlings have been found to feed mainly on *Nerine cirratulus* (a polychaete), *Bathyporeia* spp. (amphipods), and *Eurydice pulchra* (an isopod; Evans *et al.*, 1980). They probably also take *Haustorius arenarius* (an amphipod).

Sampling over a number of years has shown that *Nerine* tended to be concentrated in a band along the middle to upper part of the beach (P. R. Evans, unpublished data). Another consistent result is that *Nerine* densities have been greatest towards the south end of the beach. This might be related to the greater slope of the beach at the south end or to the possibly lesser effects of pollution at that end.

Sampling was carried out in October 1988 in order to find whether any major changes had taken place in prey distribution. Two 10cm³ samples were taken from sites at 30m, 40m, 50m, 60m, 70m, 80m, 100m and 150m below high-water mark along 6 transects separated by 500m down Coatham Sands and along two transects at Redcar (Figure 2.2). Samples were kept cool and sorted within 3 days.

The results presented in Tables 2.1 and 2.2 give the total numbers of each species found along each transect to indicate the long-shore distribution patterns. In order to provide a detailed description of prey distribution many more samples would have had to be taken so that different times of year and tidal ranges were represented. Nevertheless, taken with the results referred to above, the data confirm the broad trend of increasing *Nerine* density towards the south end of Coatham Sands; the high *Nerine* density at Redcar; and the patchiness of the distribution of crustaceans.

Banks of wrack were occasionally washed up on Redcar beach, on Marske Sands, and particularly on Coatham Sands. The invertebrates associated with these deposits and with those of coal dust (which was washed ashore mainly along Coatham Sands) provided a rich, though irregular, food source.

High tides and stormy conditions can heavily erode sandy beaches and cold weather can cause sandy substrates to freeze or the prey to burrow deeper (e.g. Evans,

Size	Transect							
	1	2	3	4	5	6	7	8
≤ 15mm	64	78	119	29	6	5	86	106
16–25mm	24	37	17	17	0	3	50	30
> 25mm	3	3	5	5	0	0	4	6
Total	91	118	141	51	6	8	140	142

Table 2.1 — Distribution of *Nerine*

Figures give the total numbers of animals found along each transect, with two samples at each of eight points. Transects 1–6 were along Coatham Sands; 7 and 8 were at Redcar (Figure 2.2).

Prey	Transect							
	1	2	3	4	5	6	7	8
<i>Bathyporeia</i> and <i>Periculodes</i>	65	100	75	76	59	145	124	142
<i>Eurydice</i>	15	33	35	13	10	6	0	1
<i>Haustorius</i>	11	5	6	8	24	13	4	4

Table 2.2 — Distribution of the Main Species of Crustacea

See legend to Table 2.1.

1976). These factors are likely to make prey densities more unpredictable than on rocky areas.

2.5 Behaviour in Relation to Tides and Seasons

Tides have an important influence on foraging, not only determining the availability of different foraging sites but also affecting prey availability through their effects on prey activity and on substrate penetrability (e.g. Connors *et al.*, 1981).

As the tide rose birds feeding on the south side of the estuary typically moved from the rocky areas which were exposed only at low tide (mainly Redcar Rocks) onto sandy areas (mainly Coatham Sands but also Marske Sands). This movement coincided approximately with the increased availability of *Nerine* as the tide reached the mid-shore zone where this species is most abundant (Section 2.4). There was a tendency for birds first to use the southern end of Coatham Sands before spreading out northwards.

Over high water in autumn and spring a roost at the Ducky at the northern end of Coatham Sands was often used (Figure 2.2). However, during some periods the birds were absent from the Redcar–Coatham Sands area over high water and no roost was found. From December through to February movement to a roost site was less frequent, sanderlings feeding for longer periods and forming high water roosting groups near the feeding sites. Birds often arrived very early on a falling tide at Redcar Rocks where they roosted at the top of the beach while the rocks were exposed. In autumn and spring sanderlings often preened and roosted at low water on Redcar Rocks. Such behaviour was less common in mid-winter (see also Section 2.6.4 and Chapter 7).

Maron and Myers (1985) also reported that sanderlings spent longer roosting in autumn than in winter. Swennen *et al.* (1989) studied the responses of captive oystercatchers, *Haematopus ostralegus*, to an artificially controlled tidal regime. They found that as the time available for feeding decreased the time spent preening and bathing was maintained at a roughly constant level. Food intake was maintained by spending less time resting and decreasing searching and handling times.

After high-water birds moved back to Redcar Rocks, either flying directly or moving in stages along the sandy beaches.

The extent to which different sites were used (both in terms of numbers of birds present and in terms of the lengths of time for which they were present) varied with the tidal range, with the season, from year to year, with the amount of disturbance, and from day to day. My observations suggested that the patterns of movement in relation to the tidal cycle and the ways in which these patterns changed through the winter were more variable than those described by Cooper (1988).

2.6 Spacing Behaviour

2.6.1 Introduction

The object of this section is to provide a description of the spacing behaviour of sanderlings at Teesmouth and of the factors affecting spacing. Detailed discussion of these factors will not be attempted.

2.6.2 Methods

Observations of flock sizes and of within-flock spacing were made between October 1987 and May 1988 at Redcar and at Coatham Sands, which was divided longitudinally into four sections. Where possible, complete checks of a site were made. Most checks were separated by a period of at least 30 minutes.

One method of differentiating flocks is to derive a maximum inter-bird distance criterion from the distribution of nearest-neighbour distances (e.g. Clutton-Brock *et al.*, 1982). If the frequency distribution of distances measured in a particular direction is bimodal, then one peak represents within-flock distances and the other represents between-flock distances. Brearey (1982) used an inter-bird distance of 10m combined with "coordinated movement" to define sanderling flocks. I found that the rocky substrate at Redcar often imposed constraints on flock spacing, especially where areas were cut off by water channels, while on the sands patchy wrack or coal dust and mussel deposits often supported discrete flocks. The 10m criterion was therefore used flexibly when other factors appeared to delineate flocks more meaningfully.

The following were noted.

- (1) The size of each flock of sanderlings (SIZE).
- (2) The total number of sanderlings present at the site at the time (TIMEPOP). This was used to find the maximum number of birds present at any one time on a given day (DAYPOP).
- (3) The distance from each individual to its nearest-neighbour. This was used to find the mean nearest-neighbour distance for the flock (MEAN) and the standard deviation of the nearest-neighbour distribution (STD).
- (4) The activities of each individual. From these the percentage of the flock which were feeding was calculated. Types of feeding method were distinguished (Section 2.3).

In the following analyses, appropriate transformations of the data were made where these resulted in an improvement in the fit to the assumptions of the statistics used. The spacing of birds using Redcar Rocks is described, followed by a comparison of the spacing of birds using different sandy areas.

2.6.3 Flock Sizes at Redcar Rocks

The dependence of flock size on the time of year, the time of day, and the time in relation to the tidal cycle was investigated by analysis of variance with the number of birds present at the site at the time of the record (TIMEPOP) as a covariate. Table 2.3 shows that only time of year had a significant effect. The time of year categories were: (1) October–November; (2) December–February; and (3) March–May. These periods approximate to the different periods described in Section 2.1. The time in relation to the tidal cycle was classed as (1) falling and low tide; and (2) rising tide. The time of day was divided arbitrarily as: (1) before 10:00; (2) 10:00–12:00; and (3) after 12:00.

The overall frequency distributions of the flock sizes observed at different times of year are given in Figure 2.3. This figure illustrates the marked decline in flock sizes through the winter.

Source of variation	SS	df	MS	F	p
Within cells	98.39	293	0.34		
Regression	3.76	1	3.76	11.21	0.001
Season	4.28	2	2.14	6.37	0.002
Tide	0.05	1	0.05	0.16	0.687
Time	0.44	2	0.22	0.66	0.519
Season by tide	0.97	2	0.48	1.44	0.239
Season by time	0.35	4	0.09	0.26	0.901
Tide by time	0.23	2	0.11	0.34	0.710
Season by tide by time	2.26	4	0.57	1.68	0.154

Table 2.3 — ANCOVA of Flock Size by Time of Year, Day and Tide

Flock size was \log_{10} -transformed so that the assumption of homogeneity of variances was met. Season categories: (1) October–November; (2) December–February; (3) March–May. Tide categories: (1) falling and low tide; (2) rising tide. Time of day categories: (1) before 10:00; (2) 10:00–12:00; (3) after 12:00. The regression term refers to the covariate of the number of birds present at Redcar Rocks at the time of the record (TIMEPOP).

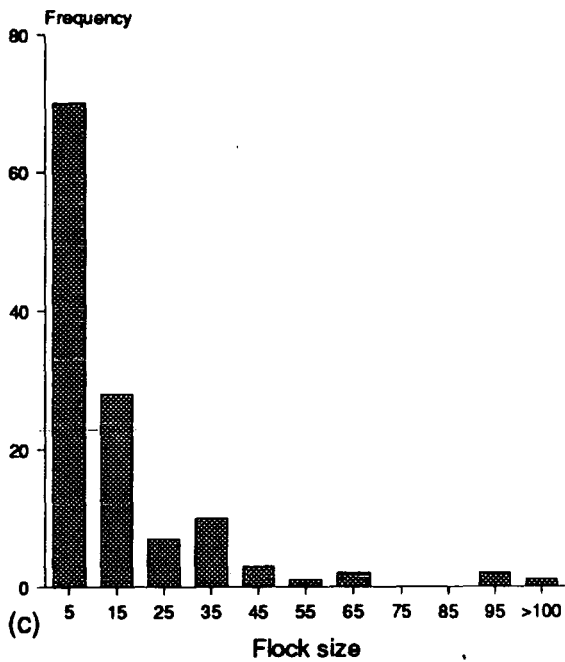
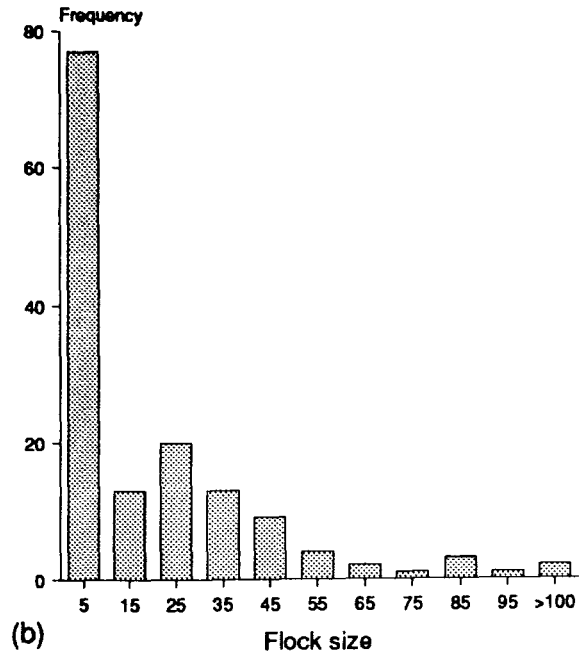
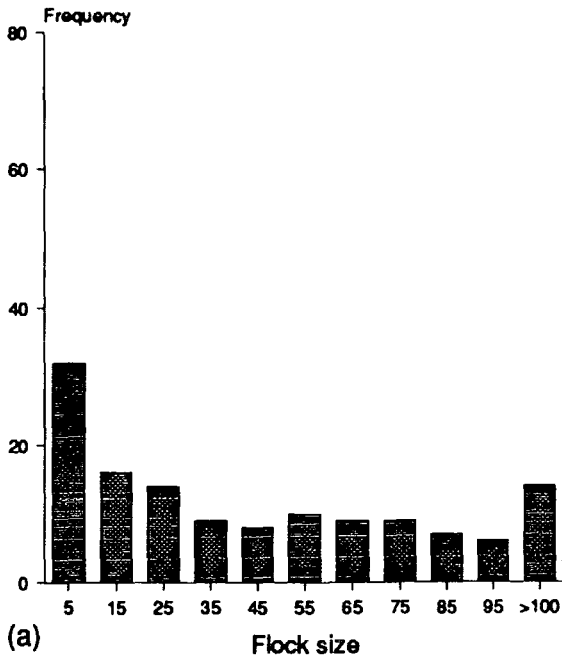


Figure 2.3 — Frequency Distributions of Flock Sizes at Redcar Rocks

(a) Autumn (October–November) mean 45.9 ± 3.6 , $n = 134$. (b) Winter (December–February) mean 19.1 ± 2.0 , $n = 145$. (c) Spring (March–May) mean 14.4 ± 1.7 , $n = 124$.

2.6.4 Activities of Birds at Redcar Rocks

The percentage of a flock which was feeding as opposed to roosting, preening or bathing varied with the time of year, the time of day, and the time in relation to the tidal cycle (Table 2.4). There were also significant interactions between these variables making interpretation of the biological meaningfulness of these effects very difficult. Examination of the means given in Table 2.5 suggests that the proportion of birds in a flock which were feeding was highest in mid-winter and lowest in autumn. This is consistent with the comments made in Section 2.5. None of the time variables gave significant effects when entered into a multiple linear regression. Non-linear effects were looked for by entering the squares of each variable: no significant effects were found. This is surprising given the results in Table 2.4. The explanation may lie in the skewed distribution of the percentages of birds feeding in flocks (*PFEED*) which means that any analyses using this variable should be treated with caution. There was a weak negative relationship between the percentage feeding and the flock size:

$$\log_{10}PFEED = 1.982(\pm 0.027) - 0.097(\pm 0.023)\log_{10}SIZE;$$

where $\text{Beta} = -0.219$; $F_{366,1} = 18.48$, $p < 0.00005$; and the t values of the constant and slope terms were significant at the $p < 0.00005$ level. Thus, there was a slight tendency for birds in larger flocks to roost, preen or bath more than birds in smaller flocks.

2.6.5 Nearest-Neighbour Distances at Redcar Rocks

The mean nearest-neighbour distance was found to decrease with flock size and increase with the proportion of the flock which were feeding. A multiple linear regression of \log_{10} -transformed mean distance gave:

$$\begin{aligned} \log_{10}MEAN = & -0.2708(\pm 0.0619) - 0.0044(\pm 0.0001)SIZE \\ & + 0.0025(\pm 0.0001)PFEED, \end{aligned}$$

(where $r = 0.43$; Beta values -0.40 and 0.20 respectively; $F_{344,2} = 50.19$, $p < 0.00005$; and the t values of all terms in the equation were significant at the $p <$

Source of variation	SS	df	MS	F	p
Within cells	20.17	349	0.06		
Regression	0.51	1	0.51	8.79	0.003
Season	0.70	2	0.35	6.07	0.003
Tide	0.21	1	0.21	3.56	0.060
Time	1.06	2	0.53	9.17	< 0.0005
Season by tide	2.22	2	1.11	19.17	< 0.0005
Season by time	3.82	4	0.96	16.53	< 0.0005
Tide by time	2.06	2	1.03	17.81	< 0.0005
Season by tide by time	3.24	4	0.81	14.02	< 0.0005

Table 2.4 — ANCOVA of Percentage Feeding by Time of Year, Day and Tide

The percentage of the flock feeding was \log_{10} -transformed so that the assumption of homogeneity of variances was met. Season, tide and time categories were as Table 2.3. The regression term refers to the covariate of flock size.

Season	Tide	Time	Mean	Std. Dev.	<i>n</i> of flocks
Autumn	Falling	1	90.00	14.14	2
Autumn	Falling	2	76.73	31.54	15
Autumn	Falling	3	83.90	28.00	59
Autumn	Rising	1	61.50	41.49	20
Autumn	Rising	2	51.67	34.99	12
Autumn	Rising	3	69.57	34.15	21
Winter	Falling	1	100.00	0.00	3
Winter	Falling	2	100.00	0.00	19
Winter	Falling	3	4.00	6.08	3
Winter	Rising	1	95.88	11.34	25
Winter	Rising	2	91.55	20.03	42
Winter	Rising	3	97.00	8.94	28
Spring	Falling	1	82.17	34.24	29
Spring	Falling	2	88.77	27.69	26
Spring	Falling	3	100.00	0.00	7
Spring	Rising	1	82.52	27.54	21
Spring	Rising	2	96.77	13.34	17
Spring	Rising	3	96.90	9.48	19

Table 2.5 — Mean Percentages of Flocks Feeding by Time of Year, Tide and Day

Categories of season, tide and time are as in Table 2.3.

0.00005 level). The standard deviation of the nearest-neighbour distances of the individuals in a flock increased with the mean nearest-neighbour distance but was unaffected by flock size or by the proportion of the flock feeding:

$$\log_{10}STD = 1.4959(\pm 0.0199) + 0.2042(\pm 0.0137)MEAN,$$

(where $r = 0.66$; $F_{1,292} = 222.65$, $p < 0.00005$; and the t values of all terms in the equation were significant at the $p < 0.00005$ level). These regressions are consistent with the partial correlations given in Table 2.6.

The decrease in nearest-neighbour distance with increasing flock size may be partly due to the decrease in the proportion of birds which will be on the edge of the flock and which are therefore less likely to have close nearest-neighbours.

2.6.6 Spacing Behaviour in Different Sandy Areas

In this section I describe the differences in spacing behaviour between birds feeding in different sandy areas. Records were divided according to the predominant feeding methods in each flock. Sample sizes were sufficient for analysis of stitching (see Section 2.3) and pecking flocks only.

In the case of stitching birds, flock sizes were appreciably greater at Redcar and in area B than in areas C or D (Table 2.7). Flocks were most dense in area B where the variability in spacing was lowest. Although dense flocks might have been expected at Redcar, these results are largely consistent with the hypothesis that birds should concentrate in the areas of greatest food density: stitching birds feed on *Nerine* which were densest at Redcar and at the south end of Coatham Sands (Section 2.4). Relationships between prey density and predator density have been found for other wading birds such as redshanks, *Tringa totanus*, (Goss-Custard, 1970) and dunlin, *Calidris alpina* (Rands and Barkham, 1981).

The patchy distribution of the crustacean prey of pecking birds makes prediction of spacing behaviour on the basis of prey distribution difficult. Flock size was greatest at Redcar (Table 2.8), followed by the south end of Coatham Sands (area C), perhaps due to its proximity to the roost site at the Ducky (Figure 2.2). Flocks in area A were most widely spaced but also showed the lowest level of variation in spacing.

Dep. var.	Indep. var.	Controlling for	corr.	<i>n</i>	<i>p</i>
MEAN	SIZE	PFEED	-0.403	344	< 0.0005
	PFEED	SIZE	0.213	344	< 0.0005
STD	SIZE	PFEED, MEAN	-0.044	289	0.227
	MEAN	SIZE, PFEED	0.612	289	< 0.0005
	PFEED	SIZE, MEAN	0.024	289	0.344

Table 2.6 — Partial Correlations between Nearest-Neighbour Distances and Flock Sizes and Activities

The dependent variables were log₁₀-transformed.

Area	Flock size			Mean nearest-neighbour distance			Std. dev. nearest-neighbour distance		
	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>
R	17.82	3.35	99	1.67	0.20	72	0.94	0.12	72
B	24.77	5.45	13	0.43	0.08	10	0.30	0.07	10
C	5.43	2.99	35	1.91	0.37	16	0.89	0.29	16
D	6.68	2.56	19	2.20	0.37	11	0.96	0.31	11

Table 2.7 — Flock Sizes and Spacing of Stitch-Feeding Birds in Different Sandy Areas

Area R is Redcar; other areas are Coatham Sands (Figure 2.2). Insufficient data were obtained for area A. Analyses of variance on the \log_{10} -transformed dependent variables gave: $F_{162,3} = 7.43, p < 0.0005$ for flock size; $F_{105,3} = 6.65, p < 0.0005$ for mean nearest-neighbour distance; and $F_{84,3} = 4.36, p = 0.007$ for the standard deviation (std. dev.) of nearest-neighbour distance.

Area	Flock size			Mean nearest-neighbour distance			Std. dev. nearest-neighbour distance		
	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>
R	10.56	1.28	331	2.00	0.12	209	0.76	0.05	209
A	4.88	1.24	25	3.41	0.65	17	0.61	0.21	17
B	5.19	0.98	96	2.45	0.22	51	0.96	0.11	51
C	7.04	2.54	27	2.14	0.45	11	1.14	0.39	11

Table 2.8 — Flock Sizes and Spacing of Birds Feeding by Pecking in Different Sandy Areas

Area R is Redcar; other areas are Coatham Sands (Figure 2.2). Insufficient data were obtained for area D. Analyses of variance on the \log_{10} -transformed dependent variables gave: $F_{475,3} = 2.47, p = 0.061$ for flock size; $F_{284,3} = 4.14, p = 0.007$ for mean nearest-neighbour distance; and $F_{207,3} = 3.62, p = 0.014$ for the standard deviation (std. dev.) of nearest-neighbour distance.

2.6.7 Spacing Behaviour on Rocky and Sandy Areas

Flocks on rocky areas were larger and more tightly spaced than those on sandy areas. Sanderlings tended to move about much more rapidly when on sand than when on rocks. These findings are similar to those of Silliman *et al.* (1977).

2.6.8 Territoriality and Aggression

Sanderlings are territorial in parts of their wintering range at certain times. Territoriality can be commonplace in California (Myers *et al.*, 1979a,b, 1981 ; Myers, 1980, 1984), but has rarely been observed in Britain (Cramp and Simmons, 1983). Only extremely rarely were sanderlings at Redcar observed to defend an area around themselves and this behaviour never lasted for more than a few minutes. The area defended was of less than 1m radius. Aggression was noted only rarely and typically involved defence of a large food item such as a *Nerine* or a mussel. In California aggression is common (e.g. Myers, 1984). Silliman *et al.* (1977) found that aggression among sanderlings increased with flock size and was greatest on sandy areas.

Chapter III

Distributions and Movements

3.1 Introduction

In this chapter, sightings of colour-ringed sanderlings are analysed in order to describe patterns of occurrence with particular reference to how individual behaviour relates to behaviour at the level of the group or the local population. Some understanding of distributions and movements is necessary before looking at the likelihood of particular individuals being found together. This chapter therefore provides a background to the work on associations in Chapter 4 where hypotheses arising from this chapter will be tested.

Sightings are also analysed in the context of intra-specific variation. The distributions and movements of individual birds can be classified in a number of ways. First, there is the degree to which individuals tend to return to the same area in different years. This may be termed their inter-year site-faithfulness. Individuals may also show intra-year site-faithfulness. That is, they may tend to remain in the same area between migrations. The degree of intra-year site-faithfulness may allow birds to be divided into residents and transients. These terms should be qualified by giving the sites at which observations were made: if they were made in an area representing only a fraction of a bird's range then it might be that a transient at one site was a resident at another. Alternatively, it might be that the bird was a floater, there being no sites where it was to be found regularly.

The number of sites used can be referred to as the home-range of a bird. Birds which are more wide-ranging must on average be seen fewer times at any given site. Therefore there is necessarily a relationship between this measure and the last. Whether or not birds with a large home-range are classed as residents or not depends on the relationship between the size of the range and the size of the area over which observations are made.

Finally birds may differ in the frequency with which they switch between sites, that is, in their vagility.

Wading birds (Charadriiformes) differ both within and between species in their tendencies to return to the same wintering areas in successive years and in the extents to which they move around in the non-breeding season. In this chapter I show that individual sanderlings vary in terms of their residency, their range, and their vagility.

3.2 Sources of Data

My analyses drew on two sources of data: (1) sightings made by a number of observers between 1976 and 1986 along the coast of N. E. England (Figure 2.1); and (2) sightings made by myself between 1986 and 1989 in the Redcar and Coatham Sands area (Figure 2.2). Cooper (1988) provides a detailed study of sanderling movements in N.E. England using data for the 1981–82, 1982–83 and 1983–84 winters and gives more details on the ringing programme, the observation schedule, and the areas searched. Brearey (1982) and Gudmundsson (1985) also provide information on numbers and movements. A summary of the numbers of sanderlings colour-ringed and sighted at different sites and at different times is given in Appendix A. Very few birds were colour-ringed after the start of this study.

Throughout this chapter data are presented for colour-ringed birds. These birds should not be taken as representative of all birds using Teesmouth. In particular, there will be a bias towards more frequently occurring birds and towards birds which tended to use the south side of the estuary.

3.3 Numbers of Colour-Ringed Birds

In this section I concentrate on sightings made from winter 1986–87 to winter 1988–89 since these are most relevant to later chapters. Data on the numbers of colour-ringed birds present in earlier years are given in Cooper (1988).

The numbers present in the winters of my study are given in Table 3.1. There was a marked decline in the mean number of colour-ringed birds present on days when thorough checks were made between winter 1986–87 and winter 1987–88. This was accompanied by a sharp decline in the total numbers of colour-ringed

birds seen at least once during the winter from 151 in winter 1986–87 to 81 in winter 1987–88 and 61 in winter 1988–89 and so the differences could not have resulted from changes in the intensity of observation. The changes in the numbers of colour-ringed birds were paralleled by changes in total numbers. The relative importance of mortality and dispersal is unknown.

During the years of my study there was no evidence for seasonal fluctuations in the numbers of colour-ringed birds present (Table 3.2). This should not be interpreted as meaning that the total numbers (including birds not colour-ringed) did not fluctuate seasonally.

However, the number of colour-ringed birds present in the Redcar–Coatham Sands area fluctuated considerably from day to day (Figure 3.1). This variation in numbers implies that a considerable proportion of individuals using the site were highly mobile.

Figure 3.2 gives the numbers of days with given numbers of birds present. There was no ‘typical’ number of birds present: the distributions are irregular and discontinuous. There was a tendency for numbers at the lower end of the range and in the middle of the range to be particularly common.

In order to quantify the degree to which the set of birds present changed through time an index of turnover was used. Following Myers (1984) the turnover of colour-ringed birds between any two days (which were not necessarily consecutive) was calculated as:

$$T = 100 \times \frac{E + I}{P_{day\ a} + P_{day\ b}}$$

where E is the number of emigrants (i.e. those seen on day a but not on day b); I is the number of immigrants; and $P_{day\ x}$ is the number of colour-ringed birds seen on day x .

Turnover was high (Figure 3.3(a)). Daily turnover was almost 40%, compared with approximately 15% found by Myers (1984). There was a slight increase in turnover with the time interval, t , between day a and day b ($F_{628,1} = 54.06, p < 0.00005, r = 0.28$):

$$T = 43.98(\pm 0.91) + 0.08(\pm 0.01)t,$$

Winter	Mean	S. E.	Min	Max	<i>n</i>
1986-87	45.17	2.55	16	68	36
1987-88	20.05	1.63	10	33	20
1988-89	21.42	2.39	10	34	12

Table 3.1 — Numbers of Colour-Ringed Birds Present on Days in Different Winters

The figures presented are the means, standard errors, minima and maxima of the numbers of birds present on days in each winter. Only days when thorough checks for colour-ringed birds were made in the Redcar and Coatham Sands areas are included. *n* is the number of such days in each year. On each of these days, 10 or more colour-ringed birds were seen.

Winter	Months	Mean	S. E.	<i>n</i>
1986-87	Oct	44.3	13.7	3
	Nov	46.0	2.0	2
	Dec	56.0	6.0	2
	Jan	48.8	4.6	6
	Feb	52.1	7.1	7
	Mar	36.6	5.9	7
	Apr	46.9	3.6	7
	May	23.5	7.5	2
1987-88	Sep-Nov	21.3	2.0	12
	Dec-Feb	14.0	3.1	3
	Mar-May	20.8	3.8	5
1988-89	Sep-Nov	22.0	2.9	9
	Dec-Feb	19.7	4.8	3

Table 3.2 — Numbers of Colour-Ringed Birds Present on a Day in Relation to Time of Year

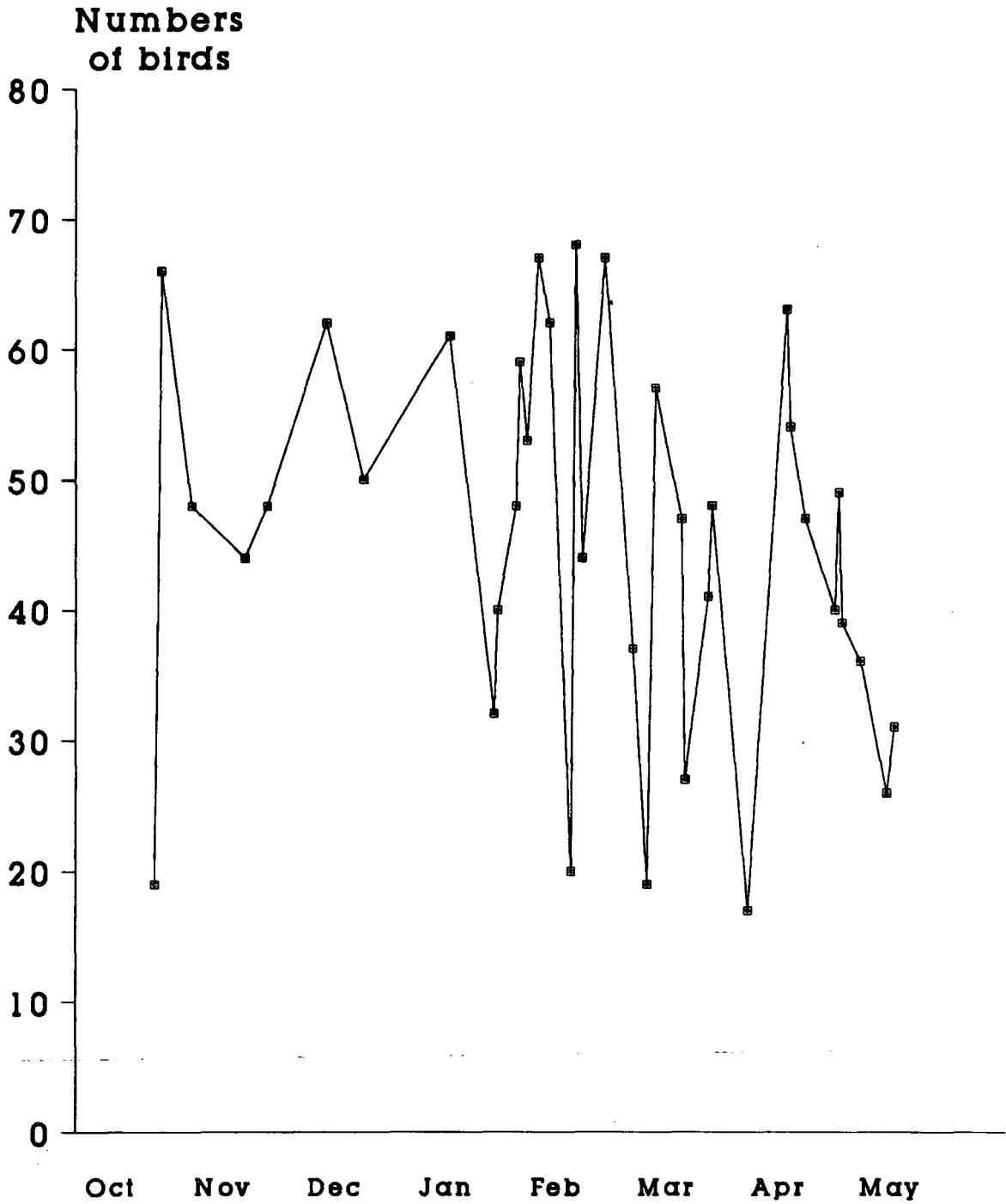


Figure 3.1 — Variations in the Numbers of Colour-Ringed Birds Present on Days in Winter 1986–87

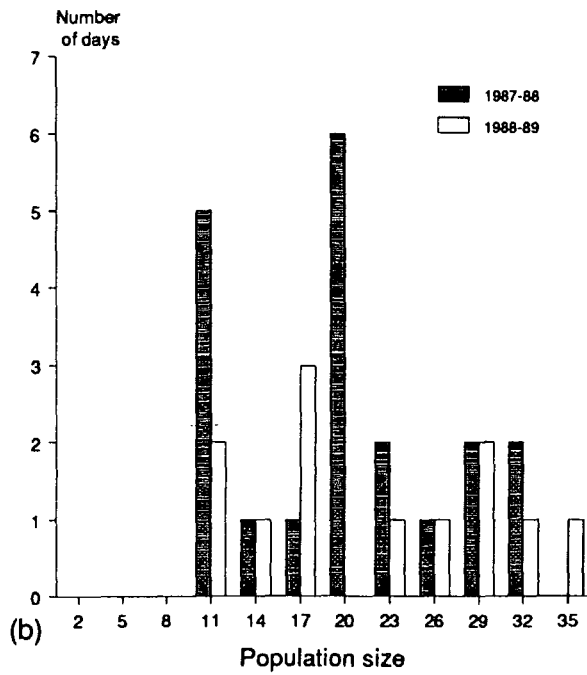
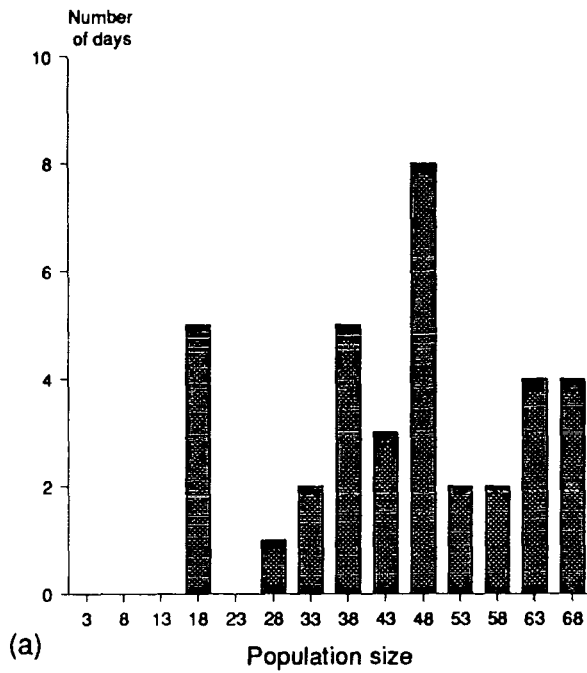


Figure 3.2 — Frequency Distributions of Numbers of Colour-Ringed Birds Present on a Day

(a) Winter 1986-87; (b) winter 1987-88 and 1988-89.

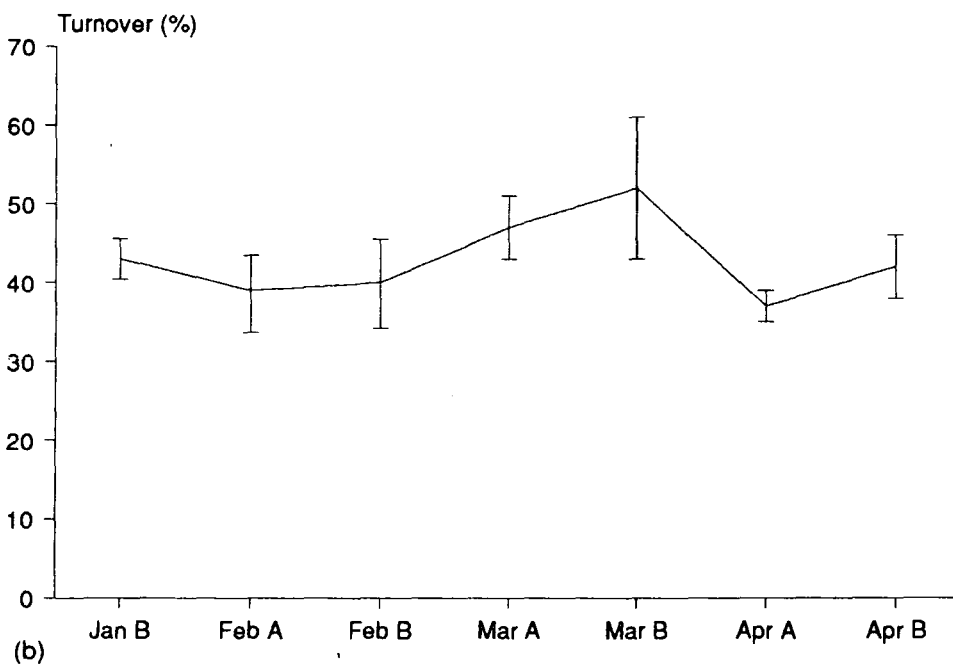
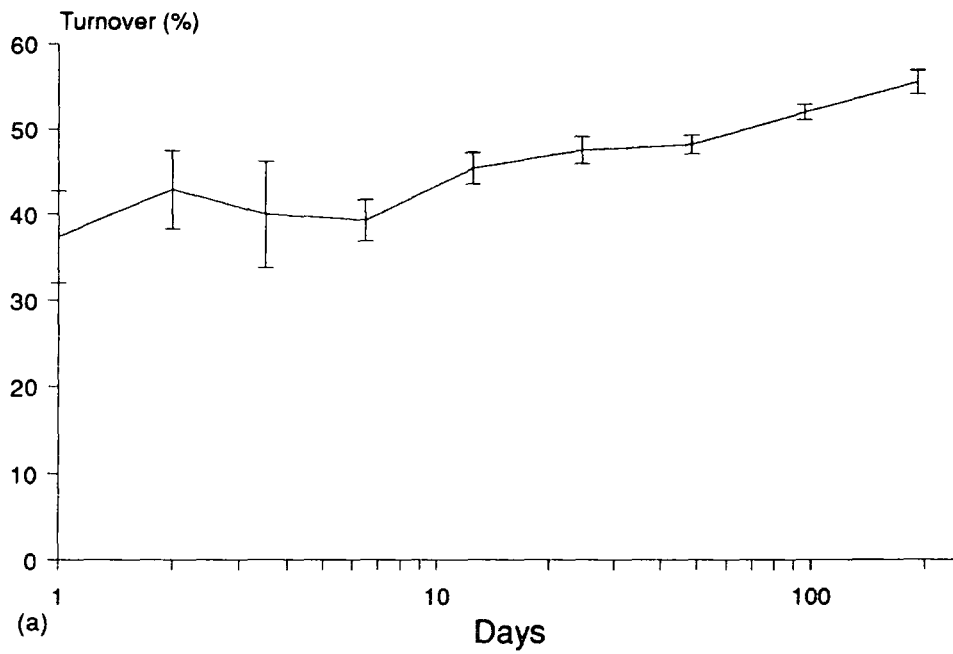


Figure 3.3 — Turnover of Colour-Ringed Birds

(a) Turnover in relation to time interval. (b) Turnover in different half-monthly periods. Bars show standard errors.

where the figures in parentheses are standard errors and the t values of the terms in the equation were significant at the $p < 0.001$ level.

Seasonal differences in turnover were investigated by dividing the winter into periods of half a month. Mean turnover rates for each of these periods were calculated from all t values for intervals starting within those periods and lasting for 14 days or less. Sample sizes were sufficient for January to April only (Figure 3.3(b)). Although the figure suggests an increase in turnover in March, there were no significant effects of season ($F_{75,6} = 1.160, p = 0.337$). The colour-ringed birds may not have been representative of the total numbers of birds using the study site so this should not be interpreted as indicating that there were no seasonal variations in turnover. The proportion of the total number of birds present which were colour-ringed varied (Cooper, 1988) and was particularly low at passage times when turnover of the total set of birds is likely to be high. However, in the case of colour-ringed birds, the high level of turnover between days swamped any seasonal effects.

3.4 Overall Site Usage: Grouping of Sites

The extent to which an individual uses a site, A , might be correlated with the extent to which it uses another site, B . In order to find whether this was the case, the frequencies of occurrence of individuals at each site were subjected to principal components analyses. Each winter was considered separately and the analyses were confined to those sites for which there were sufficient data for the appropriate winter and to those birds seen at least once during the winter. Initially, frequencies of occurrence at each site were broken down by season, but this factor accounted for only a few percent of the variance in sighting frequencies and so totals for each winter were used instead.

Tables 3.3–3.5 give examples of the analyses. The correlation matrices show that the highest correlations between frequencies of occurrence at different sites are for adjacent sites. There are differences between years in the principal components extracted, but this is to be expected given that the sites entered into the analyses differed between years due to differences in coverage and in the accuracy with which locations of birds were recorded. For example, in 1983–84 there were few records for sites north of Hartlepool and so these were grouped together in order to

(a) Correlation matrix:

	A	B	C	D	E	F	G	H	I
A									
B	0.58								
C	0.49	0.51							
D	0.36	0.32	0.34						
E	0.23			0.13					
F	0.30	0.16		0.69	0.39				
G	-0.11		-0.11	0.10	-0.11				
H	-0.26	-0.17	-0.25	-0.28	-0.16	-0.19	0.29		
I	-0.16	-0.17	-0.18	-0.23	-0.12	-0.19			

(b) Factor loadings:

	Factor 1	Factor 2	Factor 3
A	0.71		
B	0.82		
C	0.84		
D		0.72	
E		0.60	
F		0.90	
G			0.84
H			0.64
I			

Table 3.3 — Principal Components Analysis of Sighting Frequencies at Different Sites, Winter 1983–84

Key to sites (see Figure 2.1): A Saltburn; B between Saltburn and Marske; C Marske; D Redcar; E Coatham Rocks; F Coatham Sands; G Bran Sands; H Seaton Carew; I Hartlepool to St. Mary's Island. The correlation matrix gives the r values for correlations between frequencies of occurrence at the different sites where these were significant at the $p < 0.05$ level. Factor loadings are given where greater than 0.45. Analysis was by procedure FACTOR of SPSS-X (SPSS-X Inc., 1983) with varimax rotation. Extraction of 3 principal components accounted for 62.1% of the variance.

(a) Correlation matrix:

	A	B	C	D	E	F	G
A							
B	0.27						
C	-0.14	-0.10					
D		0.12	0.33				
E							
F	-0.12	-0.12		-0.10	0.41		
G		-0.11			0.16	0.22	

(b) Factor loadings:

	Factor 1	Factor 2	Factor 3
A			0.76
B			0.78
C		0.79	
D		0.83	
E	0.80		
F	0.80		
G	0.49		

Table 3.4 — Principal Components Analysis of Sighting Frequencies at Different Sites, Winter 1984–85

Key to sites: A Saltburn to Marske; B Redcar to Coatham Sands; C Seaton Carew; D Crimdon; E South and North Shields; F St. Mary's Island; G Seaton Sluice to Druridge Bay. See legend to Table 3.3. Extraction of 3 principal components accounted for 60.4% of the variance.

(a) Correlation matrix:

	A	B	C	D	E	F	G	H
A								
B	0.41							
C	0.12	0.42						
D		0.50	0.28					
E		0.24		0.18				
F					0.45			
G	-0.15			-0.18		0.30		
H								0.11

(b) Factor loadings:

	Factor 1	Factor 2	Factor 3
A	0.55		
B	0.86		
C	0.69		
D	0.59		
E		0.82	
F		0.84	
G			0.68
H			0.71

Table 3.5 — Principal Components Analysis of Sighting Frequencies at Different Sites, Winter 1985–86

Key to sites (see Figure 2.1): A Saltburn to Marske; B Redcar; C Coatham Rocks; D Coatham Sands; E North Gare Sands; F Seaton Carew; G North Sands to Crimdon; H South Shields to Blyth. See legend to Table 3.3. Extraction of 3 principal components accounted for 59.5% of the variance.

avoid having a large number of zero counts. In spite of these differences it is clear that sites to the south of the River Tees tend to be grouped together, as do sites on the north side. Thus, the number of sightings of an individual at, for example, Redcar is likely to correlate with the number of sightings of the same individual at Coatham or Saltburn but not with its number of sightings at Seaton Carew.

Sites can be grouped such that the group of sites can be considered as one site. This simplifies the analysis of distribution patterns and shows that individuals share distribution patterns to some extent. The latter follows from the predictability of an individual's frequencies of occurrence at a site B given its frequency of occurrence at A . This might come about in two ways: (1) the birds may belong to a group which moves together between the sites; or (2) birds move independently but the geography of the region is such that the particular group of sites represents a relatively discrete foraging area.

3.5 Individual Behaviour

3.5.1 Frequencies of Occurrence

Figure 3.4 gives frequency distributions of the numbers of days on which individuals were seen. The different overall numbers of sightings in different years are due to there being differences between years in (1) the number of observation days; (2) the thoroughness of the checks for colour-ringed birds on those days; and (3) the numbers of birds present.

In each winter there were large numbers of birds seen on only one day and a fairly even spread of cases across the range of sighting frequencies. It is clear that there were far more birds seen very rarely than would be expected on the basis of a Poisson distribution. However, the possibility that mistakes in reading the colour-rings contributed to the large number of birds seen only once is difficult to discount: a very small proportion of birds recorded in error would lead to a significant number of additional birds being recorded. That the number of birds seen only once is less in the later winters may reflect greater reliability in recording. Nevertheless, it is apparent that there was considerable variation between birds in their numbers of occurrences and that this variation was fairly continuous.

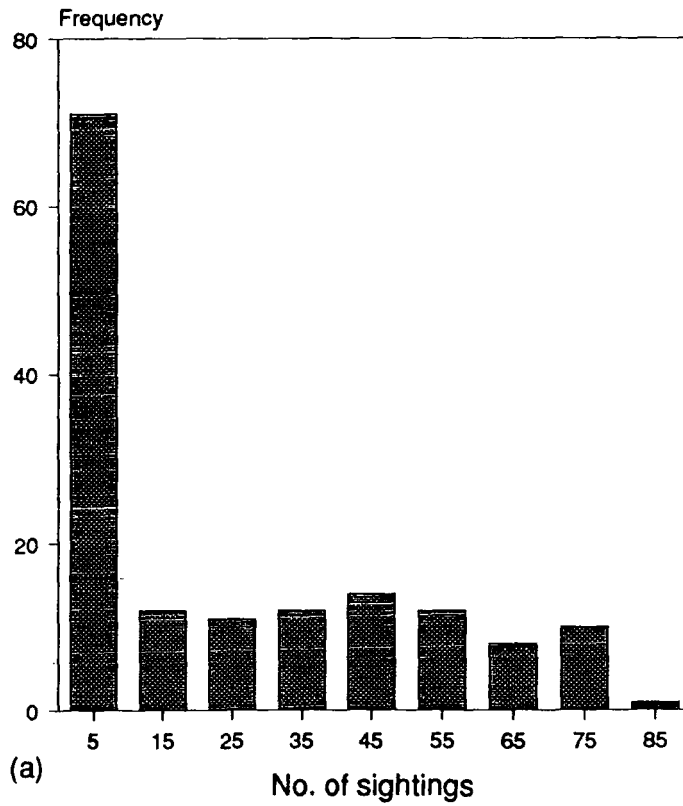
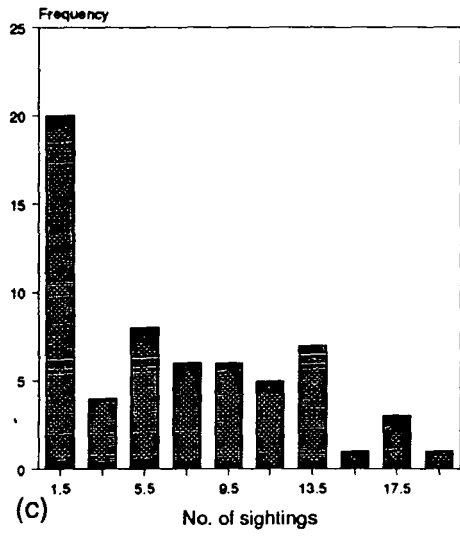
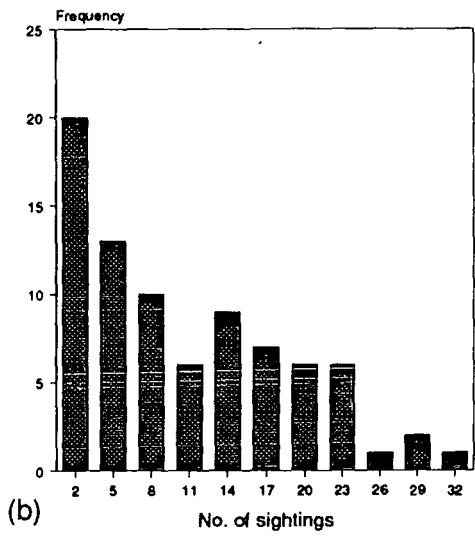


Figure 3.4 — Sighting Frequencies of Colour-Ringed Birds

(a) Winter 1986-87. (b) Winter 1987-88. (c) Winter 1988-89.

3.5.2 Vagility

Vagility is a measure of the extent to which a bird moves between sites from day to day. Following Myers (1984) an index of vagility can be computed as:

$$V. I. = \frac{\text{observed status changes}}{\text{maximum possible}} \times 100$$

A status change was taken to have occurred when a bird was present during one observation period but was absent during the next, or vice-versa. Since observations were not made every day many status changes will have been missed. Nevertheless, the measure obtained should reflect the true level of vagility.

Two methods were used to find the maximum possible number of status changes. Myers used the number of status changes which could have been made by the bird if it had alternated between presences and absences between the time of its first sighting and its last sighting. I will refer to the index calculated on this basis as Index A.

Figure 3.5(a) shows that individuals differed widely in their levels of vagility and that this variation was continuous. Thus, there is no evidence for the hypothesis that there might be classes of high and of low vagility birds (Evans, 1981). However, a problem with this index is that it is strongly dependent on the number of days on which a bird is seen (Figure 3.5(b)). Thus, birds with very small or very large numbers of sightings can make only very few status changes and will have low vagility indices. Although it can be argued that the number of presences is part of what is meant by vagility, there are advantages in having an index which is independent of this factor.

In computing Index A it is assumed that a bird could have alternated between being present and being absent. This necessarily implies a certain number of presences. If the number of presences was actually less than or greater than this implied number, then the maximum number of status changes which could have been made by the bird will be reduced. Take as an example a bird first seen on observation day 3 and last seen on day 11. Had it alternated between being present and being absent it would have made 8 status changes. This is the maximum for

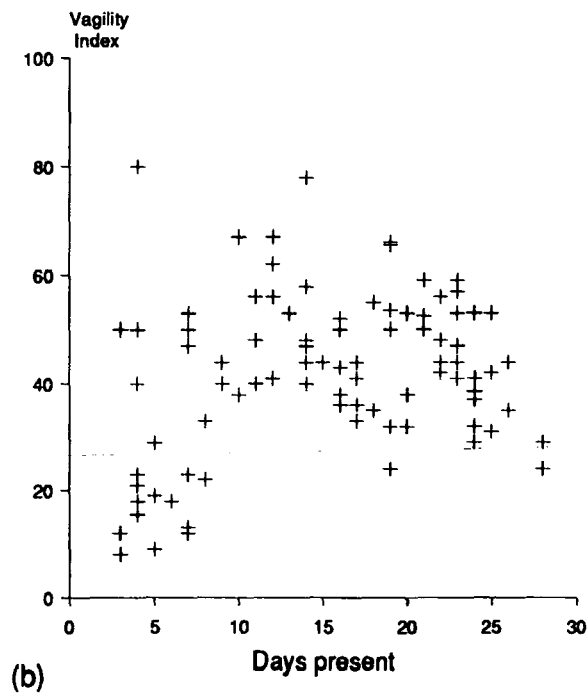
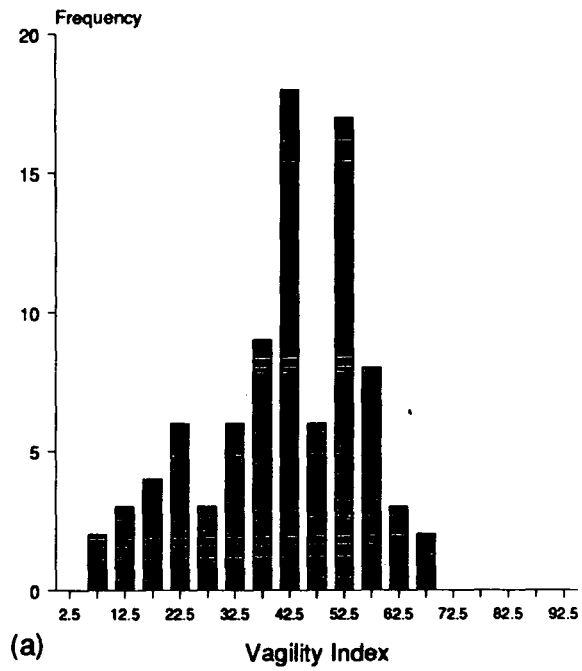


Figure 3.5 — Vagility Index A

(a) Frequency distribution of Index A values; and (b) the dependence of Index A on the number of sightings.

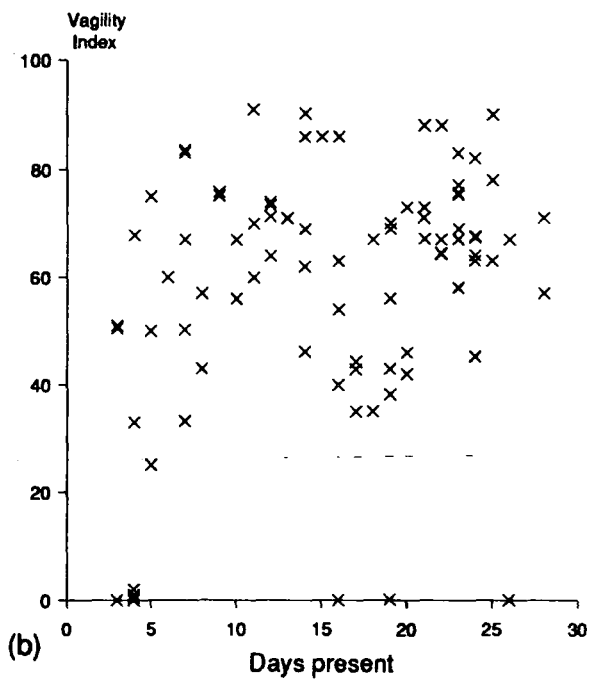
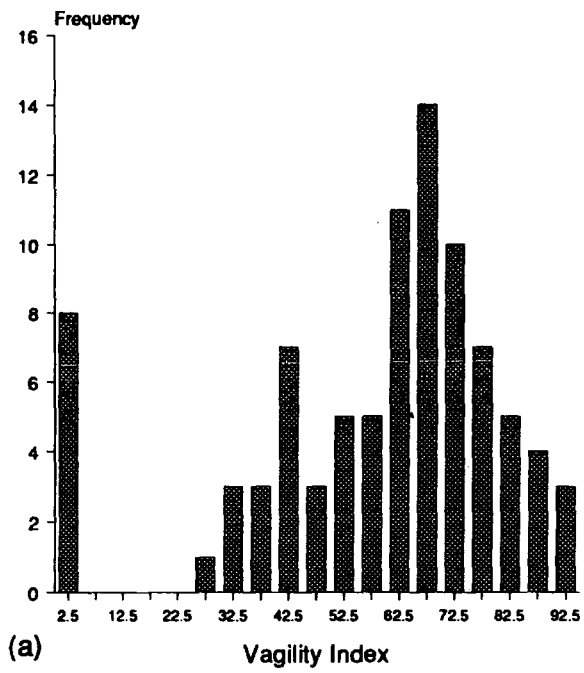


Figure 3.6 — Vagility Index B

(a) Frequency distribution of Index B values; and (b) the dependence of Index B on the number of sightings.

Index A. To have made this number of status changes the bird would have had to have been present on 5 days. Had it been present on only 4 days it could have made only 6 status changes. This latter figure is the maximum used in calculating index B.

Figure 3.6(b) shows that Index B is much less dependent on the number of presences than is Index A. Nevertheless, Figure 3.6(a) reinforces Figure 3.5(a) in showing that there is considerable variation between birds in vagility. The zero values represent birds which could not have made any status changes: that is, they were present on all observation days between their first and last sightings. These birds appear to be a distinct group. However, the gap in the frequency distribution may be an artefact of the fairly small number of observation days: given that the minimum number of status changes which could have been made was 2 and that the maximum was 27, low index values are unlikely or impossible.

3.6 Behaviour at Redcar and at Coatham Sands

In Section 2.4 reasons were given as to why the food supply on the rocky areas at Redcar was likely to be more predictable than was that on Coatham Sands. In this section I test the hypothesis that the putatively greater predictability of the food supply on the rocks at Redcar should lead to greater stability of the population at this site and lower vagility of the birds visiting it.

The following analysis was confined to days from January to May when the Redcar and Coatham Sands sites were checked most regularly. On virtually all field-work days both sites were checked thoroughly for colour-ringed birds: Redcar was checked on 24 days, Coatham Sands on 25. The total number of sightings made at Redcar was 596, compared with 825 at Coatham Sands. However, the number of birds present at Coatham Sands on any one day was not significantly greater than the number at Redcar (Table 3.6). The total number of colour-ringed birds seen was greater at Coatham Sands (122) than at Redcar (92). Table 3.6 also shows that population turnover at Redcar was similar to that at Coatham Sands but that the vagility of birds at Redcar was greater than that of birds at Coatham Sands.

These results do not support the hypothesis stated at the beginning of this section. Unfortunately, interpretation is complicated by the fact that birds often used a

Parameter	Redcar			Coatham			<i>t</i>	<i>p</i>
	Mean	S.E.	<i>n</i>	Mean	S.E.	<i>n</i>		
Population size	24.81	3.60	24	33.03	3.71	25	-1.60	0.117
Turnover	66.80	1.03	276	64.47	0.94	300	1.68	0.093
Vagility Index A	54.32	1.83	70	40.37	1.69	98	5.96	< 0.0005
Vagility Index B	80.24	2.17	70	61.71	3.16	98	4.57	< 0.0005

Table 3.6 — A Comparison of the Behaviour of Colour-Ringed Sanderlings at Redcar and at Coatham Sands

For vagility indices, t-tests were paired.

high-water roost site on Coatham Sands (Section 2.5). Thus birds may have used Coatham Sands on a regular basis because of the proximity of the feeding areas to the roost site.

3.6.1 Site Usage

In this section an attempt is made to classify birds according to their distributions. During the winters of 1981–82 to 1985–86 frequent checks for colour-ringed birds were made at sites from Saltburn in the south to Hartlepool in the north (Figure 2.1). Checks further north were less regular and so were not included in this analysis. In Section 3.4 it was shown that sites from Saltburn to Coatham Sands could be considered as one area and sites from Bran Sands to Hartlepool as another. Figures 3.7–3.11 show the number of times that individuals were seen on the north side of the estuary in relation to the number of times they were seen on the south side for five successive winters. Frequencies of observation are plotted as the numbers of times that birds were seen out of the numbers of times that the sites were visited. This measure was used to enable comparisons to be made between occurrences on the different sides of the estuary in different years given that the south side was generally visited more than was the north side and that the numbers of visits to both sites varied between years.

Cooper (1988) divided birds into the following categories.

- (1) Itinerant (less than 20% of colour-ringed birds). These birds (a) regularly moved to sites away from Teesmouth such that they were absent for several weeks of the winter; (b) were occasional visitors; or (c) moved away for part of one or more winters.
- (2) Semi-mobile (about 30%). These birds moved between the north and south sides of the estuary.
- (3) Resident (about 50%). These birds were seen predominantly on the south side.

However, Figures 3.7–3.11 provide no evidence of clusters of birds with similar distributions. Instead, there was considerable and fairly continuous variation in the extents to which different individuals used each side of the estuary with most of the possible range of behaviour being shown. Nevertheless, some distribution

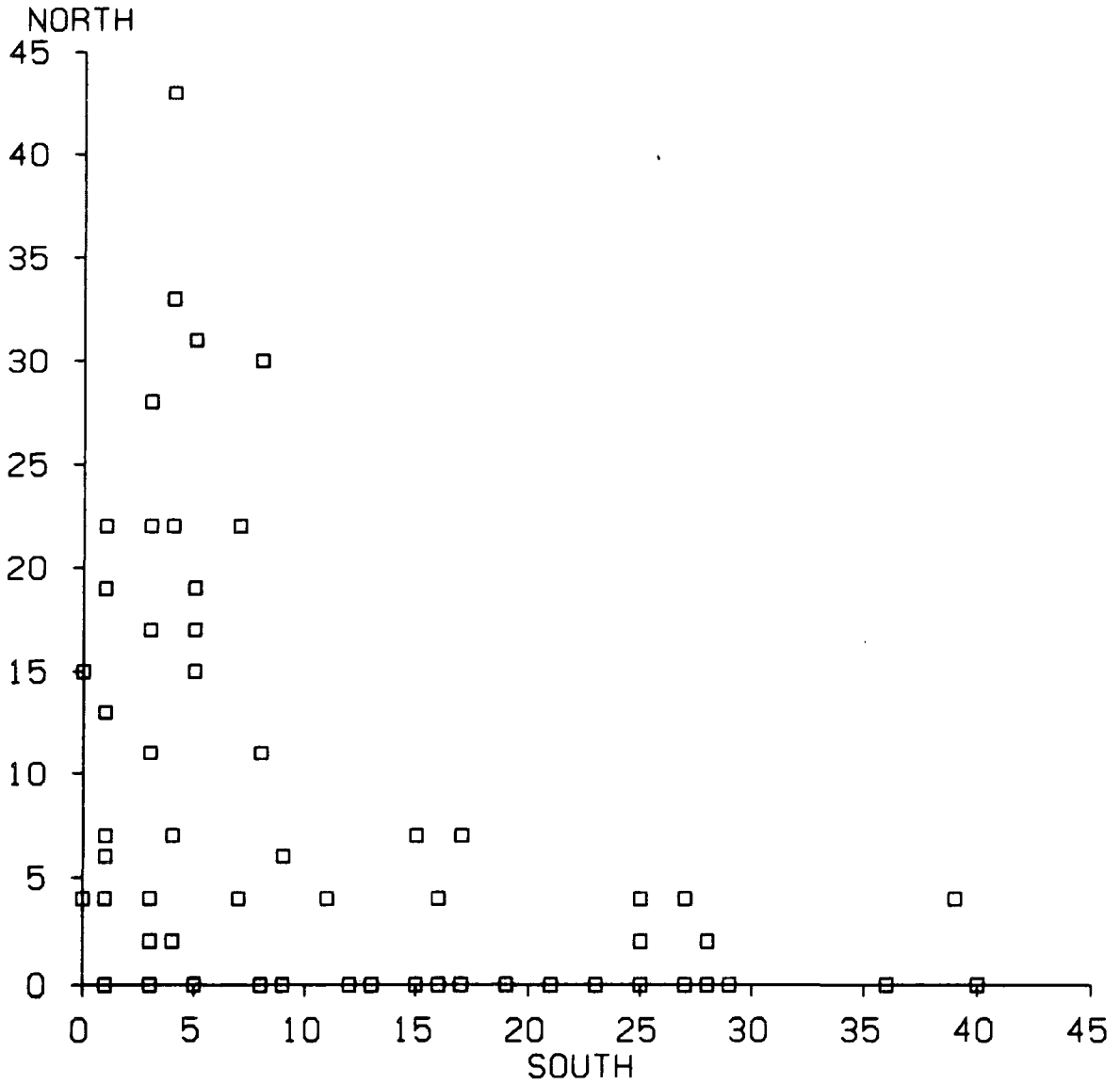


Figure 3.7 — Distributions of Colour-Ringed Birds in Winter 1981–82

Each point represents an individual colour-ringed bird. The axes give the numbers of sightings of each individual on the respective sides of the Tees in winter 1981–82 as percentages of the numbers of times that these sites were checked in that winter.

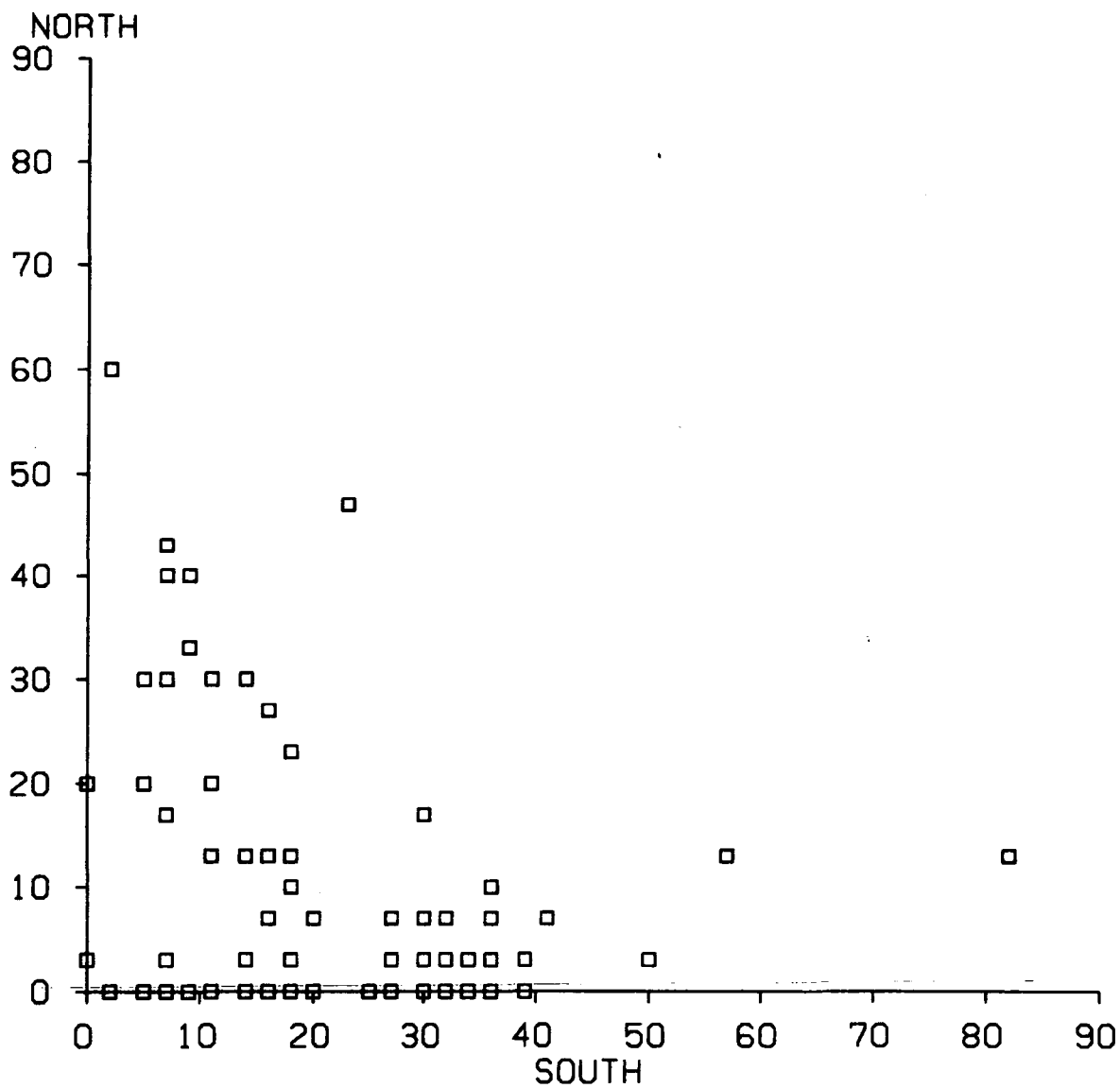


Figure 3.8 — Distributions of Colour-Ringed Birds in Winter 1982-83

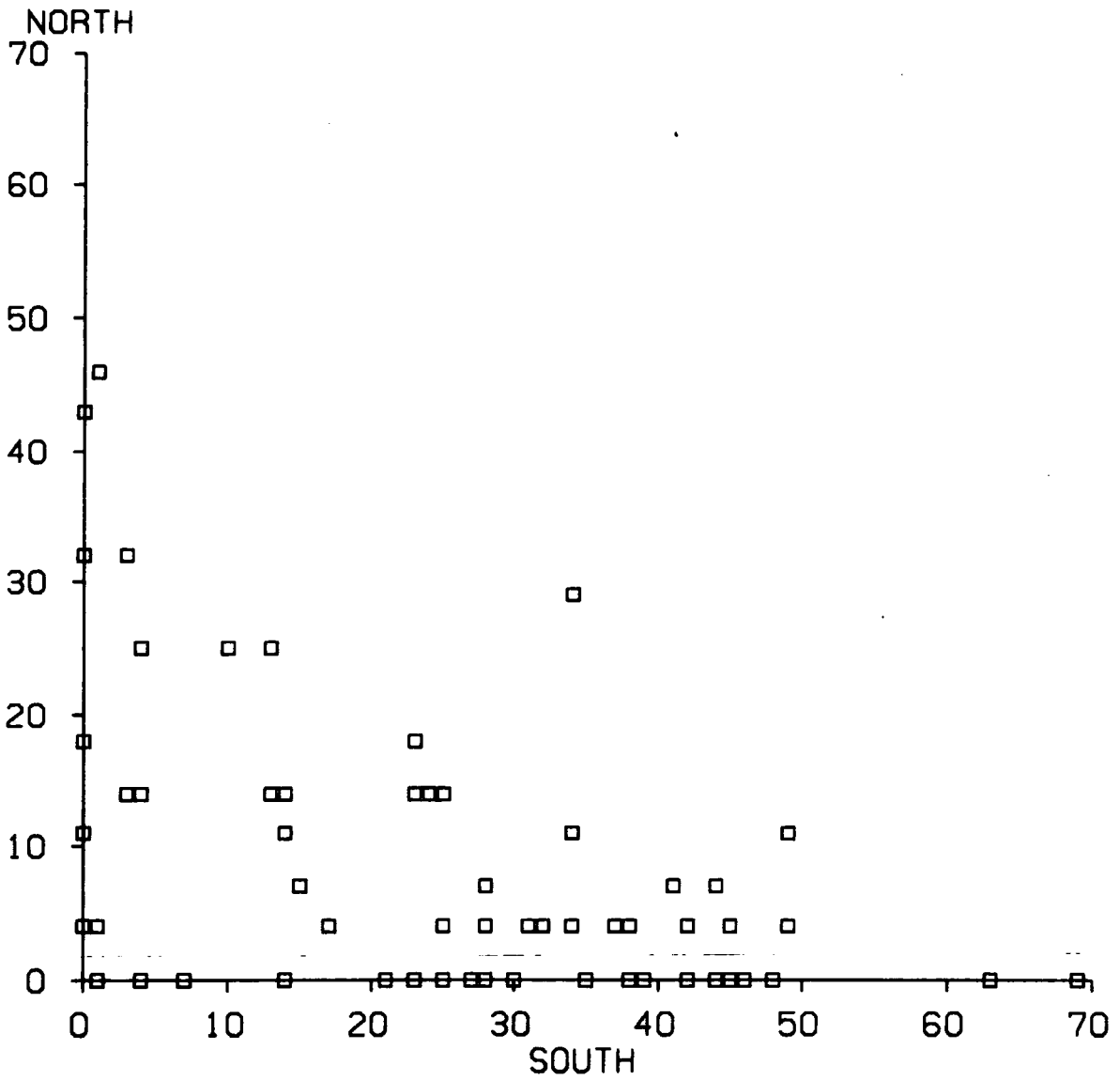


Figure 3.9 — Distributions of Colour-Ringed Birds in Winter 1983-84

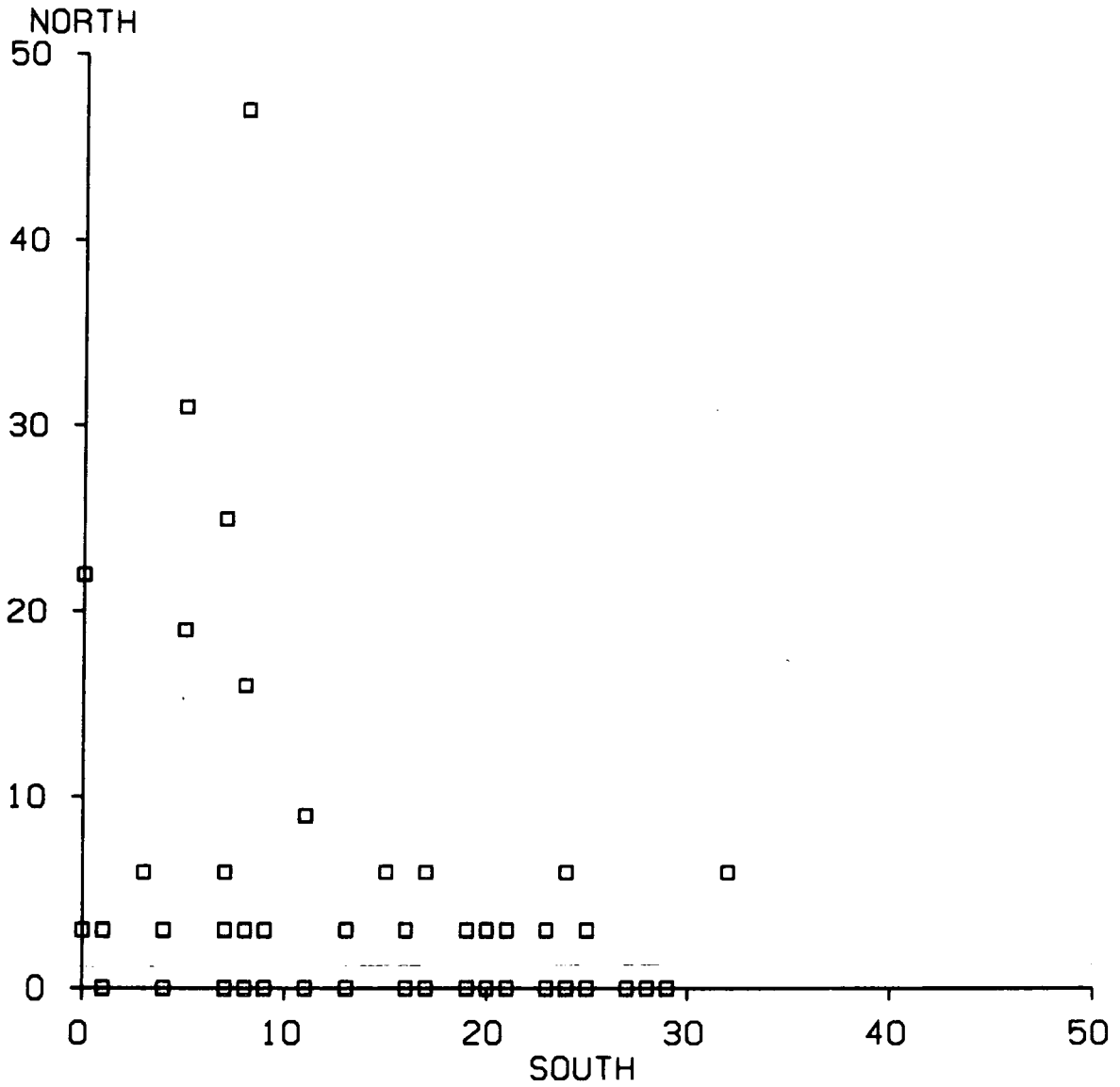


Figure 3.10 — Distributions of Colour-Ringed Birds in Winter 1984-85

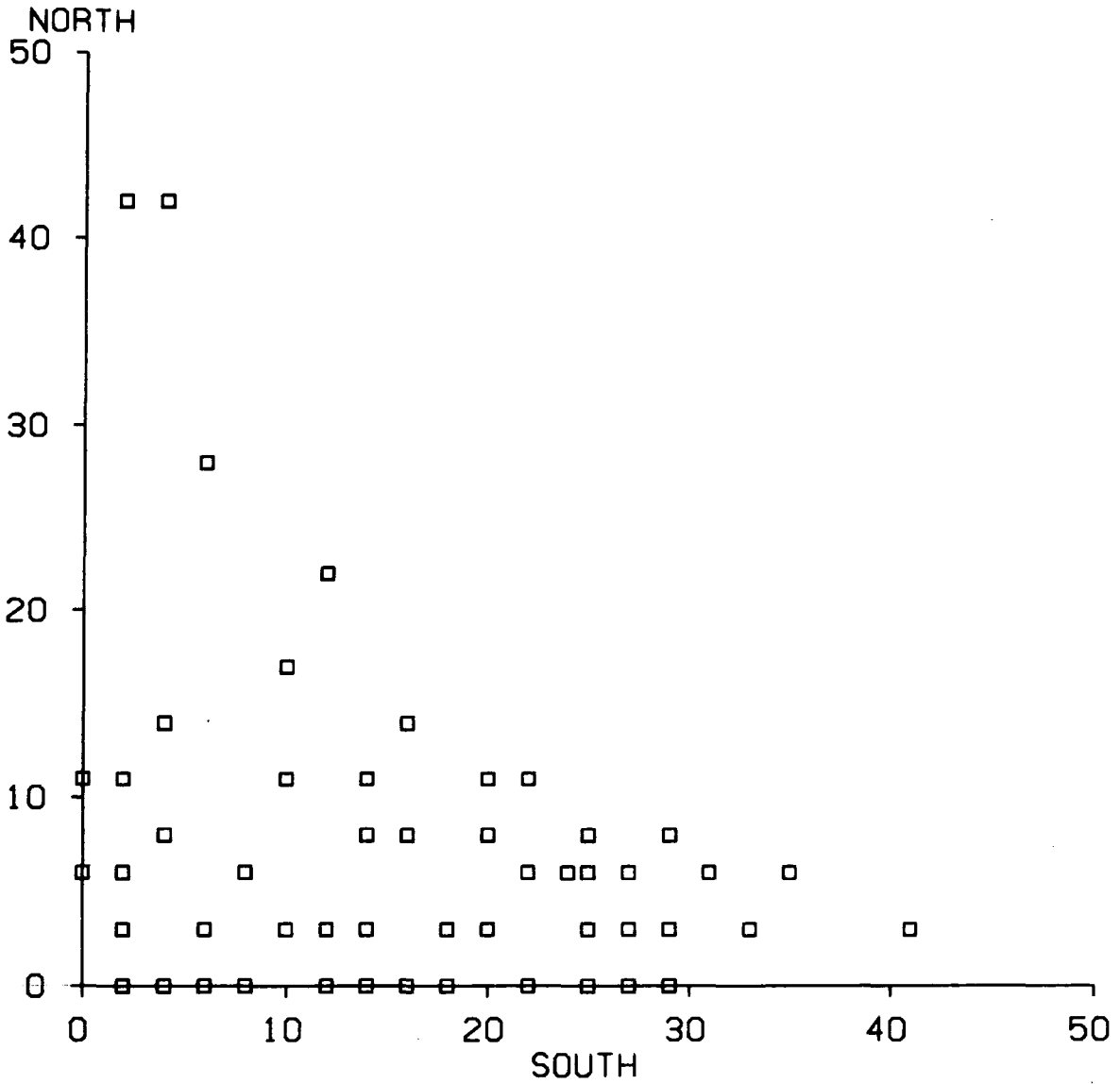


Figure 3.11 — Distributions of Colour-Ringed Birds in Winter 1985-86

patterns were more common than were others. In particular, individuals did appear to have a preference for one side of the estuary or the other, few birds being equally likely to be seen on both sides. The number of birds confining themselves to the south side was larger than the number seen only on the north side. It may be that birds from the north side were under-represented amongst the colour-ringed birds (see Appendix A) or simply that the population size was greater on the south side. Alternatively it might be that birds which normally fed on the north side were more likely to visit the south side than southern birds were to visit the north, perhaps due to food supplies being more reliable on the south side.

Apart from the fact that birds seen very frequently on one side of the river could not also be seen very frequently on the other side, the number of observations of a bird on one side is a very poor predictor of the number of times it is seen on the other. This implies (1) that individuals were frequently overlooked; and/or (2) that individuals were using other sites. Checks for colour-ringed birds were not always thorough, so the figures for the numbers of sightings as proportions of the number of observation days will be under-estimates of the numbers of presences as proportions of the total number of days. But this cannot explain the extent of the variation between birds in terms of their total numbers of sightings. It is therefore clear that individuals were using sites further afield and that there was continuous variation between birds in the extent to which they did so.

3.6.2 Individual Consistency

Figures 3.12–3.19 and Table 3.7 illustrate the high degree of consistency shown between years in the frequencies of occurrence of individual birds on the south side of the Tees. In the case of sightings made by myself (i.e. winters 1986–87 to 1988–89) I was able to confine the analysis to those sightings made on days of thorough checks for colour-ringed birds. This means that the values for the proportions of times seen are more comparable between years. Although Cooper (1988) showed that few birds belonged to different movement categories in different years, the correlation coefficients demonstrate this consistency more decisively and quantitatively.

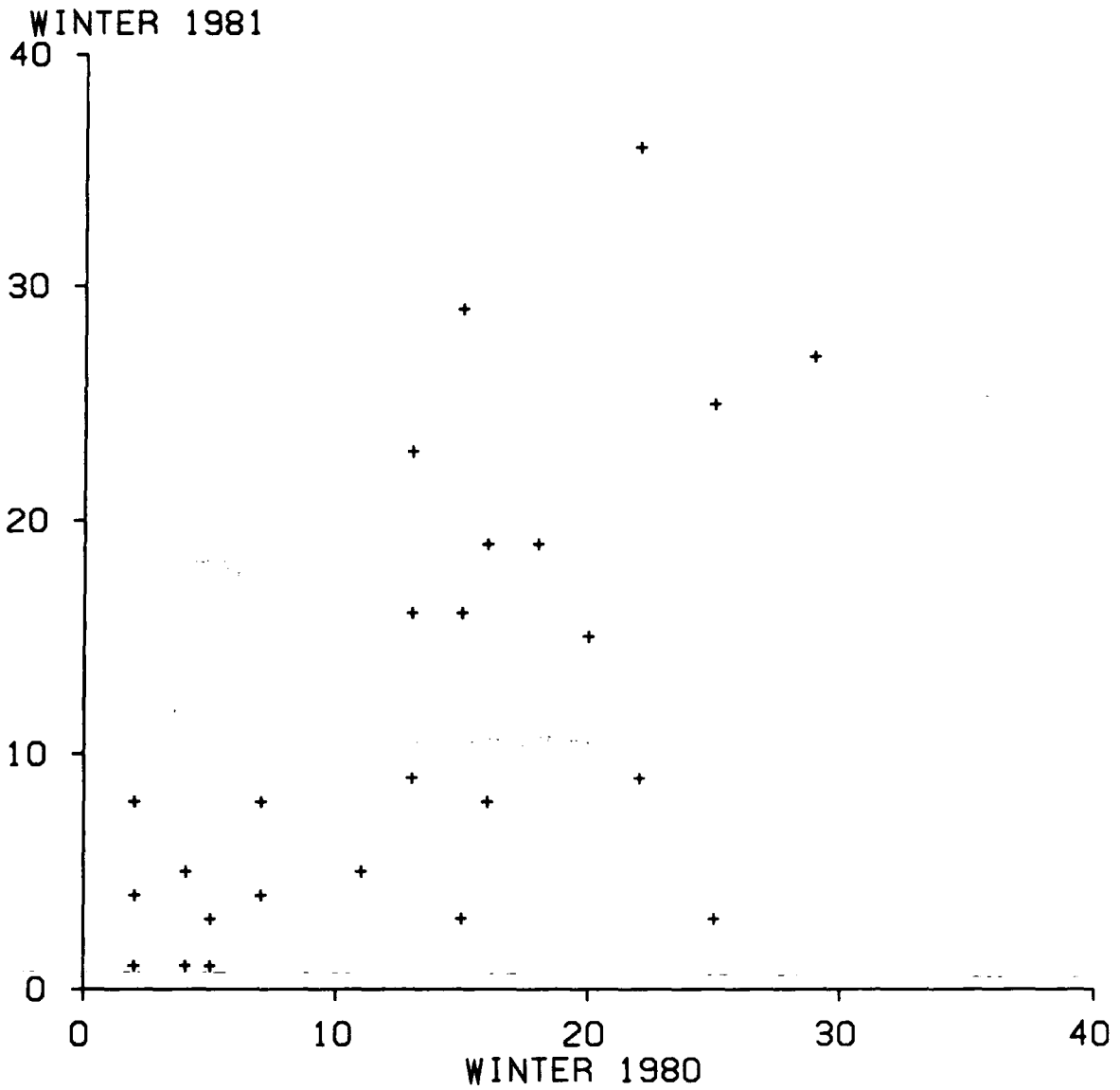


Figure 3.12 — Sightings in Winter 1980–81 and Winter 1981–82

Each point represents a colour-ringed bird. The axes give the numbers of sightings of each individual in the respective winters at sites on the south side of the River Tees as percentages of the numbers of times that these sites were checked in those winters.

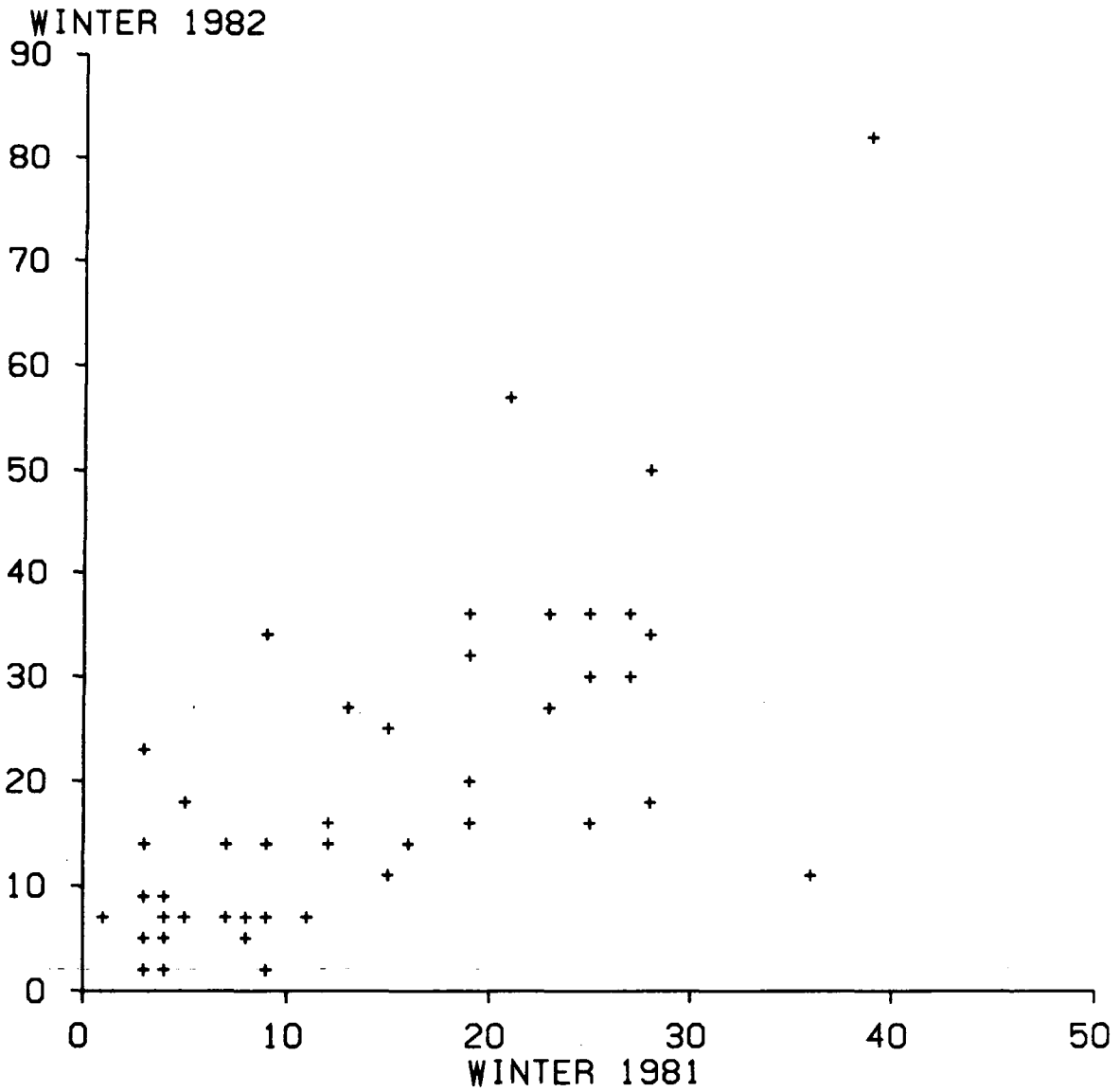


Figure 3.13 — Sightings in Winter 1981–82 and Winter 1982–83

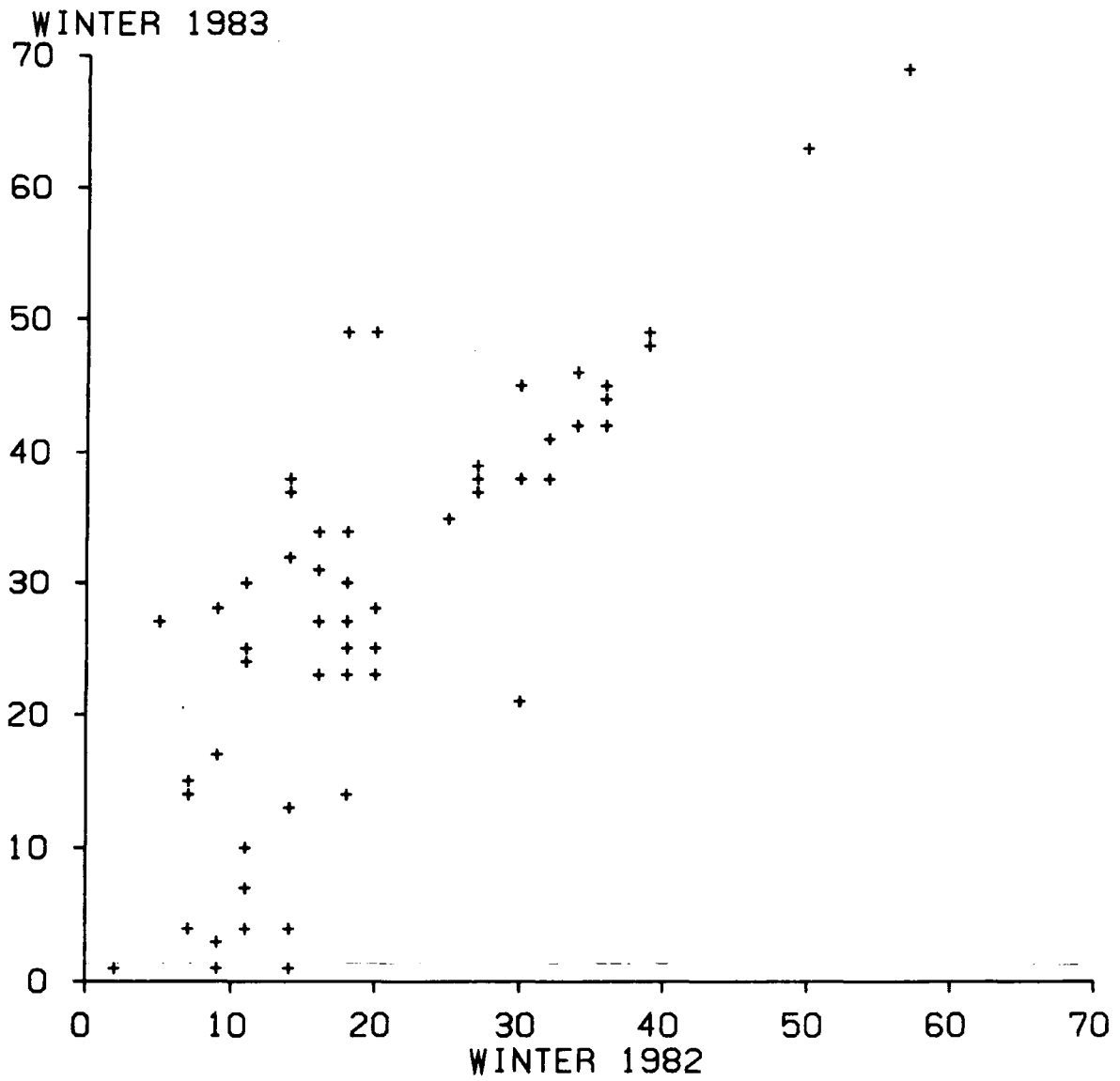


Figure 3.14 — Sightings in Winter 1982-83 and Winter 1983-84

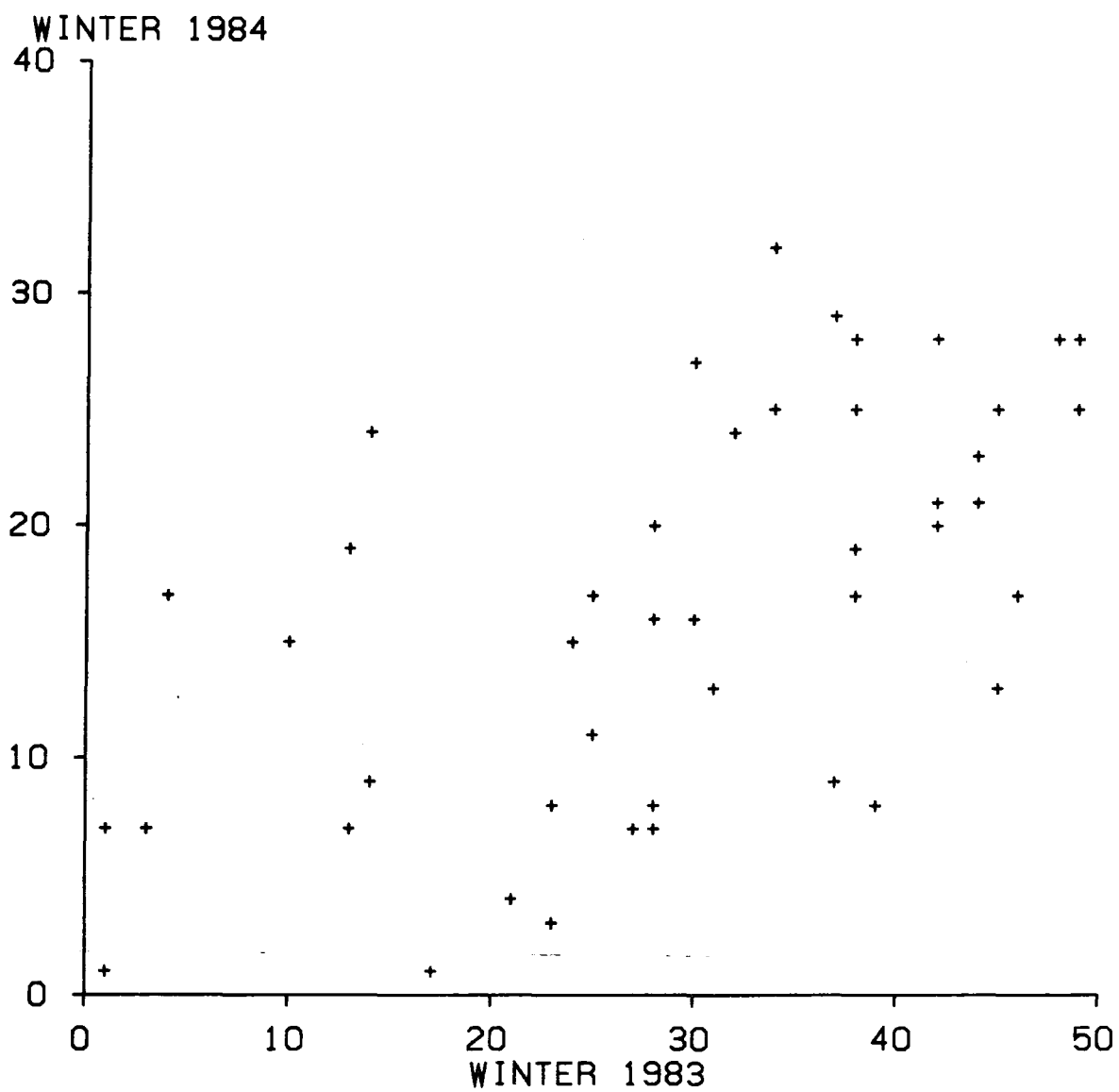


Figure 3.15 — Sightings in Winter 1983–84 and Winter 1984–85

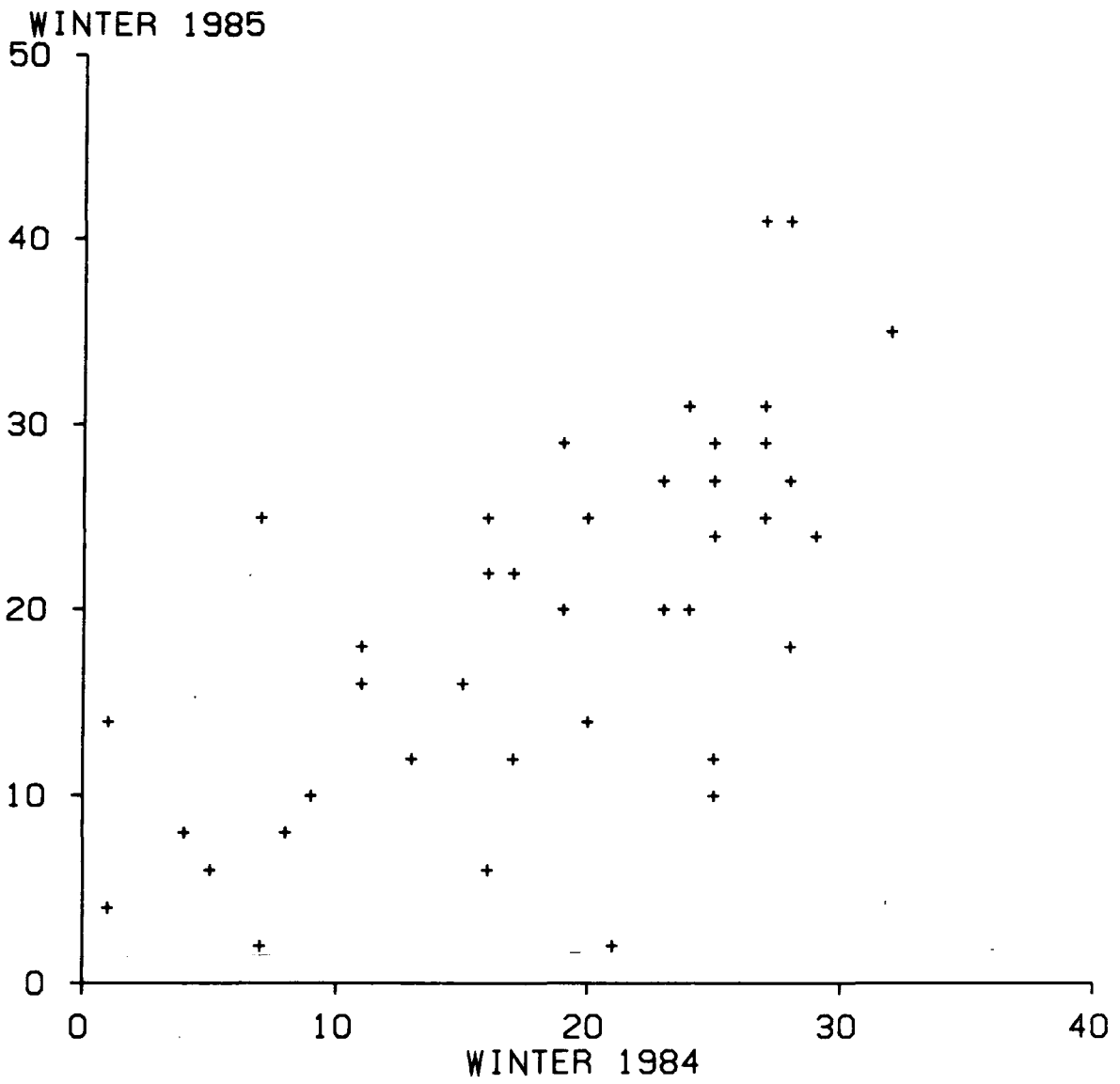


Figure 3.16 — Sightings in Winter 1984–85 and Winter 1985–86

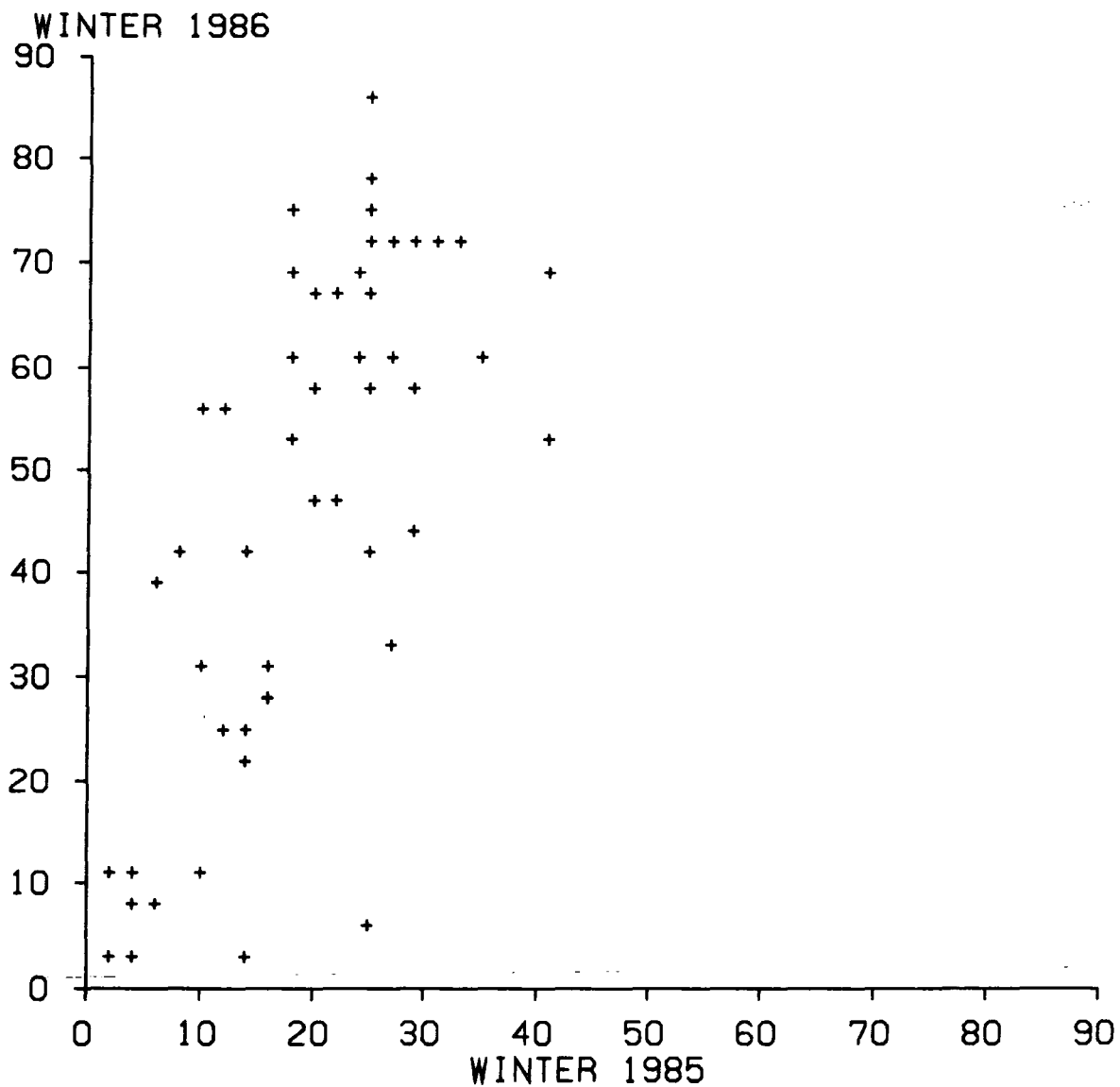


Figure 3.17 — Sightings in Winter 1985–86 and Winter 1986–87

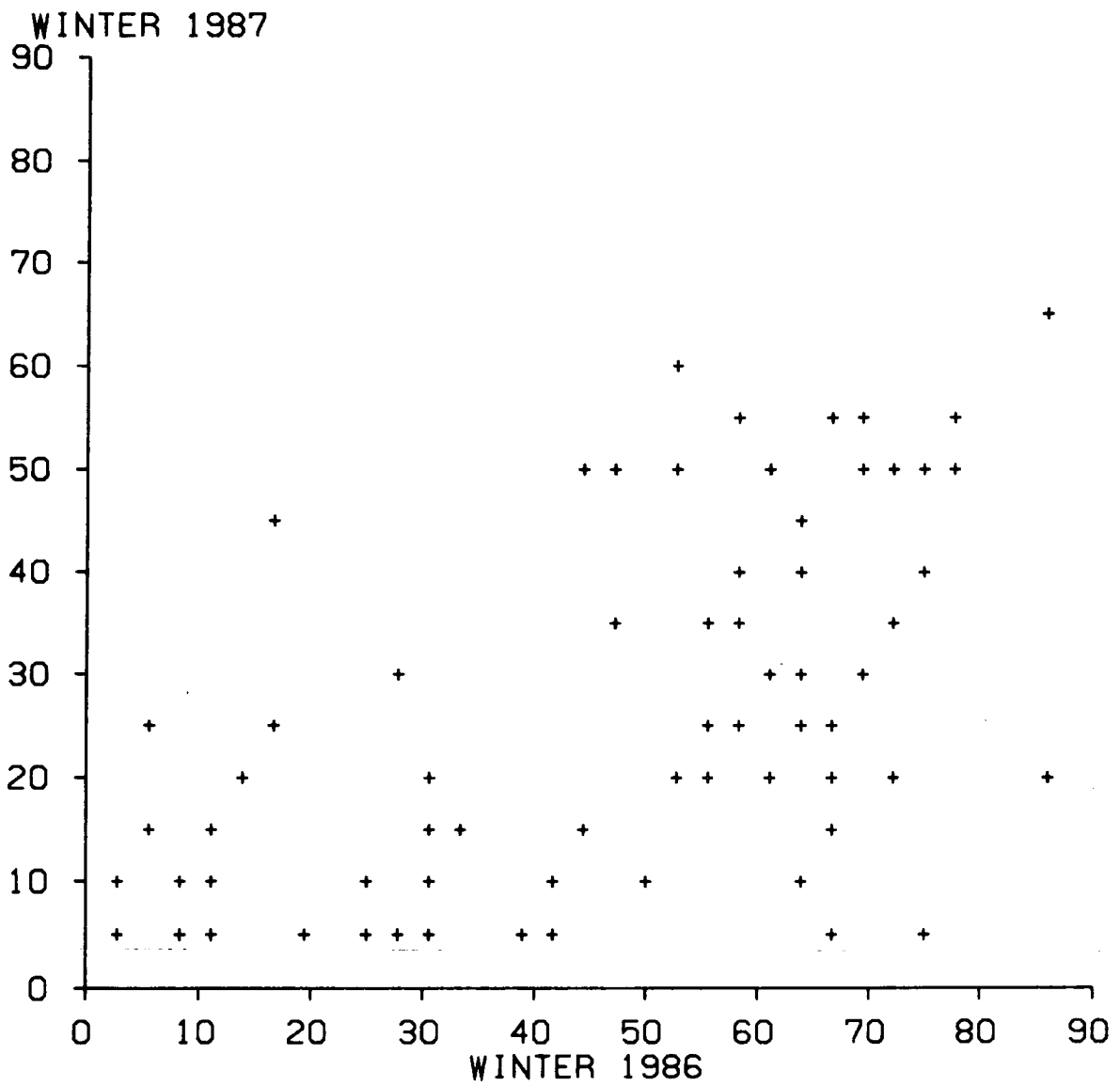


Figure 3.18 — Sightings in Winter 1986-87 and Winter 1987-88

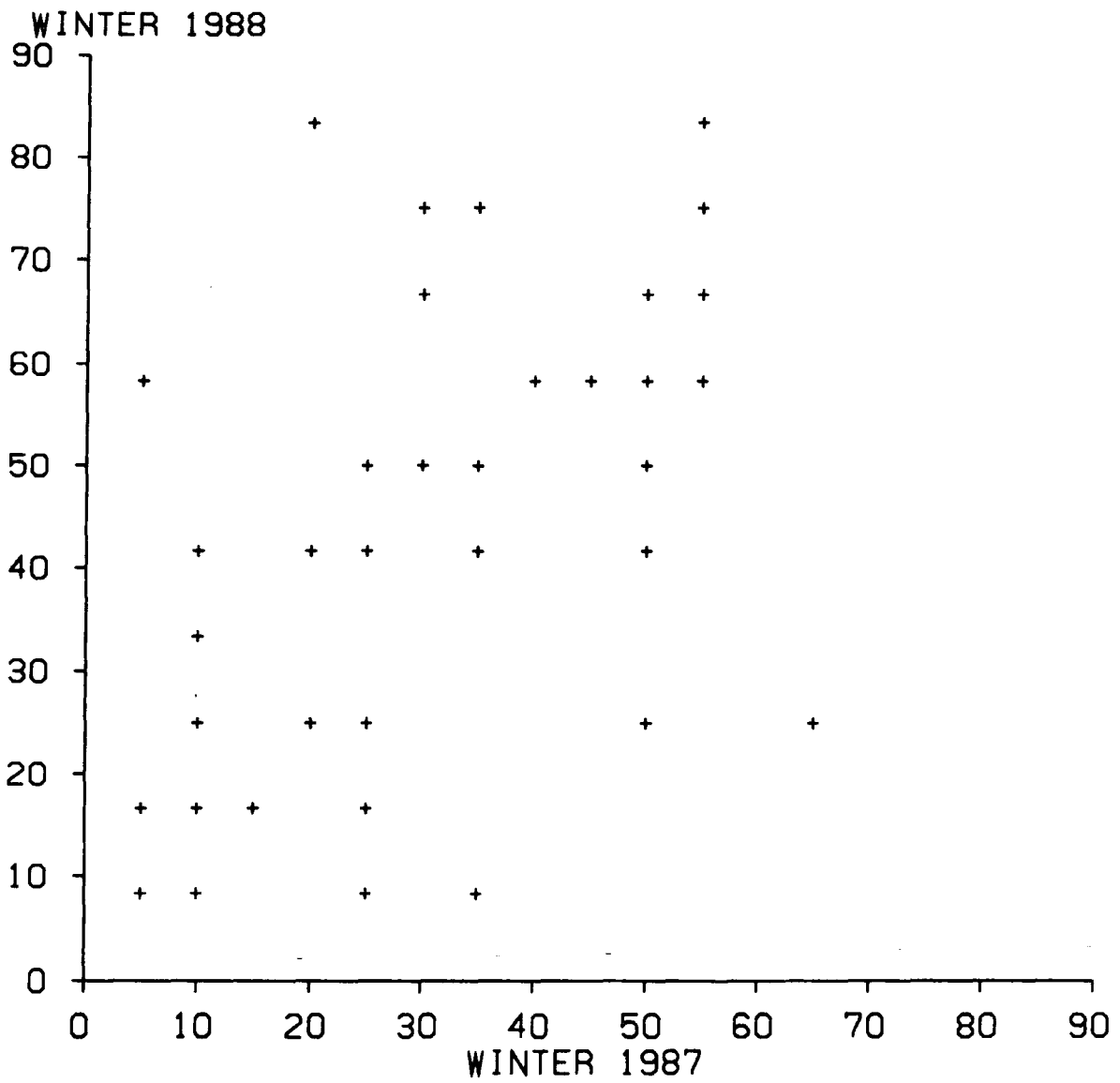


Figure 3.19 — Sightings in Winter 1987-88 and Winter 1988-89

Winter	Constant				Slope				<i>r</i>	<i>n</i>
	value	S.E.	<i>t</i>	Sig. of <i>t</i>	value	S.E.	<i>t</i>	Sig. of <i>t</i>		
1981-82	0.85	2.71	0.31	0.76	0.83	0.18	4.49	< 0.01	0.67	27
1982-83	3.89	2.85	1.37	0.18	1.11	0.16	6.72	< 0.01	0.70	49
1983-84	6.92	2.54	2.73	0.01	1.08	0.11	10.11	< 0.01	0.80	58
1984-85	5.54	2.48	2.23	0.03	0.38	0.08	4.88	< 0.01	0.59	47
1985-86	5.72	3.00	1.91	0.06	0.74	0.15	5.07	< 0.01	0.63	42
1986-87	10.74	4.99	2.15	0.04	1.81	0.24	7.61	< 0.01	0.73	53
1987-88	6.43	3.58	1.80	0.08	0.42	0.07	6.17	< 0.01	0.58	76
1988-89	21.51	5.95	3.61	< 0.01	0.64	0.17	3.75	< 0.01	0.49	46

Table 3.7 — Consistency of Individual Sighting Frequencies

The table gives the regression equations for the frequencies of occurrence of individual colour-ringed birds (as a percentage of the number of times the site was checked) in terms of their frequencies of occurrence in the previous year.

3.6.3 Changes Between Years

In the winter of 1987–88 the number of sanderlings in the Redcar–Coatham Sands area was markedly lower than in the winter of 1986–87. Considering those individuals seen in both winters ($n = 76$), the mean number of times that an individual was seen on the south side of the estuary as a proportion of the number of observation days was 46.67 ± 2.77 in 1986–87 and 26.05 ± 2.00 in 1987–88. In this section I consider how this was related to changes in individual site usage. That is, was the decline due to parallel reductions in usage of the site by all birds, or was it a more complex product of changes in behaviour by different individuals with different individuals making different decisions?

Table 3.7 shows that the correlation between sighting frequencies in winter 1986–87 and winter 1987–88 was weaker than that for most other comparisons, while Figure 3.18 shows that this was because although some birds were seen on approximately the same number of occasions, others seen frequently in 1986–87 were hardly seen at all in 1987–88. Thus, whatever the cause of the decline in overall population size, it is clear that different birds responded differently.

3.6.4 Mobility Within Days and Between Days

In the winter of 1986–87 observations were made over a period of several hours on each day so that the same birds were often seen several times during a day. In this section the possibility that the number of visits made to a site might be related to the lengths of those visits is investigated. If visits by the rarer birds tended to coincide with particularly good feeding conditions then their stays might be longer. Alternatively, if the rarer birds tended to visit to sample the site, only settling if conditions were good, then the average length of visit would be less.

However, birds seen on only a few days are seen just as many times during those days when they are present as are birds which are seen on more days (Figure 3.20). Thus, birds may vary in the amount of time that they spend at a site during each visit, but this does not correlate with the number of visits that they make to a site. Short visits might reflect sampling, though the length of time taken by an individual to sample a site can only be guessed at.

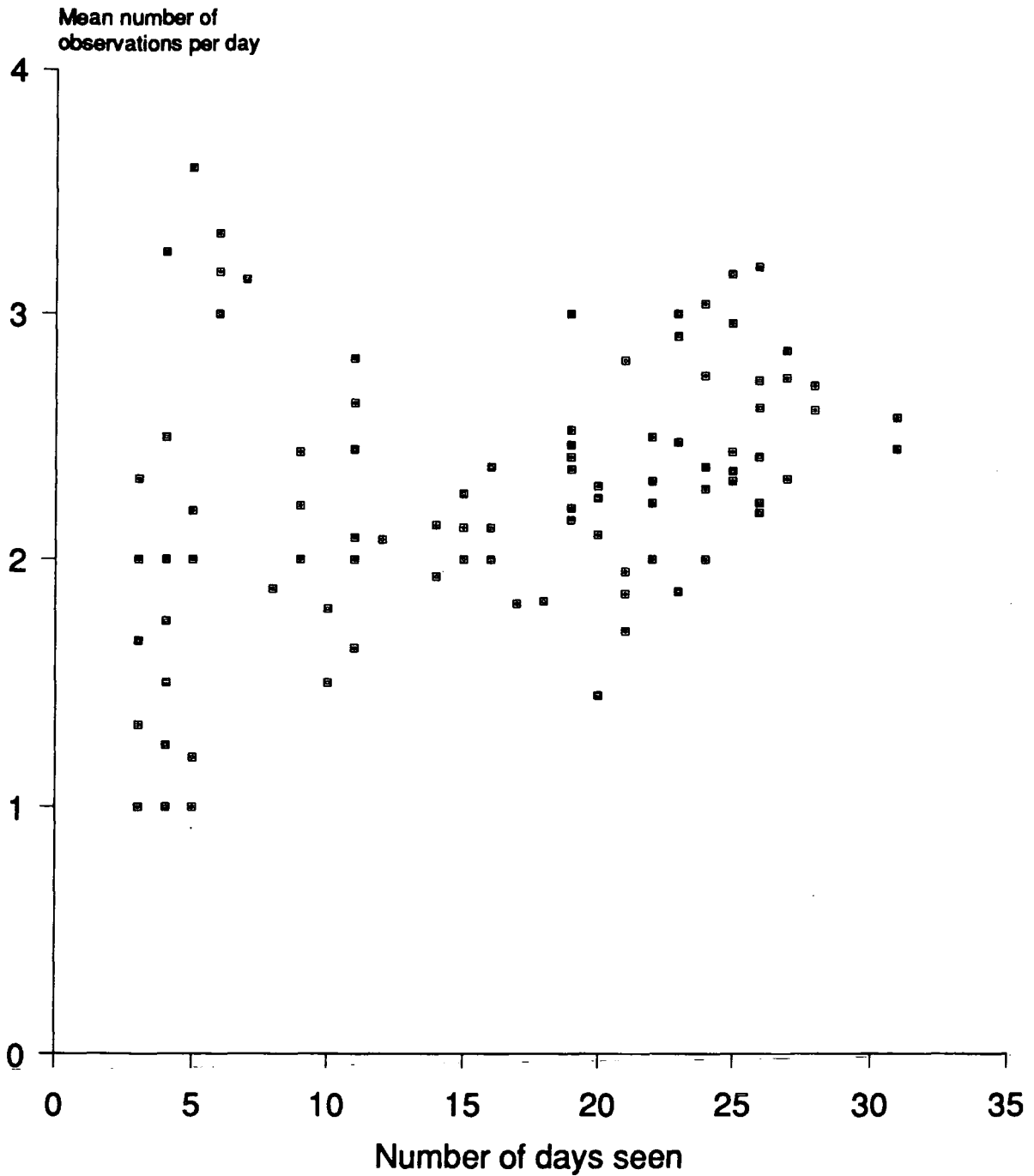
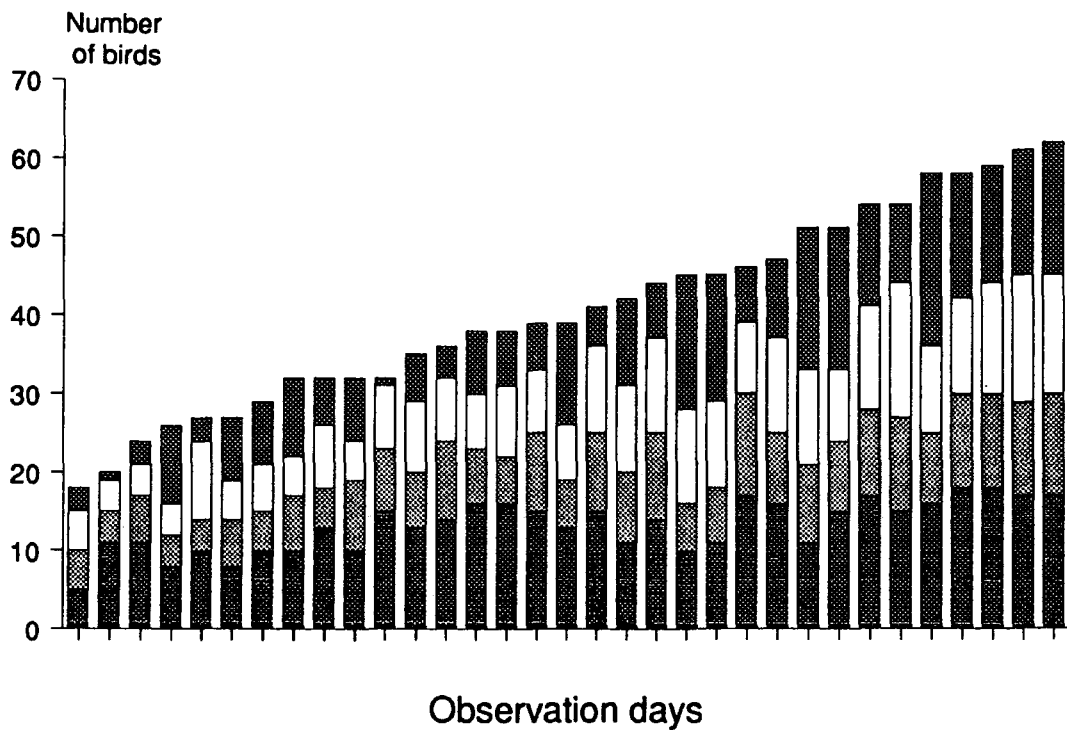


Figure 3.20 — Numbers of Sightings per Day in Relation to Numbers of Days Present

Each point represents the mean number of times that an individual was observed on a day in relation to the number of days on which it was seen.



Sighting frequencies

1-10
 11-20
 21-25
 >25

Figure 3.21 — Population Composition in Terms of Sighting Frequency Classes. 1. Actual Numbers

Each bar represents one observation day, ranked in order of increasing total numbers of birds present. The total numbers present on each day are broken down by sighting frequency classes based on the numbers of sightings of each individual in the 1986-87 winter.

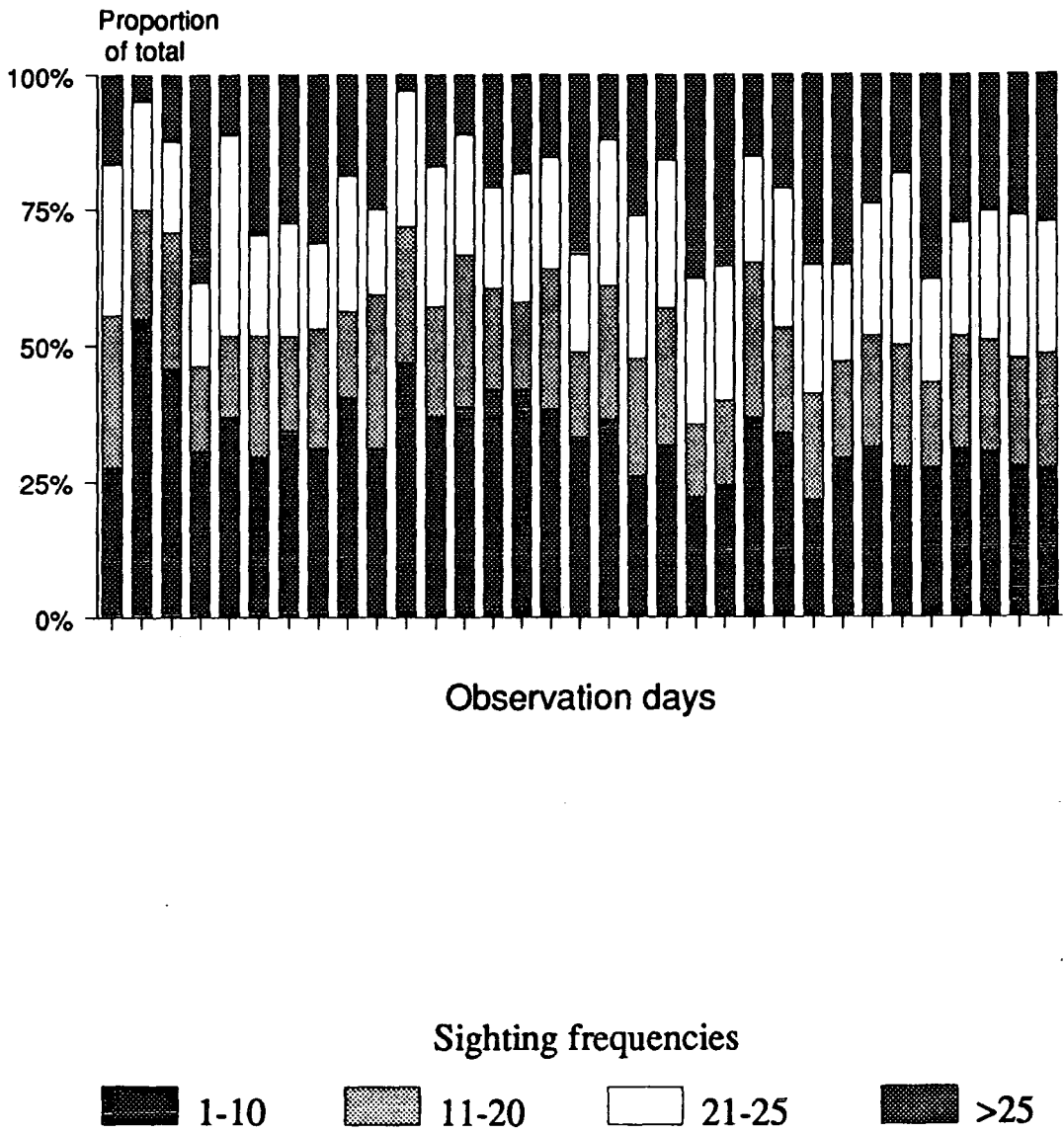


Figure 3.22 — Population Composition in Terms of Sighting Frequency Classes. 2. Proportions

As Figure 3.21 but with sighting frequency classes expressed as proportions of the total numbers present on each day.

3.7 Population Composition

Individuals were divided into sighting frequency classes in order to examine how the proportion of birds belonging to each class varied with total population size. Since there were no distinct subgroupings of birds according to sighting frequencies (Section 3.5.1), these categories were arbitrary. At one extreme it might be that the most frequently seen birds were present every day and that the size of the population (i.e. the number of birds present on a day) depended on the number of less frequently seen birds arriving on that day. At the other extreme the proportion of a particular sighting frequency class might be independent of population size.

Figures 3.21 and 3.22 show the composition of the population at Redcar in winter 1986–87 for days when a thorough check of colour-ringed birds was made. The second model appears to fit the data most closely: as population size declines, the numbers of birds belonging to all classes declines. The first model would be consistent with a situation where the most frequently seen birds tended to remain at a site whatever the feeding conditions while influxes of rarer birds occurred on days of high food availability. However, the most frequently seen birds are more mobile than this would imply, moving away on days when the population size is low while some rarer birds actually arrive. This mobility of all classes might be explained by sampling.

3.8 Summary

The set of individual birds present at a site changed considerably from day to day. The total number of marked birds present was also very variable.

There was variation between individuals in the extent to which they switched between different foraging sites, i.e. in levels of vagility.

There was some overlap in the site usage patterns of different individuals in that the usage of particular sites correlated with the usage of other particular sites.

Sanderlings used foraging sites on both the north and south sides of the River Tees as well as sites further afield. Individuals differed in the way in which they allocated their time between these areas but there was a tendency for birds to keep to one side of the estuary or the other.

There was a high degree of consistency between winters in the distributions of individual birds.

Birds which occurred only rarely at a site spent a similar length of time within a day at the site as did more regular birds.

There was no evidence for the variation in numbers of birds at a site being due to variable numbers of particularly mobile birds joining a core group of more resident birds: both rarely and commonly observed birds occurred on days of high and low numbers alike.

3.9 Discussion

Individual sanderlings at Teesmouth were found to vary in terms of their residency (individuals were seen different numbers of times at a given site); their range (some birds must have used sites outside the Teesmouth area); and their vagility (some birds switched between sites more often than did others).

Although there was variation between individuals in the extent to which they moved between sites, the number of sanderlings at Bodega Bay in California, (e.g. Myers, 1980), was fairly stable at 500–700 birds from October to February, during which period birds were largely sedentary. Thus, Myers *et al.* (1989) found that at this time the average sanderling remained within 5km of the centroid of its home range for 95% of the time. There was also a high degree of overlap in home ranges such that, at least during the winter, there was little mixing between populations centred around other areas.

The fairly discrete nature of the population at Bodega Bay contrasts with the situation at Teesmouth where there was considerable movement of birds into and out of the area. The grouping of sites around Teesmouth into areas north and south of the estuary indicates that the population is to some extent structured, in the sense of Myers *et al.* (1989), but Teesmouth birds clearly tended to have larger home-ranges and more variable distributions resulting in greater overlap between sub-populations. The population structure therefore approximated more closely to that of the Peruvian sanderlings studied by Myers *et al.* (1989) than to the structure found in California.

The behaviour of sanderlings at Teesmouth can be contrasted with that of turnstones, *Arenaria interpres*, in Scotland (Metcalf and Furness, 1985). Foraging home ranges of the latter were small and the local population size was stable throughout most of the winter. It has been hypothesized that site-faithfulness is linked to predictable food resources (e.g. Evans, 1981). However, no evidence was found in this study to support a link between high levels of vagility and unpredictable food supplies.

There are differences between individuals in the decisions made about where to feed, but each individual tends to make similar decisions in different years. The

question of why there should be such variation between individuals remains to be answered. One way in which individual variability might be maintained in the population is if the different strategies were determined by a genetic polymorphism with all strategies being equally successful. Alternatively, some strategies may be favoured over others and competition between individuals (either in all winters or in the first winter on establishment of the movement strategy) might determine which birds followed which strategy.

Given that aggression was very rarely observed and that Cooper (1988) found no body size differences between birds of different movement strategies it seems unlikely that direct competition was important in determining movement strategies. However, the possibility of there being morphological differences between birds with different strategies remains. In a transportation experiment, those juveniles which returned to Teesmouth were larger than those which remained near the release site (Evans and Townshend, 1989).

That variation between individuals is continuous does not distinguish between hypotheses, but the high level of consistency between years suggests either a genetic basis or that movement patterns are established in the first year and usually maintained thereafter. Strategies may nevertheless be sufficiently flexible to change between years, perhaps in response to environmental factors such as food conditions.

Clearly much remains to be learned about what determines where individuals feed and what are the causes and consequences of variability between individuals.

Chapter IV

Associations Between Individual Sanderlings

4.1 Introduction

The study of associations is the study of whether any particular members of a local population are found together more than are other members of that population or more than would be expected by chance. Association might be defined on two levels: that of joint flock membership and that of co-occurrence at the same site.

In this chapter I discuss the methods which have been used in studying associations and the possible problems arising. I go on to apply the results of this discussion to data on associations among sanderlings. The main aims were: (1) to describe association levels and thereby determine the stability of flock membership in different foraging habitats; (2) to uncover the factors affecting association levels and thereby determine when birds should tend to move around together and occur in the same flocks; and (3) to understand the movements of sanderlings around and away from Teesmouth, in particular whether birds move independently (meaning without other particular individuals but not necessarily singly) around Teesmouth.

4.1.1 Studies of Associations

In this section I summarize the literature on associations before going on in the following section to consider the possible reasons for associating.

Three studies have been made of associations in wading birds. Myers (1983), studying sanderlings in California, concluded that the birds in any given flock could be considered as a random sample from the local population. In contrast, Metcalfe (1986) found that turnstones, *Arenaria interpres*, foraged with only a small, stable subset of those birds that they roosted with. Whitfield (1985), working on the same species, obtained similar results. The occurrence of strongly associated individuals among turnstones appeared to be related to their small foraging home ranges and the small extent of movement and mixing which occurred.

Associations among Parids have been studied by a number of authors. Ekman (1979) found that both willow tits, *Parus montanus*, and crested tits, *P. cristatus*, tended to occur in small cohesive and territorial flocks of conspecifics during the winter. Associations among black-capped chickadees, *Parus atricapillus*, were strongest between birds which subsequently paired, and these associations strengthened through the winter (Ficken *et al.*, 1981).

Smith (1984) distinguished 'floaters' with large home ranges from resident territorial birds. But Smith and Van Buskirk (1988) found no clear distinction between birds which formed relatively stable associations and those which frequently switched between groups. The generally low association levels and low levels of flock stability found by Smith and Van Buskirk (1988) contrast with the stable group membership and high within-group association levels found by other studies of the same species (Glase, 1973; Samson and Lewis, 1979; Smith, 1984). The more strongly associated chickadees were more similar in terms of several parameters of foraging behaviour than expected when habitat preferences were taken into account (Van Buskirk and Smith, 1989).

A study of feral rock doves, *Columbia livia*, (Lefebvre, 1985) found non-random co-occurrences of individuals at a feeding site (but see Section 4.3.4). The more regular birds tended to co-occur more than expected by chance, while the opposite was true of the less regular birds.

A number of studies have been made of associations among individual mammals. These typically employ an index of association to link individuals and thereby to build up a tree of relationships representing clan structure. Studies of associations include those of Murray (1981) on impala, *Aepyceros melampus*; Guinness *et al.* (1979) and Clutton-Brock *et al.* (1982) on red deer, *Cervus elaphus*; Knight (1970) on elk, *Alces alces*; Leuthold (1979) on giraffe, *Giraffa camelopardalis*; Penzhorn (1984) on zebra, *Equus zebra*; Underwood (1981) on eland, *Taurotragus oryx*; and Lott and Minta (1983) on bison, *Bison bison*. Wilkinson (1984) reported that female vampire bats, *Desmodus rotundus*, associated non-randomly in terms of the time they spent roosting in the same trees. Associations between both related and unrelated females were found, but adult males showed few associations. Food sharing occurred between the females with high levels of association.

4.1.2 Summary of Reasons for Associating

Two types of associations can be imagined: **active** and **passive**. If individuals can recognize each other then they may be able to derive benefits from ensuring that they flock with particular other individuals: they may associate actively. But whether or not individual recognition is possible, particular individuals may tend to be found together more than they are found with particular other individuals. That is, they may associate passively.

Active associations might be favoured in the following ways.

(1) **Altruism towards relatives.** Genetic benefits may be obtained by helping close relatives (Hamilton, 1964) through such behaviour as alarm calling. Given that males, females and juveniles migrate at different times and that birds from a given breeding area go to a wide variety of wintering sites, this is unlikely to be relevant to wintering sanderlings.

(2) **Reciprocal altruism.** Where repeated encounters with recognized individuals occur, reciprocal altruism may be found (Trivers, 1971; Axelrod and Hamilton, 1981; Wilkinson, 1985). Again, this may apply to vigilance behaviour. The apparent problem of 'cheating' whereby non-vigilant birds exploit the investment of vigilant birds could mean that there would be advantages in associating with individuals whose likely investment is known. However, the 'judge' strategy of Pulliam *et al.* (1982), where birds scan if and only if other birds are scanning, would not require association with particular individuals.

(3) **Dominance hierarchies.** Knowledge of other birds could be an advantage where aggression between birds occurs. If the outcome of a contest with any particular bird can be predicted then the costs of fighting can be avoided to mutual benefit. Whitfield (1985) has demonstrated the existence of stable dominance hierarchies based on individual recognition among wintering flocks of turnstones, *Arenaria interpres*, and also found greater than expected association levels. But aggression is uncommon among sanderlings at Teesmouth, despite being frequent in California (Section 2.6.8).

(4) **Pair bond.** Pairs may form or persist in flocks. Ficken *et al.* (1981) found that attachments between males and females which subsequently mated were estab-

lished in winter flocks and suggested that such attachments might allow altruistic behaviour. This is unlikely to apply to sanderlings for the reasons stated in (1).

Passive associations might result from any of the following.

(5) Predictability of food resources. The unpredictability of food supplies (see Section 2.4) is thought to influence sociality (e.g. Pulliam and Caraco, 1984). Flock composition may be more stable where food resources are more predictable.

(6) Home Range and Itinerancy. These may reflect characteristics of the food supply such as its predictability (see above). Low levels of mobility may allow greater levels of association between individuals. Metcalfe (1986) found high levels of association among turnstones which foraged within small, stable home ranges. But he also found that increased movement during the spring brought birds into contact with more individuals thereby raising association levels.

(7) Individual differences. Birds sharing similar foraging site or substrate preferences may tend to be found together, e.g. Van Buskirk and Smith (1989).

(8) Patch use coordination. Coordinated movements of subgroups of the population may result in associations between particular birds. Coordinated movements have been described in Brent geese, *Branta bernicla*, (Prins *et al.*, 1980).

There are a number of examples of non-random dispersion in waders. Age and sex differences in the timing and nature of migration exist (e.g. Pienkowski and Evans, 1984). Stable sub-structuring of flocks has been reported by Furness and Galbraith (1980) for redshanks, *Tringa totanus*, and non-random clustering of colour-dyed knots, *Calidris canutus*, was found by Harrington and Leddy (1982). Ruiz *et al.* (1989) found non-random distributions of different age and size classes of dunlin, *Calidris alpina*, in night roosts. They also found that during a winter the population became divided into two groups, one of which moved away to roost. These birds weighed more, had more body fat, and moulted earlier.

Individual recognition by plumage seems unlikely among winter plumage sanderlings, but one cue which could conceivably be used is the carpal patch, which appears to vary in size and blackness. Calls are often given as birds fly up, and

these might be used by others following. It is possible that there is variation in these calls and that individuals respond only to particular calls.

4.1.3 Background to This Study

Observations made by those studying the sanderlings at Teesmouth suggested that certain individuals tended to be seen together. Furthermore, there were a number of reasons for supposing that the cohesion of sanderling flocks at Teesmouth might differ from that of the Californian birds studied by Myers (see Myers, 1983; Myers, 1984; Myers *et al.*, 1989).

In Chapter 3 it was shown that Teesmouth sanderlings have a wider range of distribution patterns than their Californian counterparts with some birds moving around to a considerable extent. It was also shown that the population size at a site was much less stable between days than was that in California. The associations between birds studied by Myers (1983) can be considered as within-population associations. At this level, associations were found to be effectively random. However, Myers *et al.* (1989) found that there was a high degree of between-population structuring (see Section 3.9). From Chapter 3 it is clear that the birds around Teesmouth did not form discrete populations. This will affect the nature of between-individual associations.

The situation at Teesmouth appears to differ from that in California in terms of the choices which birds have of where and on what to feed. The variety of habitats, feeding sites, and feeding methods used by sanderlings at Teesmouth provide the potential for site and method preferences which may result in non-random groupings. Birds may choose between sites, but also within sites, whether to forage on rocky areas (apparently not utilized by the Californian birds); on banks of wrack which are occasionally washed up; by probing in sand for worms or pecking for items on the surface; or by taking crustaceans from the water.

There are therefore considerable differences both in terms of the nature of the areas and in terms of the behaviour of the birds (see Chapter 3). These might lead to differences between the areas in flock cohesion and individual associations for the reasons discussed in Section 4.1.2. For example, the different degrees of itinerancy shown by the birds which visit the study site raise the possibility that there are

groups of highly mobile birds which move around together and groups of more sedentary birds (see Evans, 1981). Also, it might be that the occasional influxes of birds represent groups of birds normally found in other areas.

4.2 Fieldwork Methods

The main part of the fieldwork was carried out around Redcar between October 1986 and May 1987 on days when reasonable weather coincided with a daylight low tide. The Redcar Rocks area and the Coatham Sands area (see Figure 2.2) were covered, the former at low tide and the latter either as the tide was falling or as it was rising. At low tide, feeding is concentrated on Redcar Rocks (Section 2.5), but on spring tides when Coatham Rocks were exposed this site was occasionally also used. As it was impracticable to cover this area thoroughly due to the large area exposed and the impossibility of reaching some of the more distant parts, Coatham Rocks was not included in the study areas. Observations were carried out either on foot or from a vehicle using 8x, 40 binoculars and a 15–60x, 60 telescope. Standing in the open caused no apparent disturbance.

One check was recorded for each flock. An assessment was made as to which birds belonged to which flock (see Section 2.6.2).

Flocks were differentiated in time as well as in space. Repeated checks of the same flock were not made. However, flocks often took flight, usually as a result of a disturbance or because of a rising tide, and at such times changes in flock membership often took place. The resulting groups of birds were considered as new flocks, and so checks of these flocks were made. In order to make a more informed decision about what constitutes an independent sighting (see Section 4.3.4) no minimum time between samples was introduced at this stage.

For each flock, all colour-ringed birds were recorded along with flock size, time, foraging method used, and foraging substrate type. Where birds within the same flock were using different techniques or foraging on different substrates the predominant ones were recorded.

There were almost always other people present, mainly exercising dogs but also riding horses, riding motor-cycles, launching boats, playing, flying microlites, bait-

digging, searching the strand-line, collecting coal-dust, or simply walking and jogging. The extent of this disturbance varied between days, particularly with the season and the weather, but was most significant at weekends which were therefore avoided as fieldwork days. Disturbance, especially by dogs chasing the birds or by horses being ridden along the water's edge often prevented me from recording all of the marked birds in a flock. In such cases the data were recorded as being incomplete and were analysed separately.

Additional data were collected in the winters of 1987–88 and 1988–89. These data were in the form of presences of birds at a site on a day rather than being broken down by flock membership. Because priority was usually given to other fieldwork, daily checks tended to be less complete and so data from these years could not be included in all analyses.

4.3 Measurement of Association

4.3.1 The Meaning of Randomness: Two Approaches

Ekman (1979), Myers (1983), Metcalfe (1986), and Whitfield (1985) used an index usually referred to as Jaccard's index or Ekman's index, but also as the Twice-Weight index (Cairns and Schwager, 1987). It is given by the number of times that two birds are seen together as a fraction of the number of times that one or both of them are seen. If n_{AB} is the total number of sightings of A and B together and n_A and n_B are the total numbers of sightings of A and B respectively, whether together or apart, then Ekman's index is:

$$E_{A,B} = \frac{n_{AB}}{n_A + n_B - n_{AB}}.$$

The association levels obtained using such an index must be interpreted by comparison with other association levels. Studies of associations may aim (1) to establish whether there are non-random associations, and if so to find the magnitude of the difference from random so that its biological meaning can be interpreted; (2) to compare observed associations of different pairs; or (3) to compare observed associations in different situations.

The method followed in this study was to test for non-randomness. In order to find levels of association expected by chance, computer randomizations were carried out in which each bird actually seen was replaced by one picked at random from the population.

This was done in two ways. The simplest null hypothesis is that there is an equal chance of any bird appearing in a flock. According to this hypothesis the birds in a flock constitute a random sample from the local population. This was the approach adopted by Myers (1983) and followed by Metcalfe (1986) and by Whitfield (1985). Alternatively, the observed sighting frequencies of each individual can be taken into account. That is, a bird seen twice as often is given twice as great a chance of appearing in the computer-generated flocks. The null hypothesis is that the birds in a flock constitute a random sample from the local population weighted by the overall occurrence frequencies of individual birds. Such a null model has not been tested before.

Method 1: A computer procedure was carried out such that the number of birds in each observed flock was retained while their identities were substituted randomly, (by using a random number to specify a bird from a list of all individuals) subject to the constraint that no bird could appear more than once in the same flock. Because each bird was considered to be equally 'available' for the computer randomization, the frequency distribution of sightings had a small standard deviation: all were 'seen' approximately the same number of times.

Method 2: The second procedure retained not only the frequency distribution of flock sizes (as in method 1) but also the number of sightings of each individual. This was achieved by using a random number to specify an individual from a list of all sightings. The randomization was again subject to the constraint that no bird could appear more than once in any flock.

Birds seen fewer than six times were excluded from the data before randomization. One reason for this exclusion was that it is unlikely that reliable indices of association could be obtained on the basis of so few sightings. Furthermore, the possibility that such birds might have been erroneously recorded is difficult to discount since only a small percentage of errors can give rise to a large number of additional birds being recorded as present.

The effectiveness of the randomization procedures was tested. In files generated by method (2) there was no trend in sighting frequency with date (as might have occurred if birds of certain sighting frequency were rejected more than others as the file was worked through during the randomization) and no trend for birds of particular sighting frequencies to be found in flocks of certain sizes.

4.3.2 Monte-Carlo Randomizations

In each of the above procedures randomization was carried out only once. Monte-Carlo methods (e.g. Besag and Diggle, 1977) involve large numbers of randomizations. In the case of the 'one-off' randomizations association levels are computed for each pair, in the same way as for the observed data, and differences between observed and random are found by testing between the resulting frequency distributions of index values. In the case of Monte-Carlo randomizations an observed-random test can be carried out for each pair. Rearrangement may be systematic such that all possible versions of the data are included, or a method may be used such that the datasets obtained constitute a random sample from the set of possible datasets. The observed association index for a given pair is then ranked among the generated datasets and its rank gives the significance level for the test. For example, if only 5 of 100 generated datasets give an association index as high or higher than that obtained from the observed data then the observed data can be said to be greater than random at the 5% significance level.

Ninety-nine randomizations of the observed datasets were carried out for each test. Two different methods of producing randomized datasets were tried, both of them aiming to give a random sample of possible rearrangements.

(1) Generating random numbers successively. This was the method used for the 'one-off' randomizations. However, it was too slow to use for more than a few randomizations since as the procedure progressed more and more of the random numbers generated were rejected as having appeared already.

(2) Producing sequences of random numbers. For each randomization a sequence of random numbers equivalent to the number of sightings was generated. This was then sorted such that the magnitude of each random number determined its rank. These ranks were used to index the array of bird sightings such that if the first

random number was ranked 57, the 57th bird from the input file was taken as the first bird for the output file.

Cases where the same bird appeared more than once in a flock were then eliminated. A number of ways of doing this were tried. The most successful was simply to read through the generated data and to include in a new dataset only those birds which satisfied the constraint of not already being present in the current flock. Those birds which were unacceptable remained in the old dataset to be checked through first when a new flock was reached. This procedure inevitably meant that the datasets produced were not strictly random, but checks on the effectiveness of the randomizations (as carried out for the one-off randomizations) failed to find any evidence of non-randomness.

4.3.3 Sighting Frequency

As noted in Section 4.4.1, a criterion may be set such that birds must have at least a certain number of sightings to be included in the calculation of the association index, one reason being that where there are few sightings an accurate index value is unlikely to be obtained. The value of this minimum criterion affects the median value of Ekman's index, both for observed and for randomized data. The introduction of a minimum criterion raises the average number of sightings per bird. More specifically it raises the average number of sightings per bird in relation to the number of flocks. The theoretical limit of this process comes where all birds are seen in all flocks and all index values become 100. Thus the value of the index depends on the ratio of sighting frequencies to flocks.

The dependence of the index on the number of sightings is not important if what is being tested is the difference between observed data and random models: if the random model is generated by a method which preserves the frequency distribution of sightings then a valid comparison can be made. However, previous studies have not used such models. In the null models used each bird has had an approximately equal number of sightings. Any differences from random that are found may simply be due to differences between the sighting frequency distributions of the observed and randomized datasets. Such differences may be of interest in showing that patterns of occurrence can give rise to associations which are non-random at the simplest level of analysis. But this explanation has not been recognized explicitly.

There has been a tendency to follow the methods of other workers in order to compare the index values obtained with those obtained in previous studies. However, this is invalid if the relationship between the number of sightings and the number of flocks is not controlled for. Comparisons between studies should be confined to observed-random differences: comparing the absolute values of the indices obtained may be meaningless.

Myers (1983), Metcalfe (1986), and Whitfield (1985) all excluded birds seen fewer than four times from their analyses on the grounds that sampling error would give unreliable estimates of association when sighting frequency was low. These authors used randomizations in which all birds had approximately equal sighting frequencies. This meant that few if any birds were excluded from the randomized data. For example, in one test Myers (1983) had 58 individuals (giving 1653 pairings) in the random data, but only 49 individuals (giving 1176 pairings) in the observed data. Since birds were excluded only from the observed data, the average number of sightings in relation to the number of flocks, and therefore the average index level, would be raised only in the observed data.

If association is defined in terms of common membership of a group, then species (or populations) in which flock size is greater will tend to have higher association levels. Therefore unless it is the absolute level of association which is of interest, observed frequency distributions of flock sizes should be retained in any randomization (as in Myers, 1983; Metcalfe, 1986; and Whitfield, 1985). This illustrates the difficulty of making cross-study comparisons of association levels. I will show that a comparison of association levels according to various ecological factors reveals flock size as an important factor accounting for differences.

4.3.4 Independent Occurrences

The chances of two birds, *A* and *B*, being found in a given flock are dependent because both are more likely to be seen in large flocks than in small flocks. Lefebvre (1985) computed expected co-occurrence frequencies of feral rock doves from the products of individual occurrence frequencies. This test assumes that individual occurrences are independent. This may not hold if occurrences are dependent on some other factor such as food availability. For example, if the proportion

of regulars was greater on days of higher population size, then co-occurrences of regulars would be more than expected on the basis of independent occurrences.

4.3.5 Bias

An association index may be biased when the probability of observing one or both birds varies according to whether they are together or apart and not all individuals are located in all samples. Cairns and Schwager (1987) examined the effects of such bias on association indices by running a computer simulation incorporating different probabilities of observation of birds given that they were present.

4.3.6 Multi-Group Samples

As Cairns and Schwager (1987) point out, almost all currently used association indices were developed for measuring association between species (e.g. Dice, 1945) rather than association between individuals. One way in which the procedures may differ is that whereas each area in the study of species association constitutes a separate sample, one sample for individual association might consist of several groups. When multi-group samples are taken the possibility of recording both *A* and *B* as present but apart arises.

Even if only one group can be recorded at any given instant it may be that different groups recorded within a short space of time are properly considered as being of the same sample. If they are considered as separate samples then this raises the problem of whether successive samples are independent in the sense that the group membership found in the second sample does not depend on that found in the first.

The question of independence has been addressed by some authors but none seems to have arrived at a satisfactory solution. Myers (1983) did not state the number of groups per sample. He may have taken a complete check of a stretch of beach as one sample or each flock encountered during these checks as a sample. No mention was made of multiple sightings of birds within a sample. To lessen the dependence of successive samples Metcalfe (1986) allowed a minimum period of two hours to elapse between successive sightings of any given bird. However, if the presence of particular birds is to be ignored then the following argument suggests that it may be best to discount all records within two hours of a previous one. Even

if a bird A , seen at time t_0 , was not resighted within two hours another bird B seen within this period could be recorded and so a ' B without A ' sighting would be scored. If records of A within two hours are really not considered to be independent then this would give two contradictory records for A in the same sample. Ekman (1979) recorded only one observation per day and pair of individuals. This could mean either that second sightings of particular birds were ignored or that further sightings relevant to a pair were ignored. Lott and Minta (1983) recorded only the first identification of each individual during a 24-hour period. This technique suffers from the same problem as that of Metcalfe.

Cairns and Schwager (1987) considered that samples are likely to consist of several groups observed over a period of time during which changes in group membership are unlikely. I began with the contrary assumption that since birds are continually free to move between groups, every flock recorded is a separate sample. In practice this may mean that where there was only a short time interval between sightings, flock composition may have changed little and so individuals will be re-recorded after only a short time. An important reason for recording all flocks without a minimum time interval constraint was to find out the interval necessary for sightings to be considered as independent.

A possible bias in my method is that different flocks may stay together for different periods of time. For example, if small flocks were more transient than larger ones and A -only sightings (as opposed to AB sightings) were biased towards small flocks then the association between A and B may be under-estimated. My method may therefore be more accurately described as measuring the numbers of flocks in which birds were together or apart rather than the actual time for which they were together or apart. It would be possible to weight each record by an appropriate length of time knowing flock size and transience. On the other hand, the main objective was to identify differences from random associations. In this case measuring the true frequency of association is not necessary, although it may be valuable in interpreting the biological significance of non-randomness.

4.3.7 Maximum Likelihood

Cairns and Schwager (1987) derived maximum likelihood estimators which they found to be less biased and to have lower variance than other association indices. I

found their procedure impractical because of the difficulty of estimating the number of flocks that the entire local population was subdivided into at any given time.

4.4 Results

The following analyses are mainly of 2803 sightings made in the winter of 1986–87 of 91 colour-ringed birds on 36 days. Where only one sighting per bird per day is included, the number of sightings is reduced to 1377.

4.4.1 Flock Membership

Figure 4.1 shows that observed associations differed from those expected, where expected associations were calculated from a randomization of the data in which each bird was given an equal chance of appearing in each flock. In fact, observed associations tended to be lower than expected, there being more pairs than predicted having very low association levels and fewer having medium values of the association index. But Figure 4.2 shows that observed associations do not differ from those expected if the observed frequencies of occurrence of each individual are taken into account in the randomization.

Those pairs seen the most frequently are the most strongly associated (Table 4.1 and Figure 4.3), but these associations are no stronger than are expected given the birds' sighting frequencies. This is because of the relationship between the association index and sighting frequency discussed in Section 4.3.3.

The difference between the observed sighting frequency distribution and that in the data generated using the randomization which assumes that all birds are equally available is appreciable (Figure 4.4). The randomization in which all birds were considered equally 'available' produced a sighting frequency distribution with the same mean (30.80) but a much smaller standard deviation (2.41) than that of the observed data (18.07). Given the relationship between sighting frequency and association index value this difference is likely to have had a marked effect on the frequency distribution of association index values.

Myers (1983), using a randomization in which all birds were equally available, obtained a better fit to the null model than was found in this study.

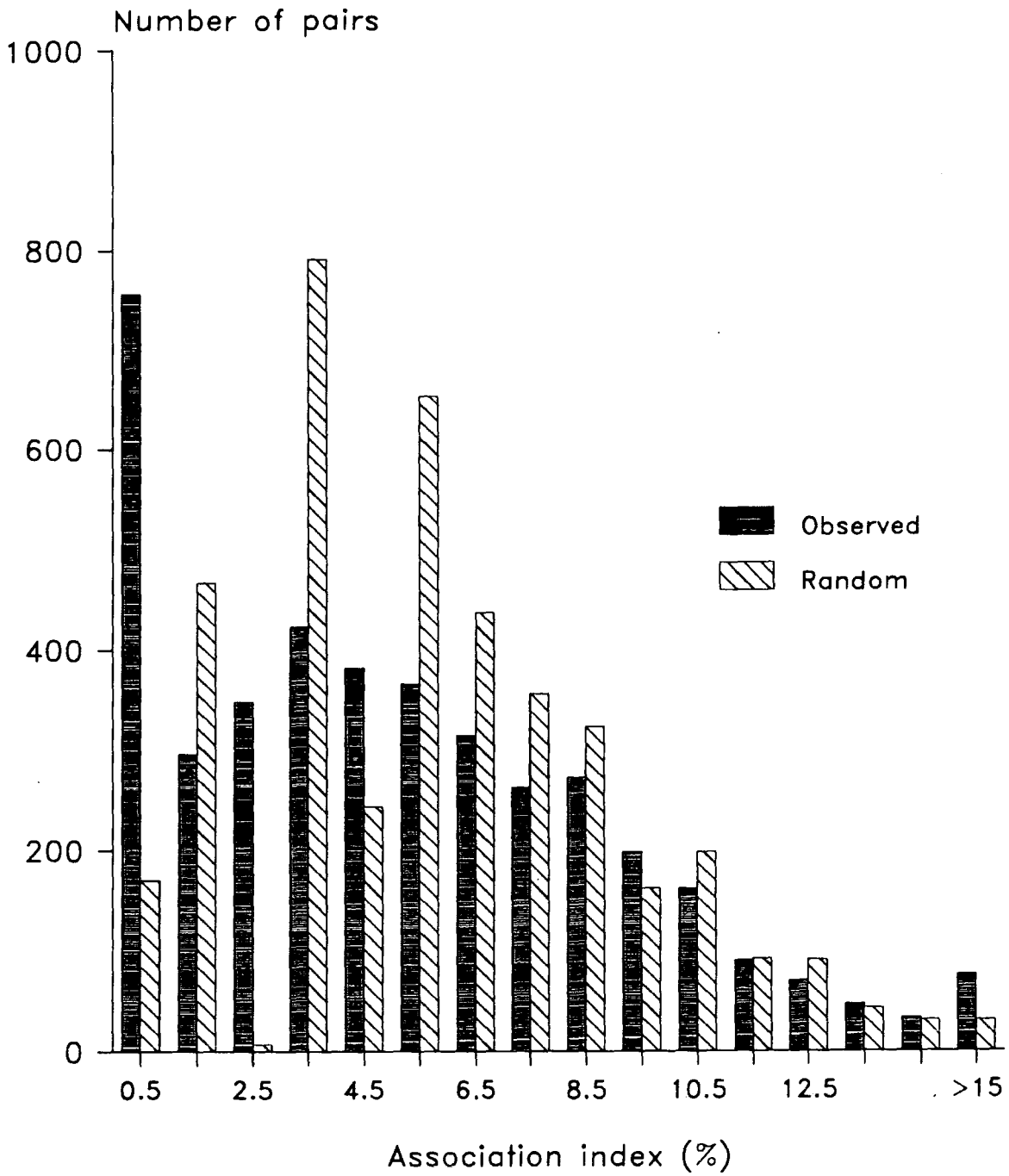


Figure 4.1 — Associations in Terms of Flock Membership (1)

Frequency distribution of association indices for observed data (median=4.545, n=4095 pairs) compared with a randomization in which all birds had approximately equal sighting frequencies (median=5.263, n=4095 pairs). A Kolmogorov-Smirnov 2-sample test on a sample of 2300 pairs showed a significant difference ($D_{max} = 0.20$, $Z = 4.78$, $p < 0.00005$) between the two frequency distributions.

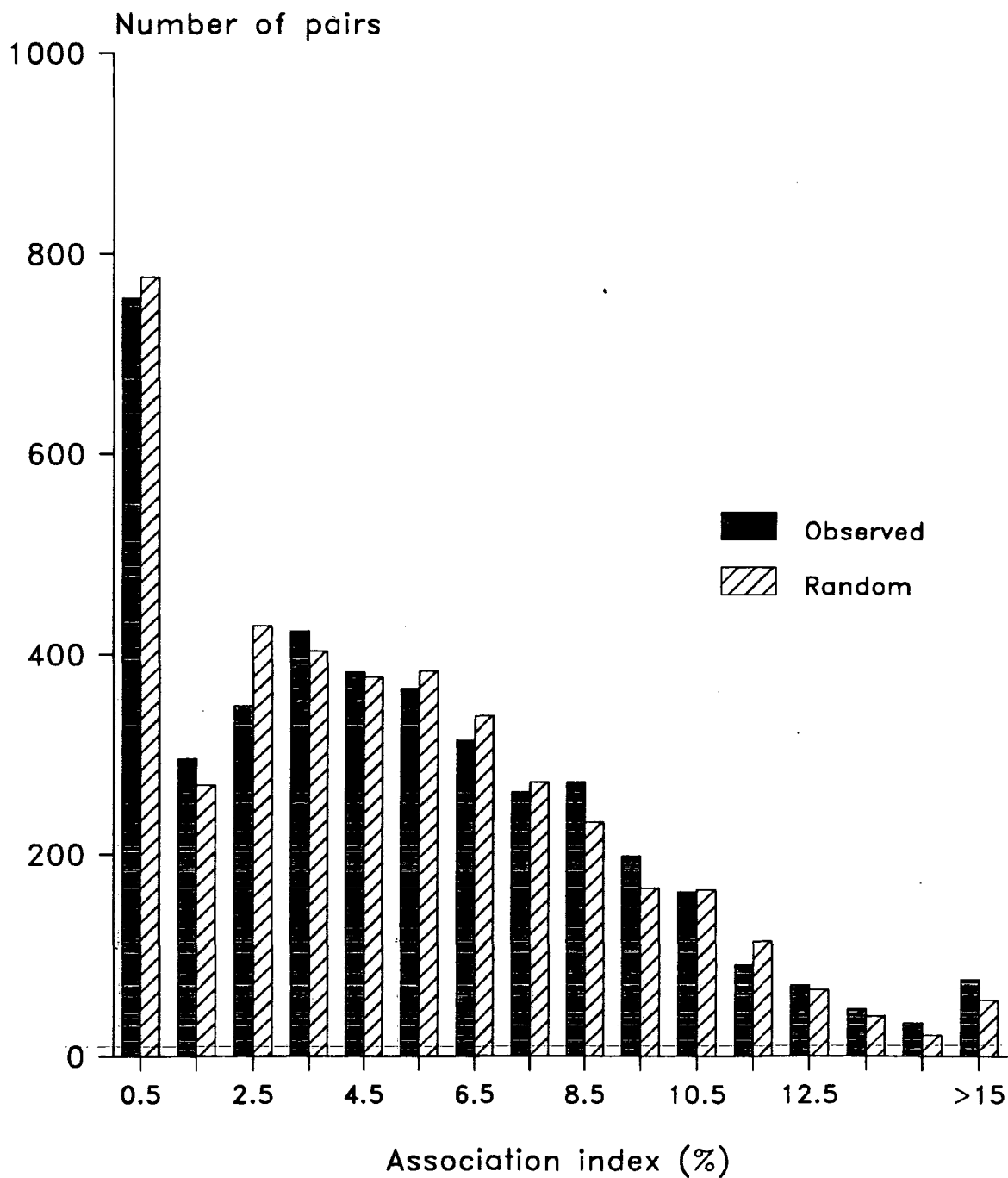


Figure 4.2 — Associations in Terms of Flock Membership (2)

Frequency distribution of association indices for observed data (median=4.545, n=4095 pairs) compared with a randomization in which sighting frequencies were retained (median=4.444, n=4095 pairs). A Kolmogorov-Smirnov 2-sample test on a sample of 2300 cases showed no significant difference ($D_{max} = 0.05$, $Z = 1.13$, $p = 0.15$).

So that any differences between observed and random associations cannot be explained by sighting frequencies, further analyses use only the randomization method which preserves these.

4.4.2 Effects of Periods of Residency

Some birds were not sighted until several weeks after the start of the study; others were last seen several weeks before the end. It can be argued that what is really of interest is the level of association between a given pair of birds while they are both present locally, as evidenced by their occasional appearance at the study site. A bird's residency period was defined as the inclusive period between its first and last sightings, and the calculation of the association index of a given pair was based only on sightings from the period during which both were resident. This procedure applied both to the observed and to the randomized datasets.

Sightings were more evenly distributed through time in the randomized datasets. This meant that more birds overlapped in residency periods (therefore the number of pairs for which an association index was computed is greater in the random data) and that overlaps were longer.

Observed associations tended to be greater than those predicted (Figure 4.5). But the difference between observed and expected was confined to birds seen rarely (Figure 4.6). At high sighting frequencies the difference was small since the period of co-residency was virtually the whole study period and the results therefore approximated to those obtained in section 4.3.1. Associations between birds seen only a few times were greater than expected, probably because of the effect of the randomization in spreading observations more evenly through time, thereby affecting the length of the co-residency period most when sighting frequencies were low. The longer the co-residency period, the less likely the two birds are to be seen together.

Strictly speaking, randomizations should be carried out separately for each pair and should be confined to the periods of joint residency. This proved to be impractical. Another possible method would be to reshuffle sightings of each bird within its residency period (compare Section 4.4.4 where flock membership is reshuffled within days). This null model could then be tested against the observed data.

Sighting Frequency	Observed	Random	Pairs	D_{max}	Z	p
All	4.55	4.41	4095	0.05	1.14	0.15
>30	8.05	8.57	946	0.03	0.80	0.54
>40	9.26	9.79	406	0.03	0.62	0.84
>50	10.89	10.88	120	0.04	0.91	0.37

Table 4.1 — Associations among Pairs of Sanderlings Seen Different Numbers of Times

The sighting frequencies given are for individual birds. Median values of the association index are given for the observed data and for a randomization in which sighting frequencies were retained. Significance levels were obtained using Kolmogorov-Smirnov two-sample tests; n.s. indicates non-significance at the $p = 0.05$ level.

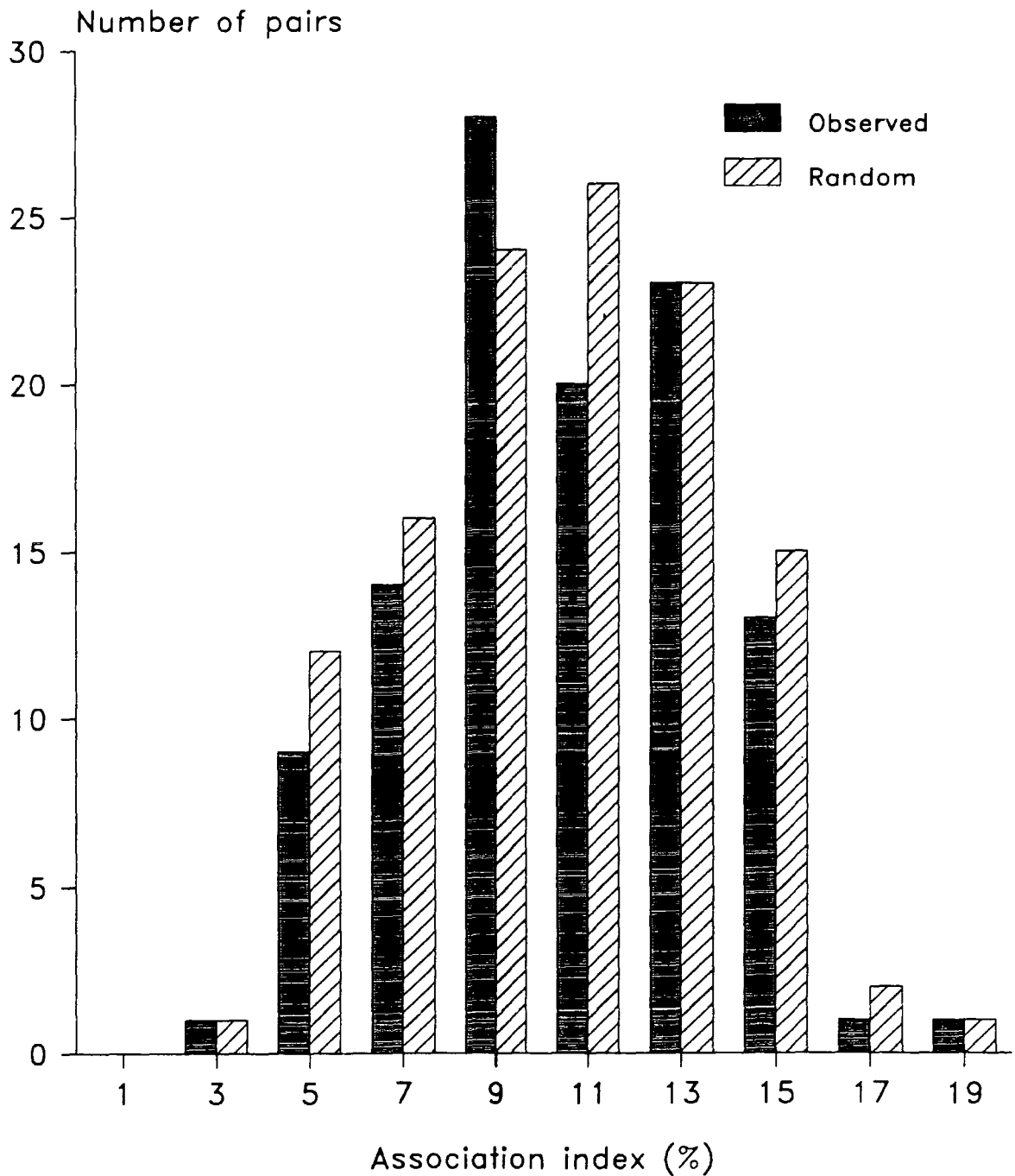


Figure 4.3 — Associations among Birds Seen Over Fifty Times

Observed frequency distribution of association indices among pairs for which the sum of the individual sighting frequencies was over 50. Statistics given in Table 3.1.

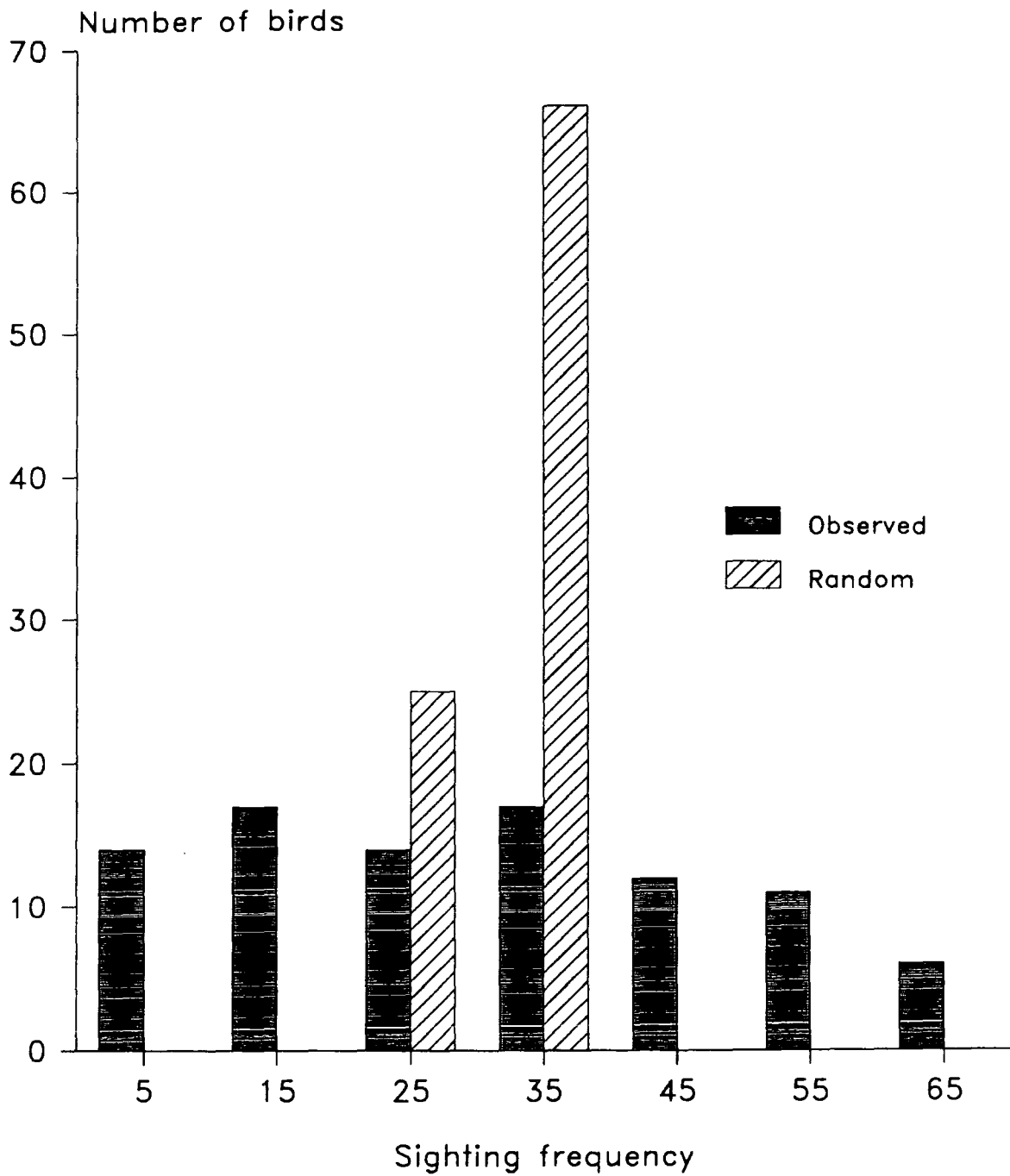


Figure 4.4 — Sighting Frequencies

'Observed' indicates the sighting frequency distribution for the observed data and for the randomization in which sighting frequencies were retained. 'Random' indicates the frequency distribution for the randomization in which all birds were 'equally available.'

This would mean that the occurrences in the null model would fit the distribution of occurrences through the winter more accurately, i.e. seasonal patterns in the occurrences of individuals would be retained. However, such a randomization proved too complex to carry out.

Because of the difficulty of interpreting the results obtained, the following analyses were not confined to periods of co-residency.

4.4.3 Daily Occurrences

The failure to find non-random associations at the level of flock membership does not preclude the possibility of associations being found at other levels. If individuals moved around between sites with particular other individuals but mixed randomly while at a site then associations might not be found at the level of flock membership but might be found at the level of co-occurrences at a site on a given day.

A test of this hypothesis found no evidence for non-random association of sanderlings by site co-occurrences. As in the case of the flock membership analysis, retaining observed sighting frequencies in the null model resulted in a good fit between the data and the null model (Figure 4.7).

4.4.4 Assortment Among Flocks

In this section observed associations are tested against those expected if the birds present on any day are reshuffled randomly between the flocks present on that day. One reason why associations might differ from those expected would be if individual sanderlings had preferences for particular foraging substrates. If birds tended to move around together such that they arrived and departed together and tended to remain together on the feeding grounds then this should be apparent as non-random association within a day. For simplicity, birds were classified as being either present or absent on any given day: in fact they may have been present only for part of the day. The results will therefore reflect both the timing of the bird's visit to the site and associations while actually there.

That there was no difference between observed and random association indices (Figure 4.8) suggests that there were neither consistent preferences for being with

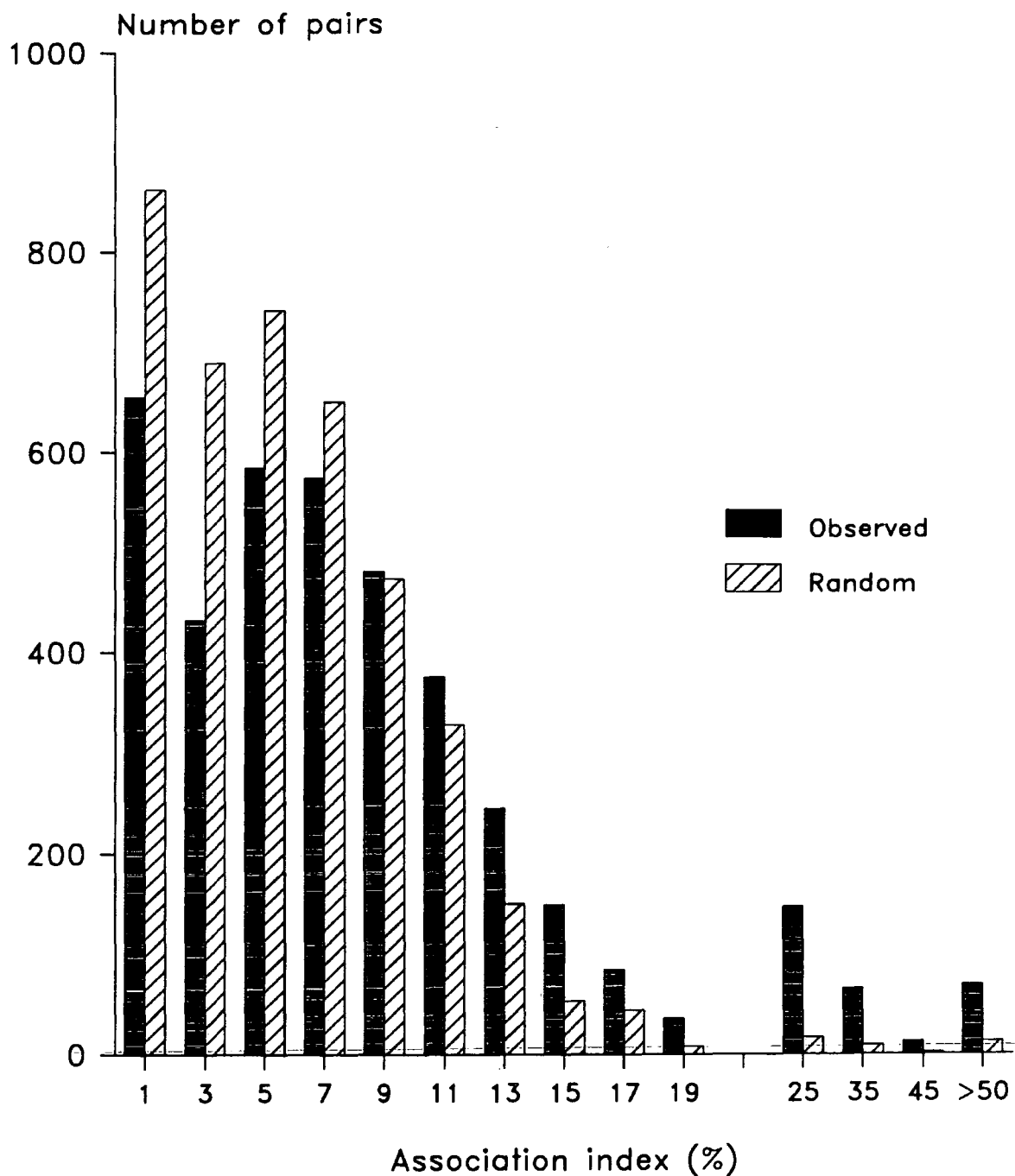


Figure 4.5 — Associations among Sanderlings While Resident at the Study Site

Frequency distribution of association indices for all pairings where sightings were included only if both of a pair were defined as being resident at the study site at the time of the sighting; observed (median=6.977, n=3909 pairs); random (median 5.263, n=4040); Kolmogorov-Smirnov 2-sample test, $D_{max} = 0.16$, $Z = 3.80$, $p < 0.00005$.

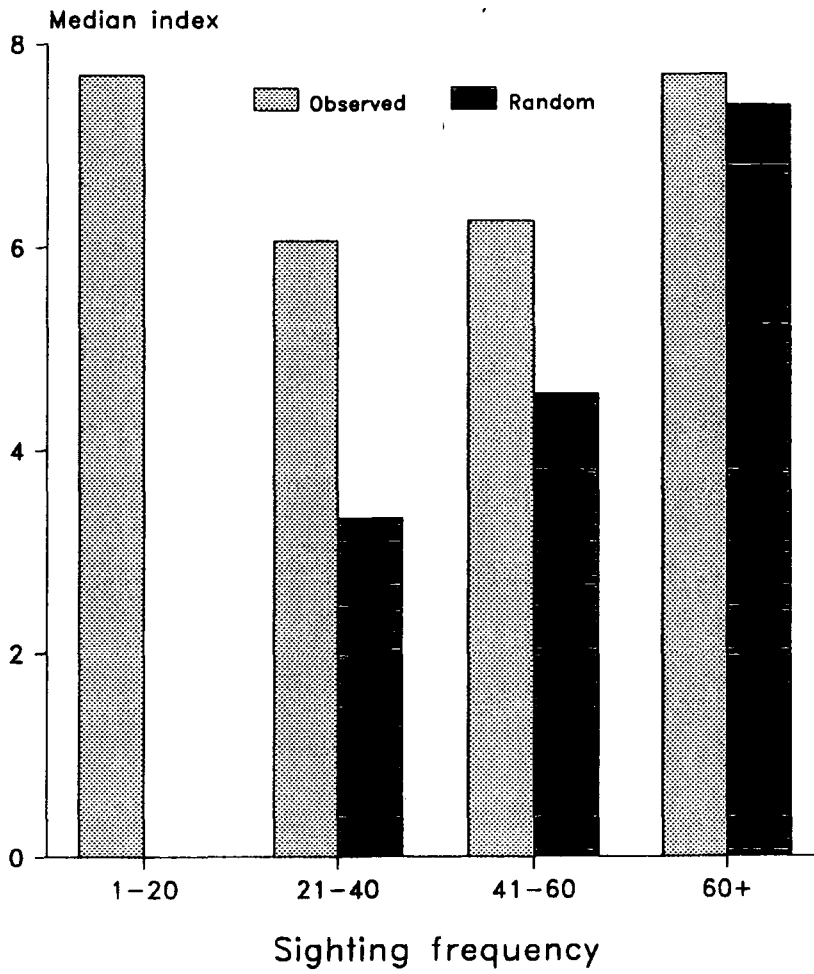


Figure 4.6 — Associations among Sanderlings while Resident, by Sighting Frequency.

The *x*-axis shows the sum of the sighting frequencies for each pair. The *y*-axis shows the median association index for each sighting frequency class. Observed and random indices differ most where sighting frequencies are low.

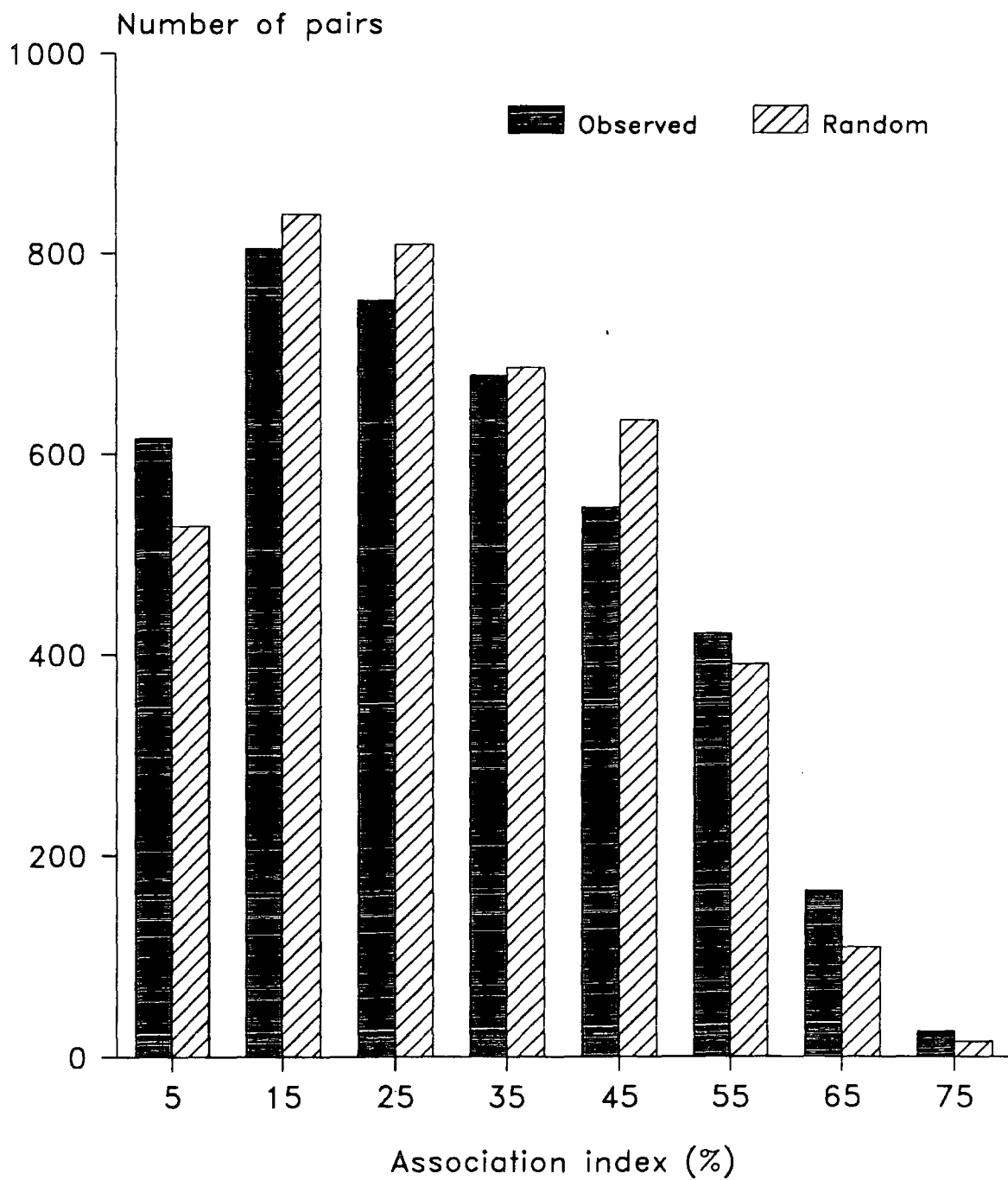


Figure 4.7 — Associations in Terms of Daily Occurrences

Frequency distributions of association indices calculated from the birds' daily presences or absences: Observed median = 27.27, $n = 4005$; random median = 27.586, $n = 4005$. Kolmogorov-Smirnov 2-sample test. $D_{max} = 0.020$, $Z = 0.501$, $p = 0.959$.

particular individuals nor shared preferences for particular feeding sites or methods.

An alternative way of testing random assortment among flocks would be to include in the calculation of the index (both for the observed and the random data) only those sightings made on days when both of the pair were present. The null model would be as derived in Section 4.4.1. This would be analogous to the joint residency analysis presented in Section 4.4.2.

4.4.5 Associations through Time

Figure 4.9 shows the proportion of occasions on which a bird *A* was seen where *B* was also present, as a function of the time since the last joint sighting. The main finding is that time is an important factor affecting association levels: the population mixes up gradually, and so sightings separated by, for example, 30 minutes will not be independent. That is, the likelihood of finding two birds together at a given time is dependent on whether they were together 30 minutes earlier. The association index values obtained in a study will depend on the time intervals between sightings.

4.4.6 Associations in Relation to Feeding Site and Substrate

Because the previous analyses may not be very statistically powerful, the next stage was to test more specific hypotheses.

One of the main objectives of the study was to find how properties of the food supplies exploited affected associations. The unpredictability of food supplies is thought to influence sociality (Section 4.1.2). Of the food supplies exploited by sanderlings (Section 2.4) the rocky areas are apparently the most predictable. Sandy areas are susceptible to being scoured by wave action but become more profitable feeding areas when wrack beds are washed up. Resource predictability might affect associations in different ways: if the rocky areas were used regularly by the same birds then associations might be higher there, but it could be argued that good feeding conditions on the sands might be exploited only by particular birds there.

Associations of birds visiting Redcar were compared with those of birds visiting Coatham Sands. The sites differed in terms of substrate type, and consequently

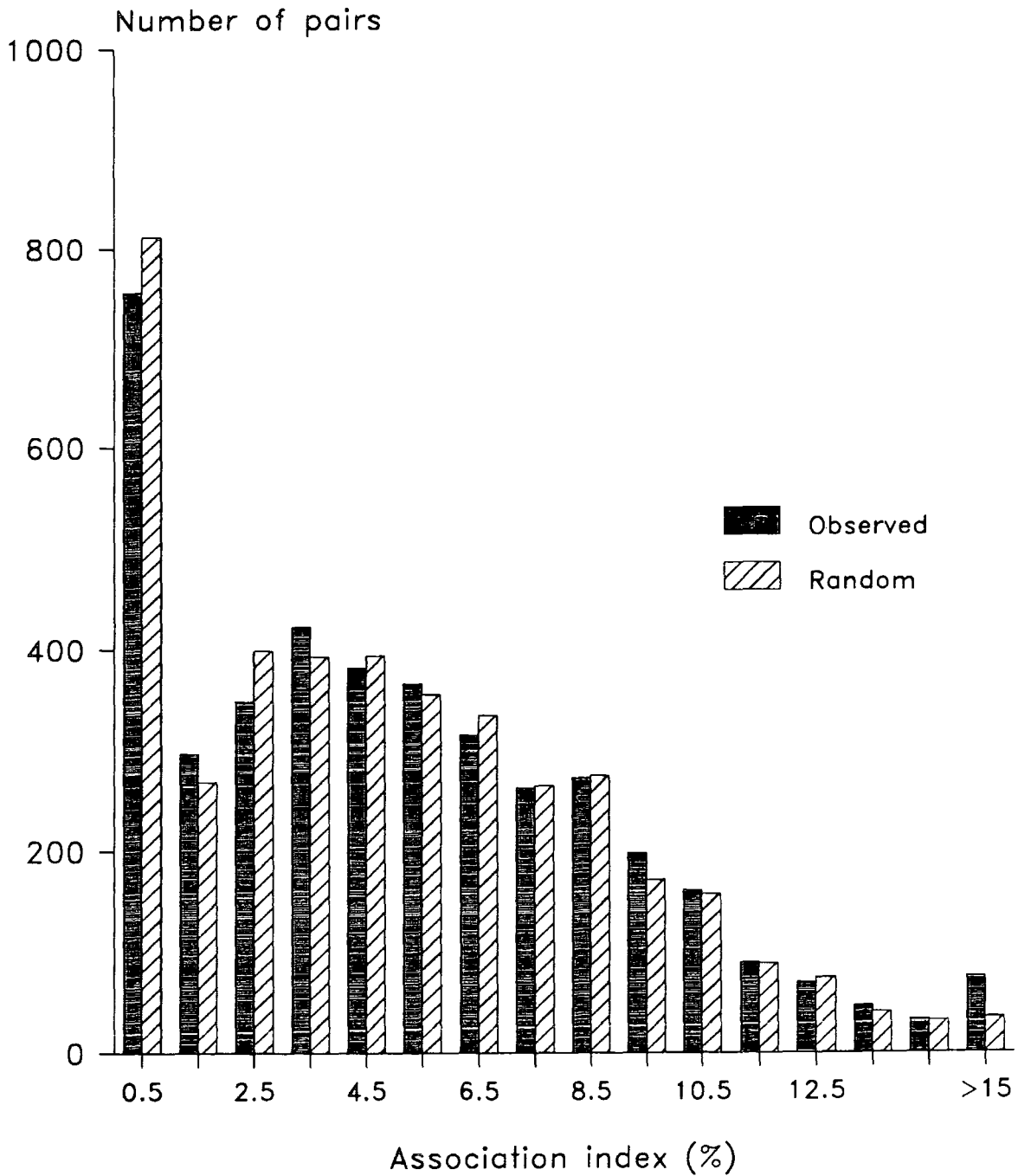


Figure 4.8 — Assortment among Sanderling Flocks

Observed frequency distribution of association indices for all pairings tested against a null model prepared by randomizing sightings among flocks while maintaining the days of the sightings. Observed median=4.545, n=4095; Random median=4.348, n=4095 pairs; Kolmogorov-Smirnov 2-sample test, $D_{max} = 0.031$, $Z = 0.662$, $p = 0.778$.

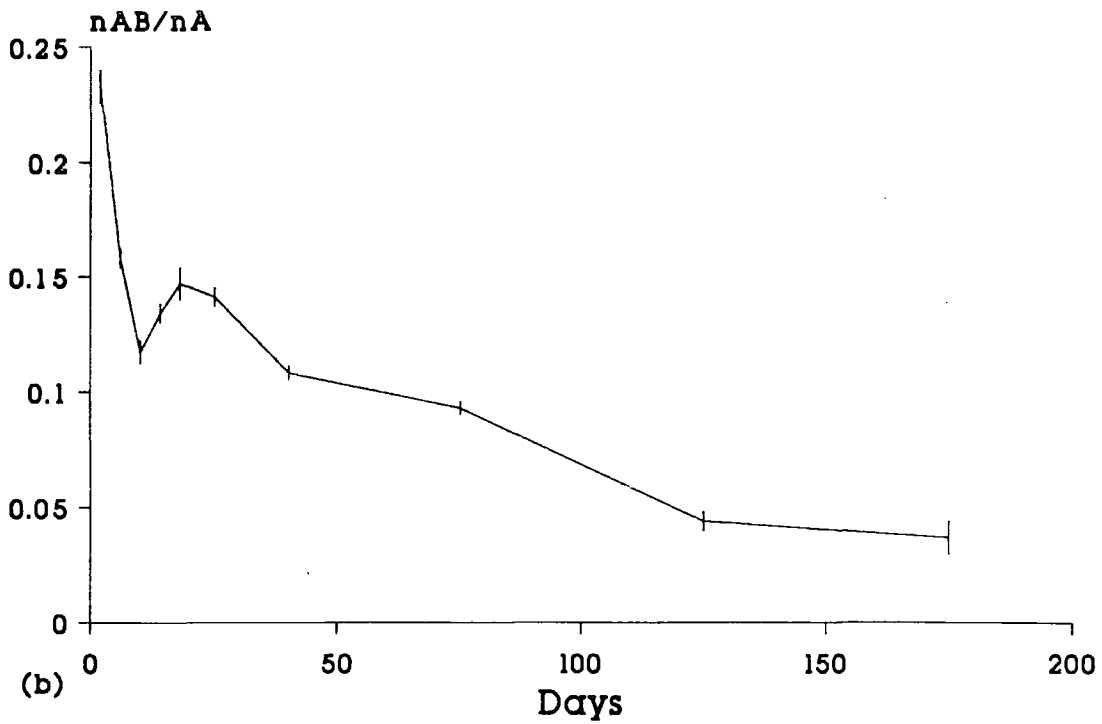
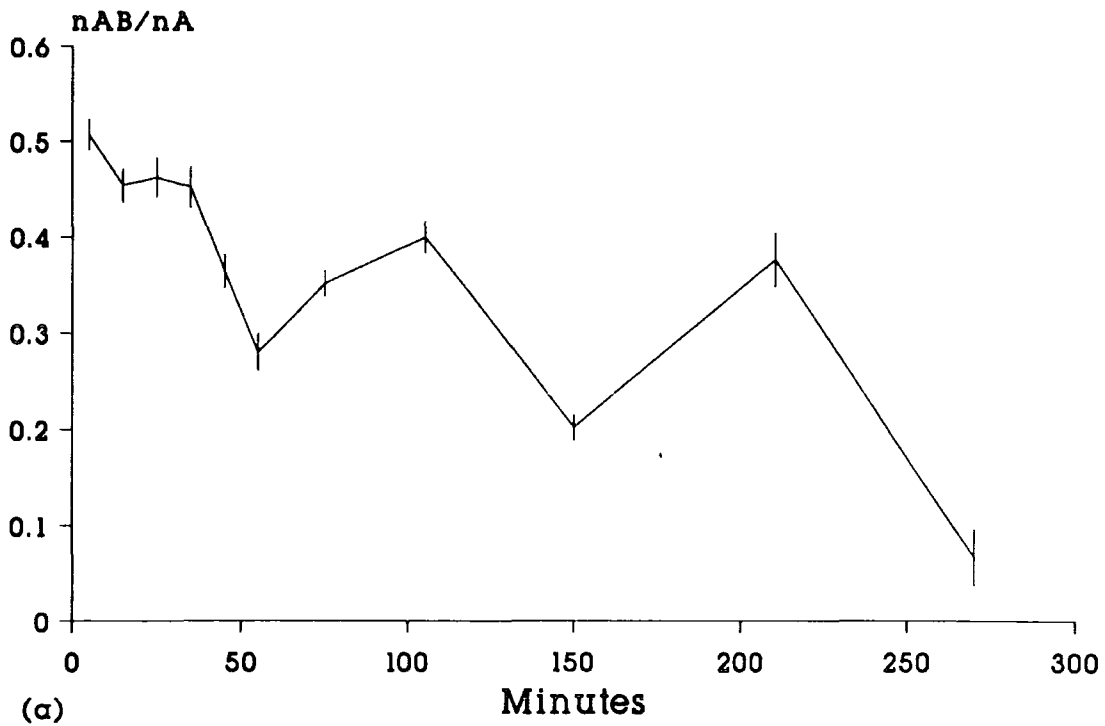


Figure 4.9 — Associations through Time

The decline in the number of joint sightings of two birds *A* and *B* (nAB) as a proportion of the total number of sightings of *A* (nA) over periods of (a) minutes and (b) days. Mean values are plotted, with standard errors.

food supply, but also in terms of disturbance, exposure period and variations thereof, and proximity to roost sites.

Associations differed from random at Redcar (observed median=4.396, $n=3916$; random median=4.255, $n=4095$ pairs; $D_{max} = 0.035$, $Z = 1.580$, $p = 0.014$) but not at Coatham Sands (observed median=4.167, $n=3916$; random median=4.257, $n=3828$ pairs; $D_{max} = 0.016$, $Z = 0.705$, $p = 0.702$). However, the difference at Redcar was only slight and would appear to be of little biological significance.

Comparing sites (Figure 4.10) there were significant differences both for the observed data ($D_{max} = 0.128$, $Z = 5.684$, $p < 0.0005$) and for the randomized data ($D_{max} = 0.100$, $Z = 4.444$, $p < 0.0005$).

The small observed–random differences within each site indicate that the differences between sites are accountable for in terms of factors which are incorporated in the null model, i.e. by the relationship between the number of sightings per bird and the overall number of flocks checked (Section 4.3.3). Thus, the greater levels of association at Redcar are due to the greater flock sizes at that site.

Substrate effects were addressed more specifically by considering only data for the Redcar area and comparing associations of birds feeding on sandy areas with those of birds feeding on rocky areas. Within each habitat significant differences between observed and random were found (Figure 4.11) but, as in the case of comparisons between sites, the magnitudes of the differences were small. (Sandy areas: observed median= 3.846, $n = 3828$; random median= 3.704, $n = 4095$ pairs; $D_{max} = 0.033$, $Z = 1.475$, $p = 0.026$. Rocky areas: observed median= 3.571, $n = 3655$; random median= 4.348, $n = 3916$; $D_{max} = 0.047$, $Z = 2.073$, $p < 0.0005$). Therefore the null models again provided good fits to the data and the null hypothesis of random associations cannot be rejected.

In the case of the observed data, there was no significant difference between substrates ($D_{max} = 0.016$, $Z = 0.716$, $p = 0.684$), although there was a significant difference for the random data ($D_{max} = 0.039$, $Z = 1.746$, $p = 0.004$).

4.4.7 Associations of Pairs with Similar Distributions

Birds showed different preferences for different sites (see Section 3.6.1) In this

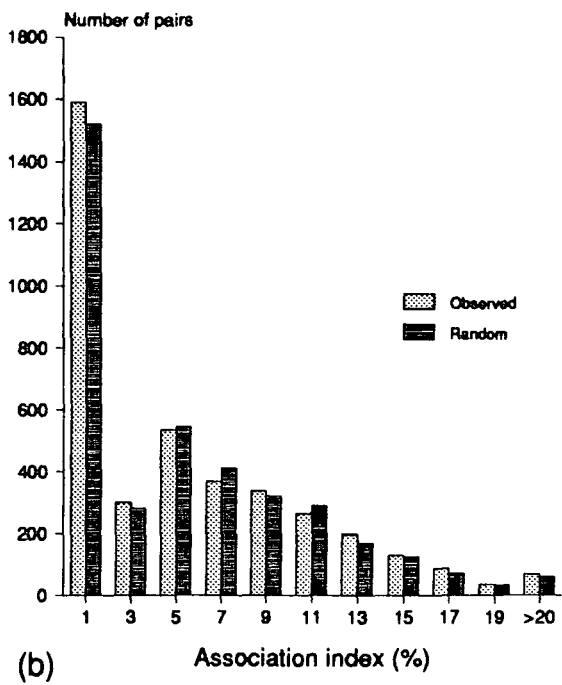
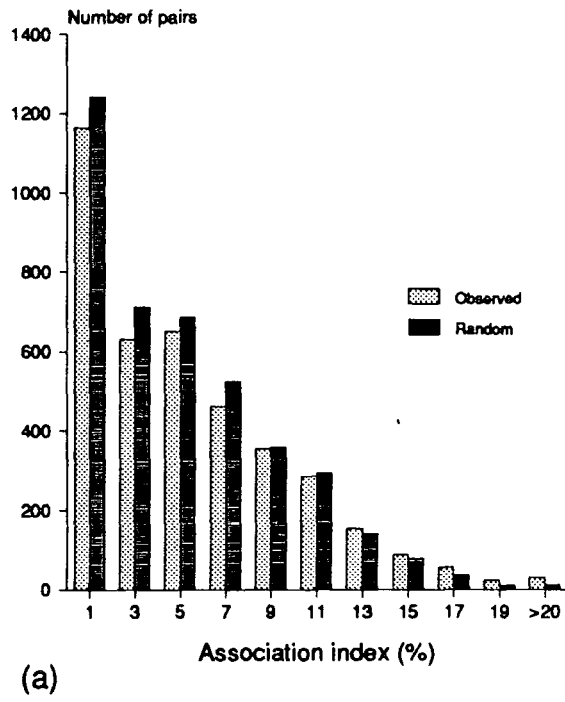
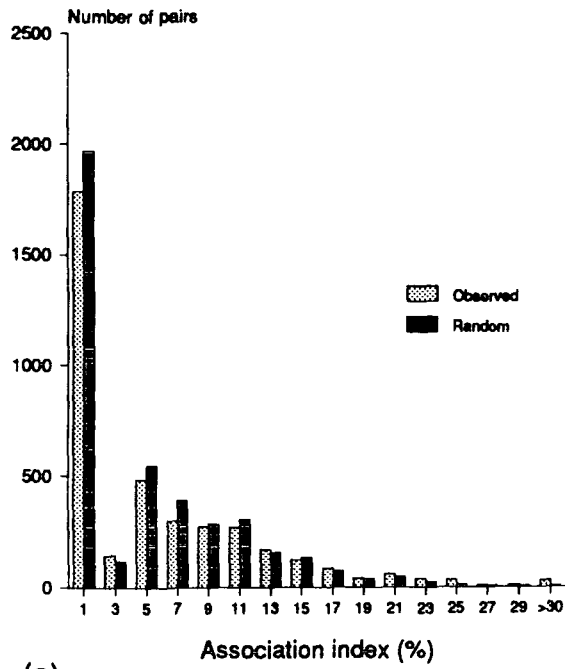
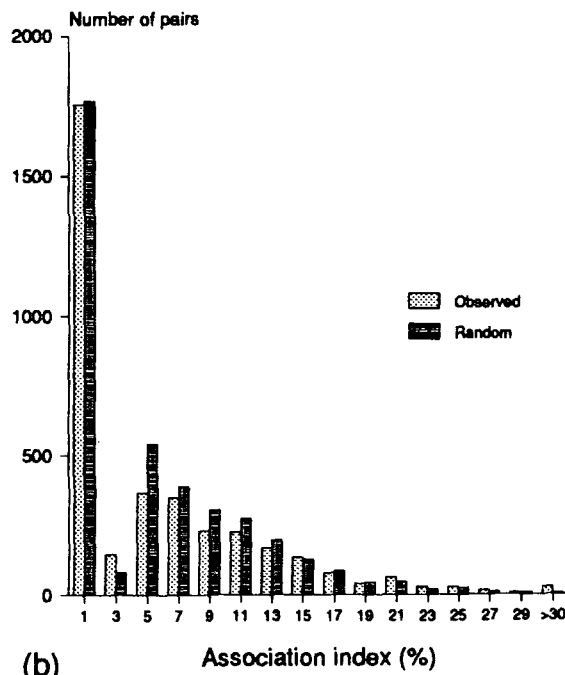


Figure 4.10 — Associations at Different Sites

Observed frequency distributions of association indices for all pairings tested against null models prepared by randomizing sightings among flocks for (a) Redcar and (b) Coatham Sands.



(a)



(b)

Figure 4.11 — Associations on Different Substrates

Observed frequency distributions of association indices for all pairings tested against null models prepared by randomizing sightings among flocks for (a) sandy areas and (b) rocky areas.

section I ask whether two birds which tend to use the same sites to similar extents also tend to use them at the same times, i.e. whether they tend to move around together. This might come about if birds normally found at a particular site deserted it on particular days in response, perhaps, to feeding conditions.

Associations between individuals on the south side of the estuary in winter 1986–87 were examined in terms of the frequencies of occurrence of those individuals on the north side in the previous winter. This was done by finding the numbers of sightings of each individual on the north side in winter 1985–86 as proportions of the numbers of observation days in that winter. Only sightings from Seal Sands to Hartlepool were included since coverage of this area was more regular than that of areas further north. Most birds (17) were seen on fewer than 5% of observation days; 8 birds were seen more frequently. This classification was arbitrary in that there was no clear bimodality in the distribution of sighting frequencies.

Table 4.2 compares association levels within and between the groups based on distributions with those expected using the association indices calculated in Section 4.4.1. No differences from randomness were found and there was therefore no evidence of birds moving around as stable groups: birds which used one side of the estuary to similar extents did not show a greater than expected tendency to visit the other side together.

4.4.8 Associations of Pairs of Similar Vagility

Vagility is a measure of the extent to which a bird moves between sites. An index of vagility was computed (Index A in Section 3.5.2) as the number of status changes made over the maximum possible number of status changes given the arrival and departure dates.

It is not easy to predict how individual vagility might affect the association of two birds. Although increasing vagility might be expected to lead to the breakdown of associations, this does not necessarily follow since birds may move around together. Birds which are more vagile will tend to come into contact with more individuals and so the associations of such birds, averaged over all possible pairings, might be higher than those of less vagile birds.

Groups	No. of pairs	Observed	Random	D_{maz}	Z	p
Both group A	190	3.897	3.974	0.095	0.923	0.361
Both group B	300	5.671	5.647	0.060	0.735	0.653
Different groups	500	4.928	4.196	0.072	1.138	0.150

Table 4.2 — Associations of Pairs with Similar Distributions

The table gives observed median association indices for pairs of birds grouped according to their distributions (see text), together with the expected median for these pairs (see text). Probabilities were obtained from Kolmogorov-Smirnov 2-sample tests.

Pairs were divided into three vagility classes: (1) where both members of a pair had vagilities less than the mean; (2) where both had vagilities above the mean; (3) where one bird's vagility was below the mean and the other's above.

The vagility index varied with sighting frequency, being greatest for birds seen an intermediate number of times (Section 3.5.2) Although the frequency distributions of sightings were maintained exactly in the null models, the vagilities of each bird could be maintained only approximately, by selecting only those cases where a pair's vagility class was the same in the random data as in the observed.

Although a significant difference from randomness was found for the high vagility birds (Figure 4.12), the magnitude was small and it appears that the null models give a good fit to the data.

The analysis was repeated using Index B from Section 3.5.2. Again, the null models fit the data and there was therefore no evidence for non-random association on the basis of vagility.

4.4.9 Correlations between Associations in Different Periods

One way in which to test whether the variation in association indices is non-random is to look at the consistency of each pair's association as measured in different periods: a correlation would suggest non-randomness. The sightings were divided into three periods: October–November; December–February; and March–May. Randomizations of the data were carried out separately for each period. Association indices for each pair were computed and the difference between observed and random calculated. This gave three difference values for each pair which were then used to compute correlations between the difference values in different seasons. Table 4.3 shows that there is no evidence of any consistency in the non-randomness of any pair's associations.

4.4.10 Monte-Carlo Randomizations

Analyses were repeated using Monte-Carlo randomizations (Section 4.3.2). The observed associations of a given pair can be said to be greater than random if fewer than 5% of the randomizations give an association level greater than or equal to that observed. This was true for only 105 out of the total of 4005 pairs,

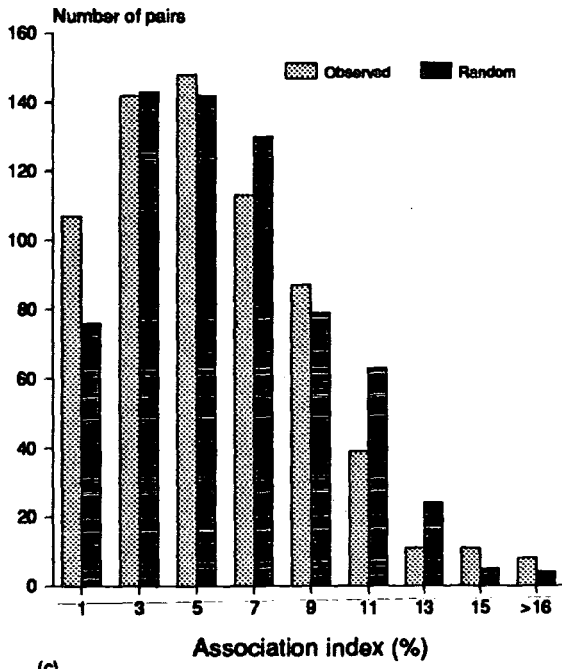
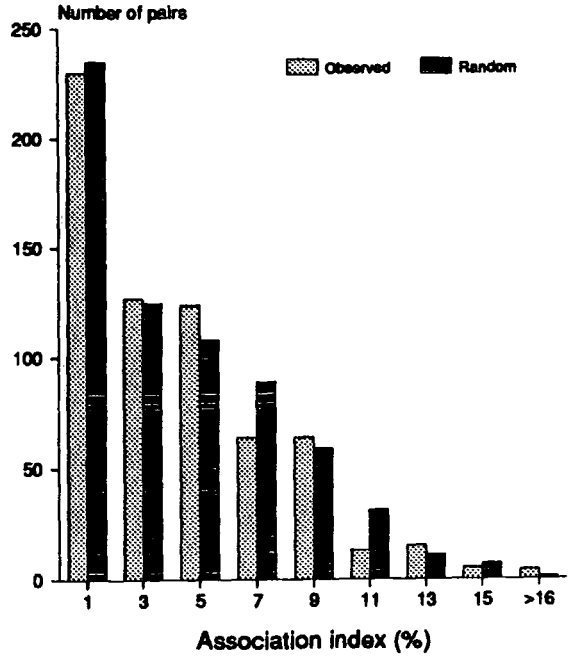
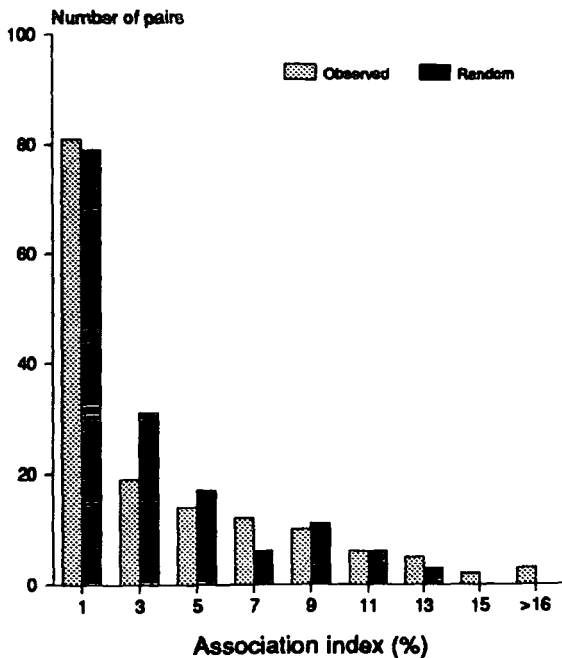


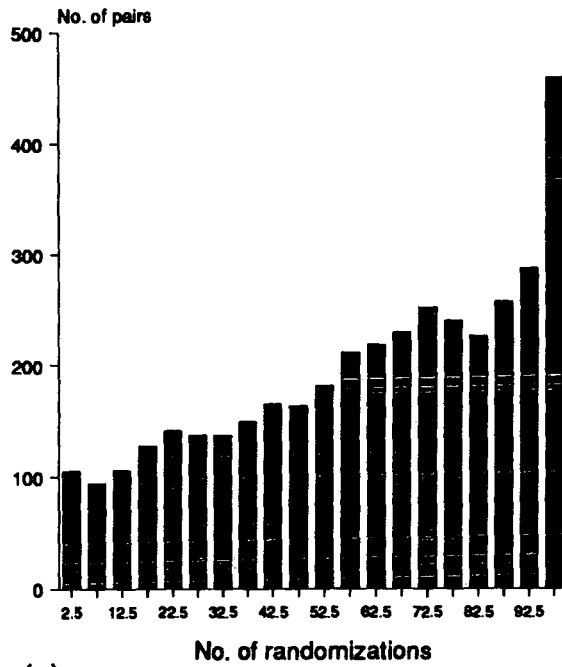
Figure 4.12 — Associations in Relation to Vagility

Observed frequency distributions of association indices for all pairings tested against null models (see text). (a) Pairs where both birds had low vagilities: observed median=1.613, n=153 pairs; random median=1.613, n=153; Kolmogorov-Smirnov 2-sample test, $D_{max} = 0.092$, $Z = 0.800$, $p = 0.544$. (b) Pairs where both birds had high vagilities: observed median=5.085, n=666 pairs; random median=5.660, n=666; $D_{max} = 0.075$, $Z = 1.370$, $p = 0.047$. (c) Pairs of differing vagilities: observed median=3.727, n=666 pairs; random median=3.571, n=666; $D_{max} = 0.027$, $Z = 0.493$, $p = 0.968$.

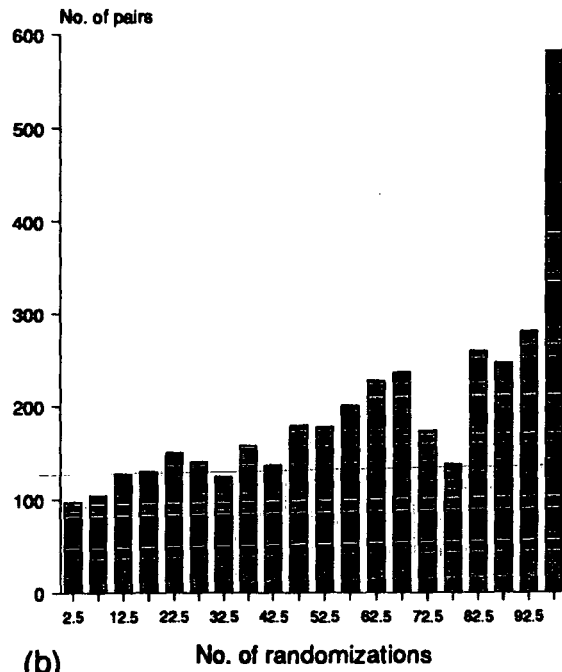
Seasons	overall		5+ sightings		no zeroes	
	<i>r</i>	<i>n</i>	<i>r</i>	<i>n</i>	<i>r</i>	<i>n</i>
Autumn and Winter	0.00	2850	-0.02	861	0.03	938
Autumn and Spring	-0.01	2850	0.02	780	0.04	796
Winter and Spring	0.03	3321	0.03	1830	0.08	1597

Table 4.3 — Correlations Between Differences from Randomness in Different Seasons

The table gives the Pearson *r* values for correlations between seasons in the difference between observed and expected association levels for each pair (a) overall; (b) including only cases where each bird had five or more sightings; and (c) including only pairs which were seen together at least once in each year.



(a)



(b)

Figure 4.13 — Monte-Carlo Randomizations

Frequency distributions of numbers of pairs having associations (a) greater than or equal to random and (b) less than or equal to random.



i.e. for 2.6% of pairs (Figure 4.13). Using a corresponding procedure 97, or 2.4% , of pairs had associations less than random.

It is clear that a large number of randomizations gave association levels exactly equal to those observed. The power of the test must therefore be questioned: a much larger number of sightings per bird is apparently needed in order to allow for a greater spread of association values among the randomizations.

Further analyses are not presented because of the doubts over the power of the methods and the failure to find any effects which differed from those obtained in the one-off randomizations.

4.5 Summary

If each individual was considered to have an equal chance of appearing in each flock then associations differed from those expected by chance.

But if the different numbers of times that each individual occurred at the study site were taken into account then associations were as expected by chance.

This was also true if associations were calculated for the sanderlings present at the study site on each day (rather than for the birds present in each flock).

Birds which used the same feeding areas to the same extents did not show a greater than expected tendency to use those areas on the same days.

There was no evidence for birds moving around as stable groups: each individual appeared to decide where to feed independently of other particular individuals despite tending to feed in flocks.

This was true of birds using both predictable and unpredictable food supplies.

Taking into account the different distributions of different individuals, the population of birds present on any day represented a random sample from the population of birds seen during the winter.

4.6 Discussion

Studies of associations are important as baseline studies, indicating the types of behavioural interactions and the degree of social organization to be expected in a population. However, a number of methodological problems arise when trying to measure and interpret association levels. The questions being asked must be framed precisely so that appropriate assumptions are built into any null models used.

It was shown that association index values needed to be qualified (according to the observed flock size frequency distribution, the interval between records, etc.)

and so absolute values of a particular index characteristic of a population and comparable between populations, whether of the same or of different species, may not be obtainable. Instead, differences in index values from those expected by chance should be compared.

Some evidence of non-random association between sanderlings was found in this study, but this could be accounted for by the fact that different birds used the study site to different extents. If frequencies of occurrence were taken for granted then birds were found together at random. Despite being gregarious, sanderlings are independent in that they respond to the choices available to them in terms of where and when to feed in ways which may depend on what other birds are doing but do not depend on the behaviour of any other particular individuals or of any sub-groupings of the population. Although they frequently move around in flocks, these do not represent stable groups. Birds which share similar distributions appear to have independently reached similar decisions in terms of how to distribute their time between sites.

It follows from this that when the number of sanderlings at a site peaks there is simply a larger random sample from the local population present, weighted by overall sighting frequencies. That is, birds do not use sites independently of each other (because on some days there are large numbers and on others few) but there is no tendency for birds to arrive with particular other individuals beyond that due to their overall frequencies of occurrence.

Further studies of associations in other gregarious species are needed in order to understand the ecological factors determining levels of cohesion. A study of geese and swans might be profitable: there appears to be variation between species and situations in the extent to which birds move around as family groups and possibly as larger groups (Cramp and Simmons, 1977; Prevett *et al.*, 1980).

Chapter V

Flock Dynamics

5.1 Introduction

In this chapter I examine a number of aspects of the dynamics of flocks. In particular, I look at how cohesive flocks are and at how they build up and break down. Few studies have taken this mechanistic approach to flocking behaviour. Krebs (1974) showed how flocks of great blue herons, *Ardea herodias*, built up on the feeding grounds; Barnard (1980*b*) looked at changes in flock sizes of house sparrows, *Passer domesticus*; Barnard and Thompson (1985) described how flock sizes of golden plovers, *Pluvialis apricaria*, lapwings, *Vanellus vanellus*, and black-headed gulls, *Larus ridibundus*, changed through time and discussed how the tendencies of birds to join, remain in, or leave flocks could be understood in economic terms; and Caraco (1979*a, b*, 1980; Caraco and Pulliam, 1980) modelled and tested the interaction between flock sizes and time budgeting in yellow-eyed juncos, *Junco phaeonotus*.

At one end of the spectrum flocks might be open and dynamic, continually losing and gaining birds which move between flocks singly or in small groups. At the other extreme flocks might be closed, moving around as units. In order to find which is the better description of sanderling flocks I look at the group sizes in which birds move around, concentrating on the group sizes in which they leave flocks.

The general pattern of flock build-up and break-down over the low-water period is then described.

I go on to try to explain the observed frequency distribution of flock sizes for a given set of conditions in terms of the splitting and joining of flocks, that is, in terms of the rates at which birds arrive and depart. This allows a discussion of the decisions which birds are making in terms of which flock sizes to join and which to leave.

The question of whether flocks have an equilibrium level about which they fluctuate, or whether they are always either building up or breaking down is then addressed.

I go on to look in more detail at the choices which birds are apparently making when they join flocks. Do they choose the largest or the smallest of available flocks, the nearest or the furthest? How are these choices related to movements between habitats? When do birds tend to form new flocks?

I test the hypothesis that the group sizes in which birds fly should be larger when they are flying further since they are likely to be at greater risk of predation and increased group size reduces individual risk (Hamilton, 1971).

Finally, I examine the dynamics of disturbed flocks. How do disturbances affect the group sizes in which birds move around and consequently how do they affect flock size and cohesiveness?

5.2 Methods

In the following the term 'flock' refers to aggregations of birds on the ground, whereas the term 'group' refers to parties of birds joining or leaving such flocks.

Data were collected by concentrating on one flock at a time and recording as many of the movements involving flight as possible. These can be classified as:

- (1) groups of sanderlings flying in to join a flock (part-flock arrivals);
- (2) birds flying in to form a new ground flock (whole-flock arrivals, or founding flocks);
- (3) groups of birds leaving a flock (part-flock departures);
- (4) whole flocks taking flight (whole-flock departures); and
- (5) flocks splitting or joining in flight.

The numbers of sanderlings in a flock may also change if flocks split or merge while on the ground: birds may be said to have split from a flock if the distance to the nearest bird in the original flock exceeds 10m. As these events do not involve flights they are not considered here. This means that the record of changes in flock size will not be complete. Observations suggest that ground flocks tend to split more often than they join in that birds may spread out more over a feeding area through

time. As the tide rises, flocks at Redcar Rocks tend to be compacted. Whether this results in the splitting or merging of flocks depends on the local topography. The impression is that splitting predominates as the tide floods areas between ribs of rock which jut out into the sea.

Data were collected both on days devoted solely to these observations and on days when other data were being collected. On the latter days in particular, observations could not be comprehensive and as such may be biased in terms of the flocks watched, the types of events noted, or the conditions under which events were recorded. Where appropriate, analyses are confined to days when more complete data were collected.

Sometimes birds took off but landed within the same flock. This occurred particularly on Coatham Sands where flocks often extended for long distances along the shore-line and on Redcar Rocks when some individuals were forced to move inland a few metres within their flocks due to a rising tide covering their rocky feeding sites. Such movements were not recorded.

The study concentrates on the Redcar Rocks area and on periods when the tide was rising, which was when flights were most frequent.

5.3 Flock Cohesion

In this section flock cohesion is examined by looking at the sizes of groups which leave flocks.

Figure 5.1 and Table 5.1 show the group sizes of departures expressed as proportions of the flocks left. The peaks representing departures of complete flocks are well removed from the rest of the distributions, and account for considerable proportions of the cases when records are weighted by group size. This is true for flocks of all sizes.

It is clear that flock sizes are very flexible in the sense that individuals or small groups of birds do frequently arrive and depart. That is, flock sizes are not constrained in the way that they might be if birds rarely moved in small groups. If there are advantages in remaining within foraging flocks (e.g. in terms of a reduced

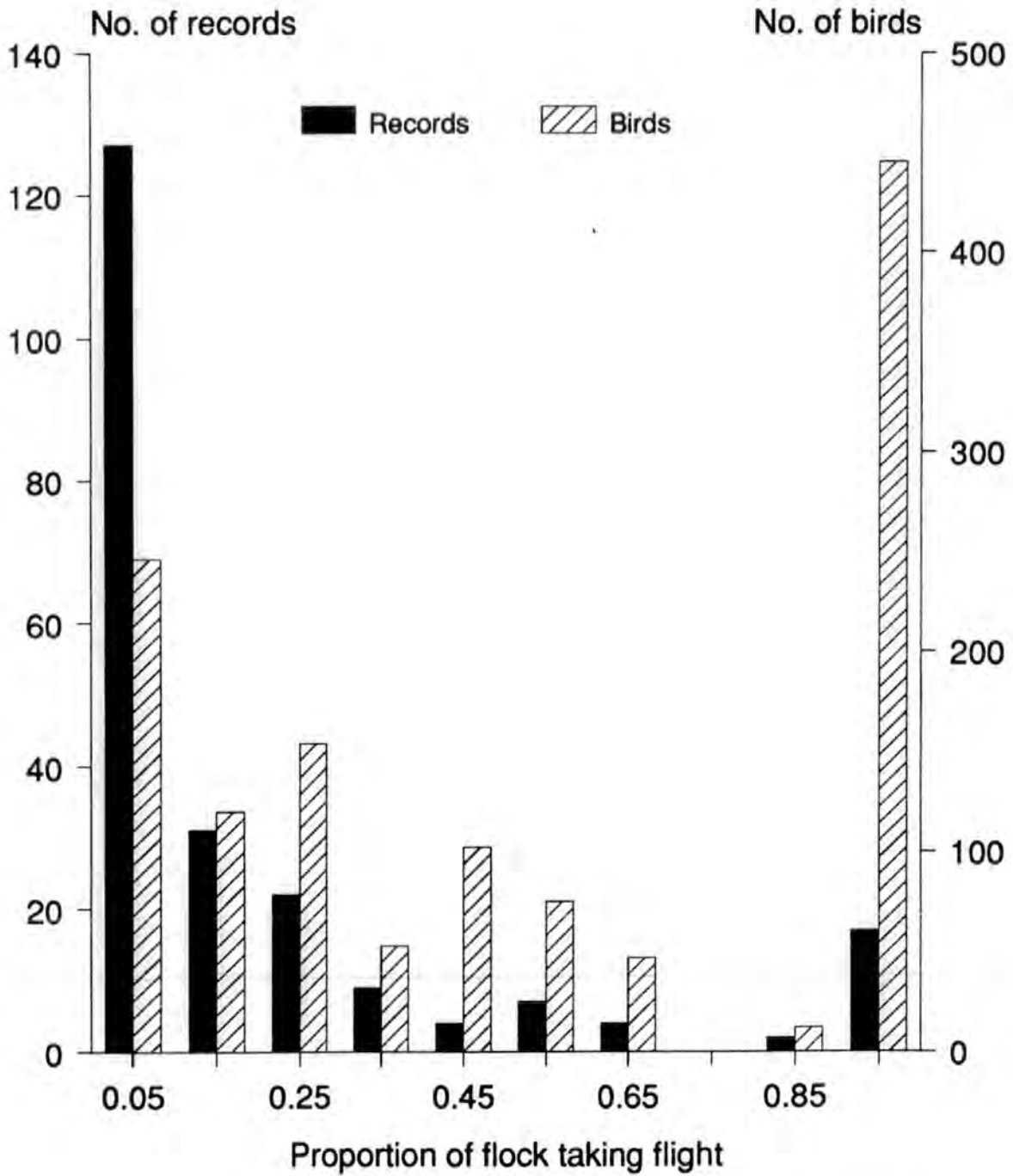


Figure 5.1 — Departure Group Sizes as Proportions of Flock Sizes

Numbers are given in terms of (a) the numbers of groups and (b) the total numbers of birds involved.

Flock size	Departure group size as a					<i>n</i>
	proportion of flock size (midpoint) of flocks					
	0.1	0.3	0.5	0.7	0.9	
11-20	50	14	2	1	9	76
21-30	40	6	1	0	9	56
31-50	43	10	4	1	5	63
51-80	49	4	1	4	4	62
> 80	59	2	3	0	6	70

Table 5.1 — Proportions of Flocks Taking Flight

individual risk of predation) then these are frequently overridden by advantages of moving to other flocks, even if this means doing so singly or in small groups.

The following analysis was carried out in order to determine the likelihood that a bird would take flight given that a certain number of other birds took flight. First, the proportion of birds taking flight, given that at least one took flight, was computed by taking all records where one or more birds left a flock and dividing the sum of all the birds flying up by the sum of all the birds in each flock from which at least one bird departed. Then the proportion of birds taking flight, given that two flew, was computed, and so on.

The graphs shown in Figure 5.2 are summarized in Table 5.2. The table shows the points at which birds are as likely to depart as to stay. For flocks of 11 to 20 birds this point comes where only 1 to 2 birds have left, whereas for flocks of over 50 it comes when about 10 birds have left. The number of birds leaving before birds were equally likely to leave as to stay increased roughly in proportion to flock size. There was no evidence for any fixed cut-off point such that, for example, when 5 birds had flown then all others tended to fly, regardless of flock size. It seems that as a flock gets larger it takes more birds to put the flock to flight: a group of 8 birds might leave a flock of 80 without the rest of the flock taking flight, but they are unlikely to leave a flock of 20 without the rest flying.

Any explanation for the occurrence of the dichotomy between flights involving one or a few birds and flights involving a whole flock must be in terms of the reactions of individuals to the departures of others. The following scenarios, which are not necessarily exclusive, have been put forward to explain apparent coordination within flocks.

- (1) The **chain reaction hypothesis** proposes that each bird makes a decision as to whether or not to leave based on the numbers of other birds which have left. Working on the similar problem of in-flight flock coordination, Davis (1980) suggested that a turn resulted from a threshold number of birds making preliminary movements which indicated that a turn was imminent.
- (2) The **chorus line hypothesis** (Potts, 1984) proposed that the reaction is made to the initiator rather than to neighbours. A number of birds may therefore

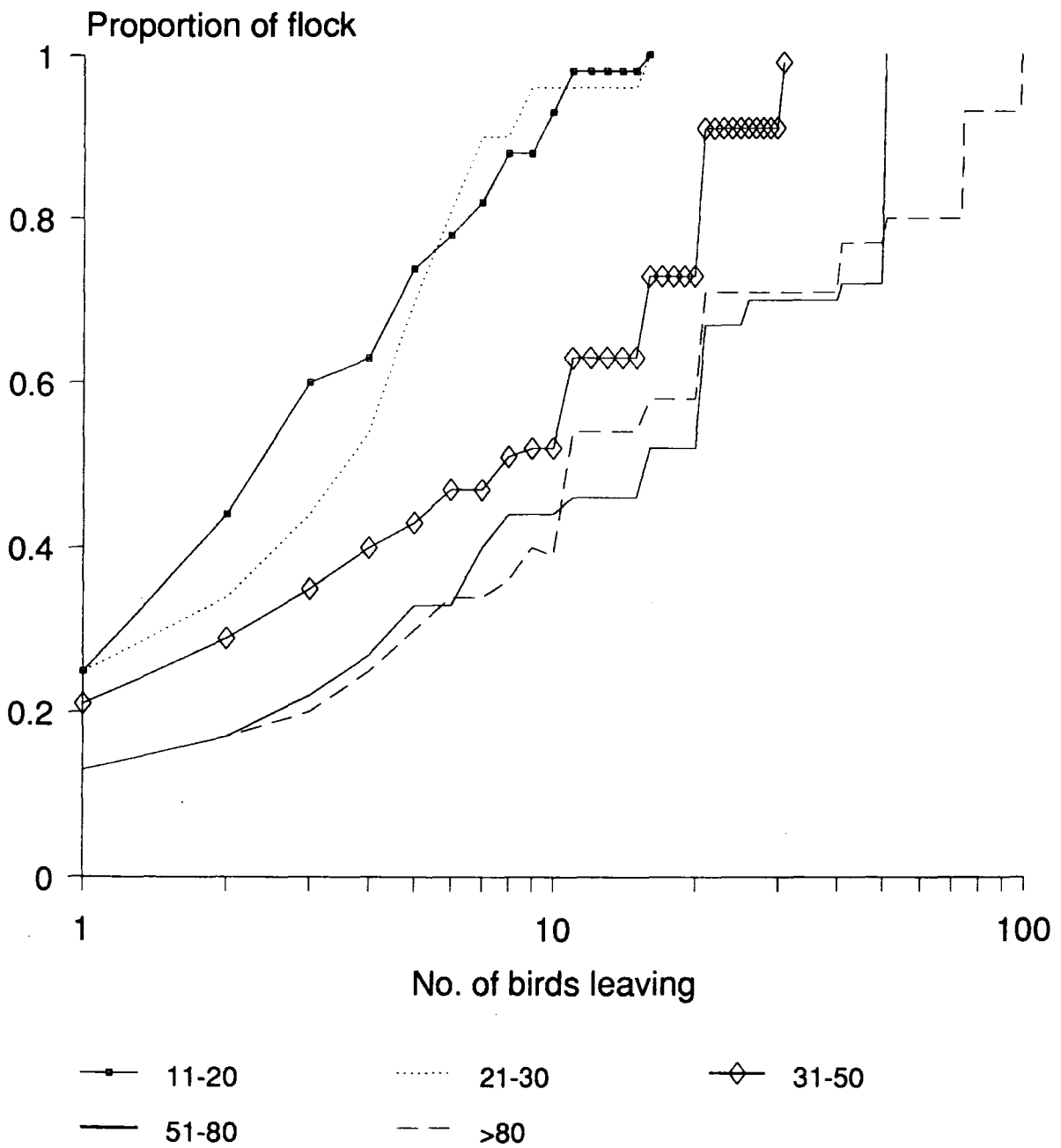


Figure 5.2 — The Proportions of Flocks Taking Flight

The y -axis gives the sum of all birds flying when at least x flock members flew divided by the sum of all birds in flocks from which at least x birds flew.

Initial flock size	% of birds in flock which leave when group sizes given are exceeded		
	50%	75%	90%
11-20	1-2	4-5	8-9
21-30	2-3	4-5	6
31-50	6-7	15-20	15-20
51-80	10-15	40-50	40-50
> 80	9-10	30-40	50-75

Table 5.2 — Proportions of a Flock Taking Flight

As an example, for flock sizes of 11-20 birds are equally likely to leave as to stay when there are more than 1 or 2 birds departing.

decide simultaneously whether to fly, given that one or a few are flying.

The important point here is that the take off of a whole flock is not necessarily the result of a critical number of birds taking off and the remainder responding to this: it may be that each bird decides virtually simultaneously and independently to follow the initiator(s).

5.4 The Build Up and Breakdown of Flocks over Low Water

In this section the question of flock cohesion is examined by describing the pattern of arrivals and departures through time.

Barnard and Thompson (1985) observed changes in the flock sizes of black-headed gulls, lapwings and golden plovers through time. On the basis of these observations they classified flocks into three types (Figure 5.3).

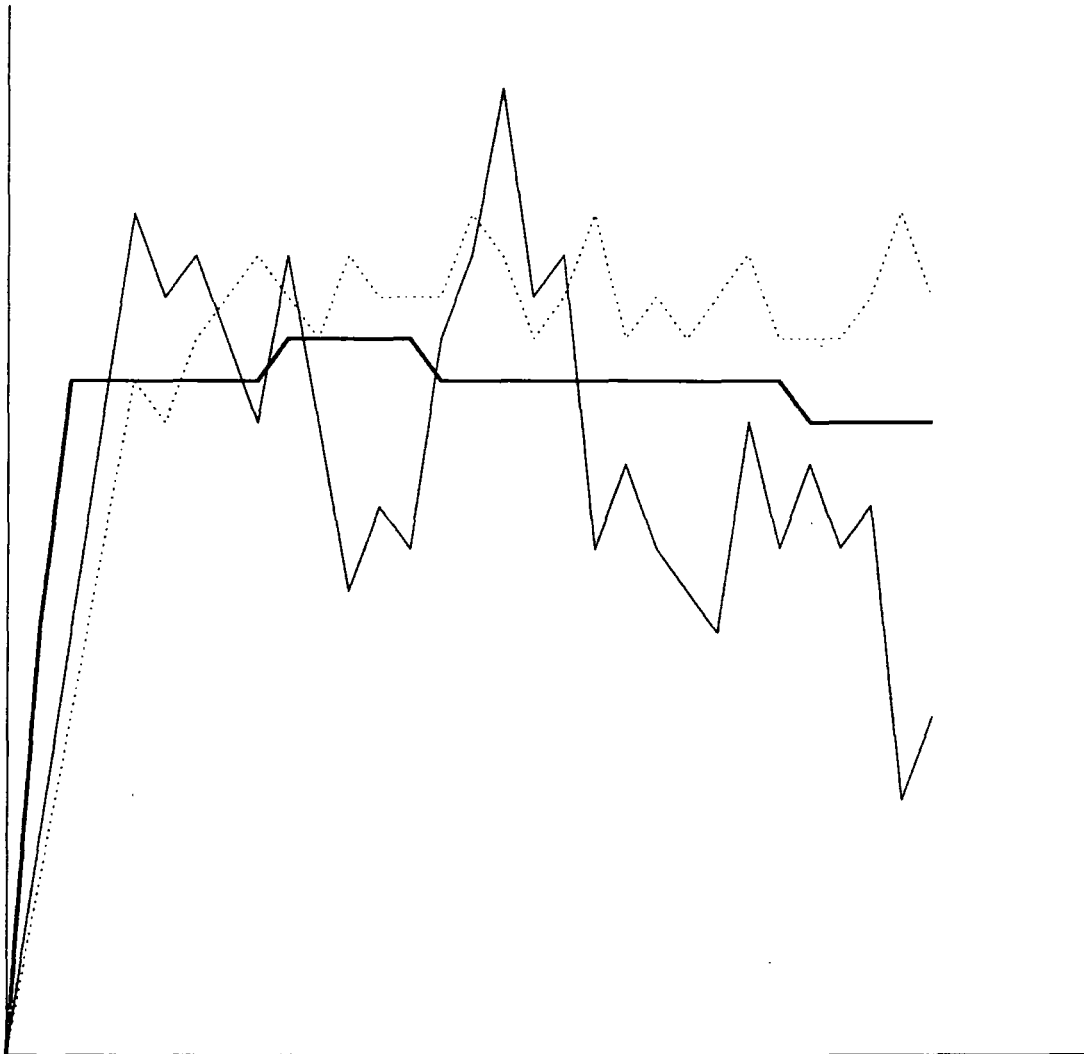
- (1) **Equilibrium flocks.** Flock size fluctuates around a mean level which represents the capacity of the site. As birds continue to arrive there is a compensatory loss of birds.
- (2) **Static flocks.** These remain at a more or less constant size but this does not represent a dynamic equilibrium.
- (3) **Variable flocks.** These undergo large and unpredictable changes in size.

The general pattern of sanderling movements with the tidal cycle was described in Section 2.5.

Figure 5.4 gives an example sequence of flock size changes on a rising tide. At this stage of the tidal cycle arrivals and departures occurred in rapid succession (as indicated by the large number of changes recorded in the 15 minute sample shown). Birds tended to be forced off the rocks and onto the sand. Flock size changes were gradual indicating a tendency to move in small groups.

Because most movements occurred on rising tides, sampling effort was concentrated at such times. This means that much of this chapter will be concerned with flock dynamics on rising tides with other tidal stages being discussed for comparative purposes.

Flock size



Time

— Variable

— Static

..... Equilibrium

Figure 5.3 — Flock Types

Ways in which flock size may change through time, based on Barnard and Thompson (1985).

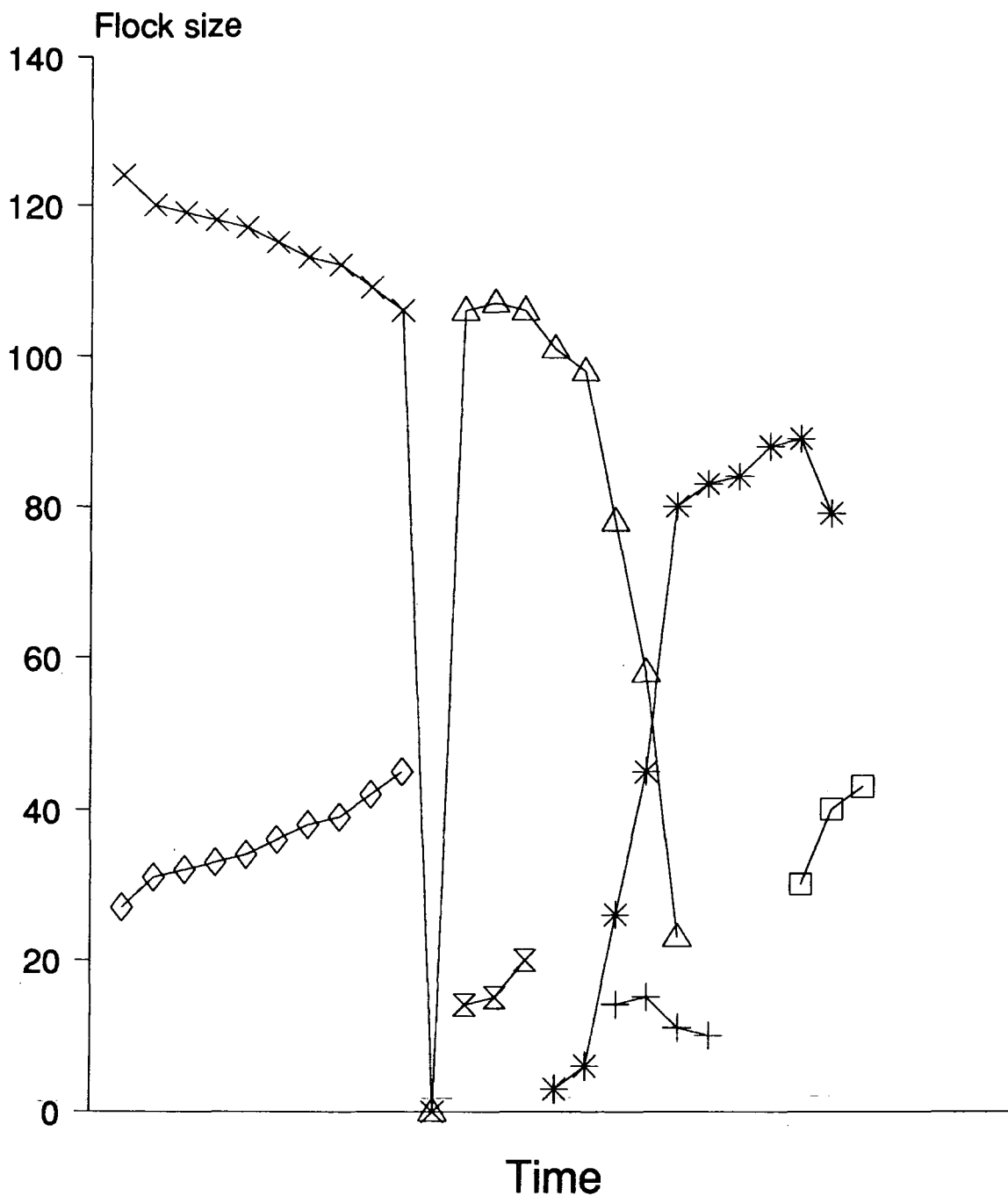


Figure 5.4 — Changes in Flock Sizes through Time on a Rising Tide

The graph gives an example of the changes in size of a number of flocks (each represented by a different symbol) over a 15 minute period on a rising tide. Flock size changes are shown chronologically but the time axis is non-linear.

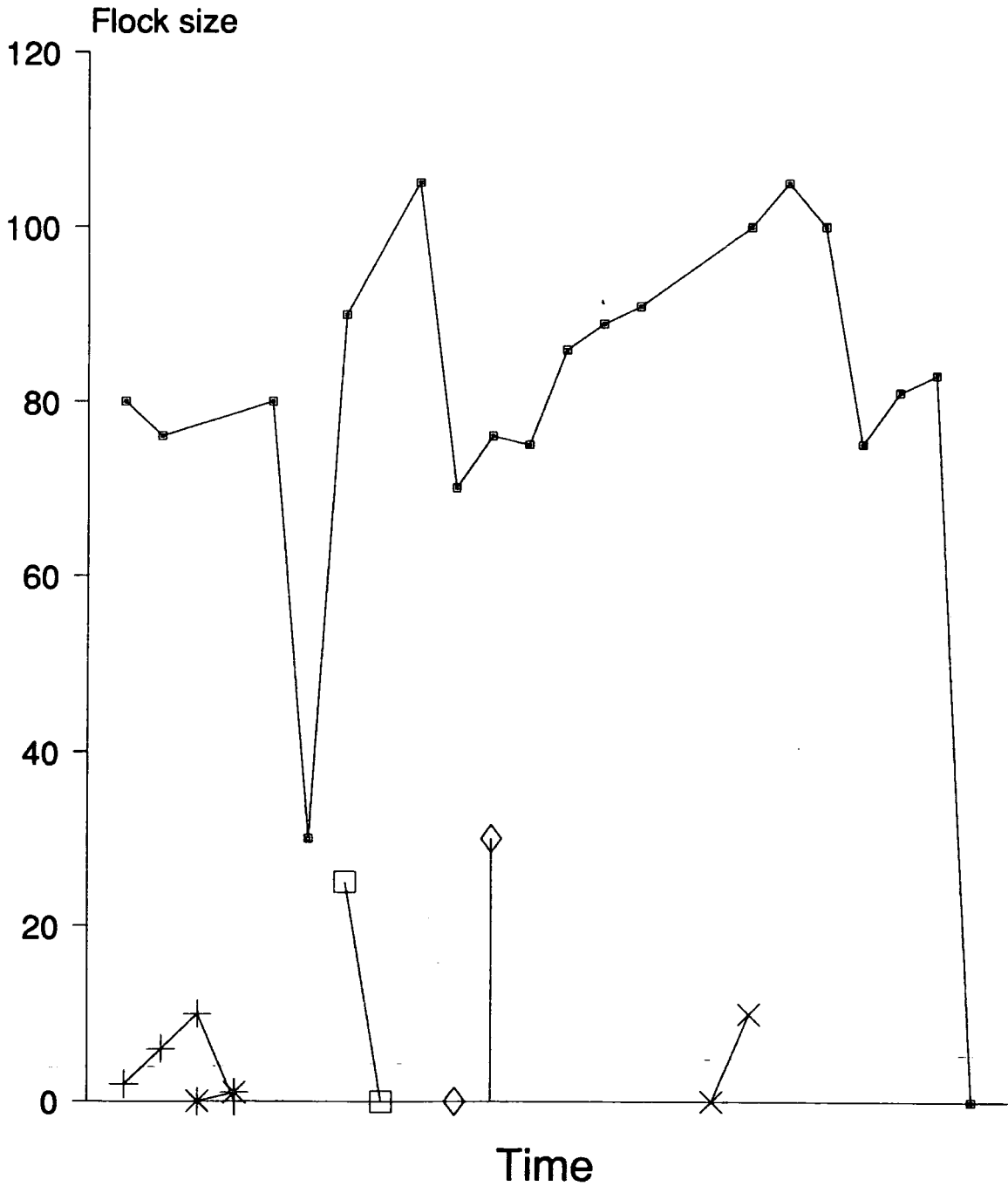


Figure 5.5 — Changes in Flock Size through Time at Low Tide

The graph gives an example of the changes in flock size observed over a 40 minute period at low tide. One main flock was observed but some other flock size changes are shown, each symbol representing a different flock. Flock size changes are shown chronologically but the time axis is non-linear.

Figure 5.5 gives an example sequence of flock size changes over a low tide period. Although the number of flock size changes shown is similar to the number shown in the rising tide example, the sample was of 40 minutes rather than 15. This reflects the lower frequency with which flock size changes occur on falling tides and at low tide. At times, the number of changes taking place is so small that flocks may be considered as Static flocks. This applies particularly when a large proportion of the flock is roosting or preening. Observations showed that such behaviour was most frequent towards low tide outside of the mid-winter period. At such times flocks sometimes remained of approximately the same size for an hour or more.

On the whole, sanderling flocks appear to be best described as Variable flocks. Where flocks are Variable, observed flock size distributions cannot be explained simply in terms of there being favoured flock sizes for different conditions which are achieved either through a balance of arrivals and departures (Equilibrium flocks) or by the appropriate numbers of birds arriving at a site (Static flocks). The distribution results from complex series of arrivals and departures of birds and of splitting and joining of flocks. There is presumably an equilibrium flock size (for a given set of conditions) in the sense that flocks below a certain size are more likely to grow than to shrink and flocks above that size have the reverse tendency, but watching single short-lived flocks is unlikely to reveal this. It could only be shown statistically: this is attempted in the next section.

5.5 The Dynamics of the Build-Up and Breakdown of Flocks

5.5.1 Introduction

The aim of this section is to show how the observed frequency distribution of sanderling flock sizes for a given set of conditions can be explained in terms of the interaction of arrivals and departures, which can in turn be viewed as products of flock size but also of the attractiveness of a site to foragers.

A number of attempts have been made to model flock dynamics. Krebs (1974) presents a graphical model to show how flock size is a consequence of arrival and departure rates. Models of Birth-Immigration-Death-Emigration (BIDE processes) have been applied (mainly to groups with longer persistence times than those considered here) by a number of authors (see references in Pulliam and Caraco,

1984), while Caraco (1980) has developed and tested stochastic models of flock size in juncos.

The key processes of flock dynamics are the arrival rate and the departure rate. The nature of each will depend on the ecology of the particular species and situation studied.

5.5.2 Arrival Rate

This is a measure of the rate at which birds join a flock through time. Arrival rate can be considered to have two components: the site-dependent arrival rate and the flock size-dependent arrival rate. The former represents the attractiveness of a site and the latter represents the differing attractiveness of flocks of different sizes, due to the effects of flock size on feeding and other activities. Krebs (1974), using model birds, found that the rate of joining was a negatively accelerating function of flock size. But in this case birds were attracted to flocks because they indicated profitable patches rather than flocking itself enhancing feeding efficiency. The distinction between the components of arrival rates is therefore unclear. Poysa (1987a) working on teal, *Anas crecca*, also demonstrated the attractiveness of flocks using models. Juncos tended not to join larger flocks because of increased aggression (Caraco, 1980; see below). Barnard and Thompson (1985) found that aspects of both the physical environment and of flock composition affected arrival rates, and that these factors could be related to individual time budgeting and feeding efficiency.

Arrival rate may be constrained by local population size: as a flock increases in size the number of potential arrivals may decline and so arrival rate should decline. Caraco (1980) incorporated this factor into one of his models.

5.5.3 Departure Rate

This may depend on foraging success at the site. Krebs (1974) found that birds left a patch if the interval between captures exceeded a certain time, the 'giving up time.' Flock size had no effect on giving up time so departure rate was taken as being proportional to the number of birds present: the number of birds exceeding their giving up time depends simply on the number present. Caraco (1980) found

that as time allocated to aggression increased (with increased flock size, temperature and food density) then the component of arrival rate dependent on group size decreased and departure rate increased. Barnard and Thompson (1985) found a number of relationships between departure rates and time budgeting, feeding efficiency and risk. For example, lapwings were more likely to depart when kleptoparasitized by gulls. It might be that interference (e.g. Goss-Custard, 1980) reduces food intake such that birds can do better by foraging elsewhere. Departure rate may increase simply because the number of birds present increases: if each bird has an equal probability of leaving a flock at any time then an increase in flock size will result in an increase in the number of birds leaving.

The frequency distribution of flock sizes was found to depend on a number of factors (Chapter 2). In particular, flocks on rocky substrates tended to be much larger than those found on sand. It is also clear from Section 5.4 that there are fewer arrivals and departures over the low water period than there are on rising tides. So the decisions which birds are making about which flocks to join and which to leave appear to differ according to the situation. The dynamics of flocks were therefore considered separately for each situation and then compared to find the factors leading to the differences in flock sizes.

5.5.4 Ratios of Arrivals to Departures

There is presumably an intermediate flock size below which a flock is statistically more likely to grow and above which it is more likely to decrease in numbers. The flock size at which this balance point occurs represents the equilibrium flock size. In order to find where this equilibrium occurred, the ratio of arrivals to departures was expressed first in terms of the number of birds involved (the bird A:D ratio) and then broken down in terms of (1) the number of groups arriving and departing (the group A:D ratio); and (2) the sizes of those groups.

Another way of finding where the balance point lies is to find the **median flock size** joined and left under different conditions. If the median flock size left exceeds that joined then arrivals must predominate in small flocks while departures predominate in large flocks.

5.5.5 Notes on Sampling Methods and Data Interpretation

Arrival and departure rates for flocks of different sizes were not recorded as such. This would have required continuous observation on single flocks for long periods of time. Thus, if there are more cases of arrivals for small flocks as opposed to large flocks, this does not imply that the arrival rate was greater in the former case. This may be so, but it could be that there are simply more records for small flocks because these are more frequent or because of a sampling bias. The main assumption made is that arrivals are as likely to be observed as are departures. Table 5.3 shows that, overall, the number of birds observed arriving is very close to the number observed departing. Rather more arrivals than departures were observed on the rocks on falling and low tides and on the sands (all tidal stages). These are likely to reflect the movement of birds into those sites at those times.

The analyses presented in this section involving group or flock sizes are repeated using values weighted by group size. Thus, a record of a group size of 40 becomes 40 records each representing the group size in which an individual was found. The level of analysis therefore becomes the individual rather than the group. This has the advantage that the decision of one bird to fly in a group of 1 is not equated with the decisions of 40 birds to fly in a group of 40.

Cases where the whole flock departed or a group of birds arrived to form a new flock were not included. The former events were shown in Section 5.3 to be distinct from part-flock departures and the latter represent the foundation of flocks rather than changes in their size.

5.5.6 Correlations between Group Size and Flock Size

The sizes of departing groups were significantly correlated with flock size in all three situations considered (Table 5.4). This was to be expected given that large numbers of birds could not leave small flocks. The low r_s values show that only a small proportion of the variance in departure group size is explained by flock size variation. On rising tides on the rocks there was a significant though only slight decline in the size of arriving groups with increasing flock size; on falling and low tides on the rocks there was no relationship; and on the sands there was a strong positive relationship. It appears that on the sands large flocks attract larger groups

Site; habitat; tidal stage	Arrivals		Departures	
	Groups	Birds	Groups	Birds
Redcar; rocks; rise	142	849	191	846
Redcar; rocks; fall, low	59	725	68	626
Redcar; sands	134	800	71	698
Other	35	371	58	641
Overall	370	2745	388	2811

Table 5.3 — Numbers of Arrivals and Departures Recorded

Situation	Arrivals			Departures		
	r_s	n	p	r_s	n	p
Rocks; rise	-0.162	762	< 0.0005	0.381	549	< 0.0005
Rocks; fall & low	0.089	254	0.079	0.282	338	< 0.0005
Sand	0.672	402	< 0.0005	0.505	518	< 0.0005

Table 5.4 — Correlations between Group Sizes and Flock Sizes

Spearman rank correlation coefficients for the relationships between arrival group sizes and flock sizes joined and between departure group sizes and flock sizes left. Includes only cases where part of a flock arrived or left. All sizes weighted by group size.

Flock size	Arrivals				Departures				A:D ratio	
	Groups		Birds		Groups		Birds		Groups	Birds
	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>		
1-10	2	76	5	246	1	52	2	97	1.46	2.54
11-20	1	36	20	339	1	61	4	142	0.59	1.68
21-30	2	39	19	263	2	46	4	126	0.85	2.09
31-60	2	58	35	459	2	79	17	507	0.73	0.91
61-90	4	38	20	355	3	54	20	357	0.70	0.99
> 90	2	30	5	97	3	47	50	590	0.63	0.16

**Table 5.5 — Arrivals and Departures for Flocks of Different Sizes:
Overall Results**

Arrivals and departures were classified according to the flock size joined or left. In each instance the number of cases and the median group sizes are given, first in terms of the number of groups, and secondly in terms of the total numbers of birds involved. The latter figures were obtained from the former by weighting by group size.

Flock size	Arrivals				Departures				A:D ratio	
	Groups		Birds		Groups		Birds		Groups	Birds
	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>		
1-10	2	19	20	91	1	25	2	49	0.76	1.86
11-20	2	22	20	149	1	38	4	77	0.58	1.94
21-30	2	23	19	127	2	28	3.5	66	0.82	1.92
31-60	2	22	25	118	2	52	7	180	0.42	0.66
61-90	4.5	22	12	186	3	17	6	66	1.29	2.82
> 90	2	28	6	91	2	22	56	111	1.27	0.82

Table 5.6 — Arrivals and Departures for Flocks of Different Sizes on Rocky Areas on Rising Tides.

See legend to Table 5.5.

Flock size	Arrivals				Departures				A:D ratio	
	Groups		Birds		Groups		Birds		Groups	Birds
	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>		
1-10	1.5	8	22	34	1	8	2	12	1.00	2.83
11-20	1	9	50	74	1	4	1	5	2.25	14.80
21-30	1.5	6	30	39	3	4	12	20	1.50	1.95
31-60	1.5	4	20	24	3	9	30	131	0.44	0.18
61-90	2	9	50	78	2	26	50	157	0.35	0.50
> 90	5	1	5	5	3	3	9	13	0.33	0.38

Table 5.7 — Arrivals and Departures for Flocks of Different Sizes on Rocky Areas on Falling and Low Tides

See legend to Table 5.5.

Flock size	Arrivals				Departures				A:D ratio	
	Groups		Birds		Groups		Birds		Groups	Birds
	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>	med	<i>n</i>		
1-10	1	45	4	113	1	11	4	22	4.09	5.14
11-30	3.5	14	10	73	2.5	12	5	46	1.17	1.59
> 30	2	18	50	216	9	32	20	450	0.56	0.48

Table 5.8 — Arrivals and Departures for Flocks of Different Sizes on Sandy Areas on all Tidal Stages

See legend to Table 5.5.

Situation	Arrivals		Departures		<i>U</i>	<i>p</i>
	median	<i>n</i>	med	<i>n</i>		
Overall	2	277	2	339	45862	0.61
Rocks; Rise	2	136	2	182	10779	0.04
Rocks; Fall & Low	2	37	2	54	981	0.88
Sands	2	77	4	55	1504	< 0.005
χ^2	0.8		17.4			
<i>p</i>	0.69		< 0.005			

Table 5.9 — Arrival and Departure Group Sizes

Rows give Mann-Whitney U-tests between arrivals and departures while columns give Kruskal-Wallis ANOVA tests between the three situations.

Situation	Arrivals		Departures		<i>U</i>	<i>p</i>
	med	<i>n</i>	med	<i>n</i>		
Overall	20	1659	15	1819	593692	0.01
Rocks; Rise	15	762	4	549	119319	< 0.005
Rocks; Fall & Low	30	254	30	338	41088	0.36
Sands	15	402	20	518	95962	0.04
χ^2	23.6		322.1			
<i>p</i>	< 0.005		< 0.005			

Table 5.10 — Weighted Arrival and Departure Group Sizes

As Table 5.9 but weighted by group size.

Situation	Arrivals		Departures		<i>U</i>	<i>p</i>
	med	<i>n</i>	med	<i>n</i>		
Overall	28	277	34	339	40123	< 0.005
Rocks; Rise	33.5	136	30.5	182	11358	0.21
Rocks; Fall & Low	26	37	68	54	658	0.01
Sands	7	77	59	55	852	< 0.005
χ^2	45.9		7.7			
<i>p</i>	< 0.005		0.02			

Table 5.11 — Flock Sizes Joined and Left

Rows give Mann-Whitney U-tests between flock sizes joined and those left while columns give Kruskal-Wallis ANOVA tests between the three situations.

Situation	Arrivals		Departures		<i>U</i>	<i>p</i>
	med	<i>n</i>	med	<i>n</i>		
Overall	40	1659	67	1819	385504	< 0.005
Rocks; Rise	35	762	40	549	187692	< 0.005
Rocks; Fall & Low	30	254	63	338	21676	< 0.005
Sands	37.5	402	98	518	26402	< 0.005
χ^2	30.2		230.0			
<i>p</i>	< 0.005		< 0.005			

Table 5.12 — Weighted Flock Sizes Joined and Left

As Table 5.11 but with flock sizes weighted by the sizes of arriving and departing groups.

Situation	Groups		Birds			
	Whole	Part	Propn.	Whole	Part	Propn.
Rocks; rise	6	136	0.04	87	762	0.10
Rocks; fall & low	22	37	0.37	471	254	0.65
Sands	57	77	0.43	398	402	0.50

Table 5.13 — Arrivals of Whole Flocks

Proportions represent the fractions of the total numbers of arrivals which were of complete flocks.

Situation	Groups		Birds			
	Whole	Part	Propn.	Whole	Part	Propn.
Rocks; rise	9	182	0.05	315	549	0.36
Rocks; fall & low	14	54	0.21	288	338	0.46
Sands	16	55	0.23	180	518	0.26

Table 5.14 — Departures of Whole Flocks

Proportions represent the fractions of the total numbers of departures which were of complete flocks.

but that this is not the case in other situations. That arrival group sizes were not necessarily larger in all situations in which flocks were larger implies that the sizes of the groups in which birds move around are not simply a function of foraging flock size. But the difference between situations in the relationship with flock size implies that group sizes are influenced by tidal stage and substrate type.

5.5.7 Arrival: Departure Ratios for Flocks of Different Sizes

Part-flock arrivals and departures were broken down according to the size of the flock joined or left. The bird and flock A:D ratios are given in Tables 5.5–5.8 and the overall median sizes of flocks joined and left are given in Tables 5.11 and 5.12.

Overall, there was a decrease in the ratio of arrivals to departures with increasing flock size, and the median flock size joined was lower than that left. These results were most pronounced when the numbers of birds involved, as opposed to the numbers of groups, were considered. This is because of the correlation between departure group size and flock size (see above).

There were marked differences between tidal stages. On the rocks on rising tides neither the group nor the bird A:D ratio showed a clear trend with flock size. This finding is consistent with the fact that the median flock size joined was similar to the median flock size left. On falling and low tides on the rocks the A:D ratio, in terms of both birds and groups, declined with flock size. This trend is consistent with the fact that the weighted median flock size joined was significantly and appreciably lower than that left.

On the sands the A:D ratios were highest for the smallest flock size class and lowest for the largest. The weighted median flock size joined was again significantly and appreciably smaller than that left. The A:D ratios for birds and for groups changed similarly with flock size as both arrival and departure group sizes were correlated with flock size (see above). The results illustrate the extent to which sand flocks tended to build up through time. Sand flocks were highly mobile in that individuals moved about considerably while foraging, and the flocks were highly transient in that they often moved off soon after forming, either southwards to Marske Sands (Figure 2.2), northwards to Coatham Sands, or back onto the rocks. Therefore flocks did not remain in one place for long enough to act as a focus for incoming

birds, as did flocks on rocky areas, and in fact they were too transient for arrival and departure rates for single flocks to be compared with those of rock flocks.

In situations where part-flock arrivals and departures balance for flocks of all sizes then, provided that there is no imbalance in terms of arriving and departing whole flocks, the frequency distribution of flock sizes should stay approximately the same through time. This should also be true where there is a tendency for small flocks to get larger which is balanced by a tendency for large flocks to get smaller. The changes in the frequency distribution of flock sizes through the tidal cycle could be quantified by taking scan samples of flock sizes at different times.

5.5.8 Arrival and Departure Group Sizes

On rising tides on the rocks, arrival group sizes were significantly greater than departure group sizes, the difference being greater when weighted (Figure 5.9 and 5.10). This suggests that groups were joining in flight; that large arrival groups tended to be from another site or substrate type; that small departure groups tended to be leaving the site or substrate type; or that there was a sampling bias. Observations suggested that the most likely explanation was that birds moving off onto sandy areas moved in small groups. On falling and on low tides there was no difference between sizes of arrival and of departure groups. Departure group sizes were significantly greater than arrival group sizes on the sands, reflecting the tendency of flocks to build up gradually but move off in larger groups.

5.5.9 Comparison of Group Sizes

Arrival group sizes differed significantly between situations only when weighted, those on the rocks on falling and low tides being greater than others. The sizes of the flocks joined were greatest on the rocks on a rising tide, and lowest on the sands. This trend remains significant but is less clear when weighted. Departure group sizes were larger on the sands than on the rocks (where flock sizes were higher), and the flock sizes left also tended to be larger.

Arrival and departure group sizes were lower on rising tides than on falling tides (Tables 5.9–5.10). It may be that feeding conditions are better on the rising tide or that there is more pressure on birds to feed before the high water period than there

is over the falling and low tides when they have a long period of food availability ahead. If so, then birds might be more ready to accept the putatively higher level of risk involved in flying around in small groups at this time in order to make the most of the foraging opportunities. Or it may be that moving in small groups is much more risky on a falling tide: if the available area is increasing then independent movements may leave birds at considerable distances from the main flocks, whereas if the area is decreasing birds have much less risk of becoming isolated. In Section 5.8 it is shown that group size correlates with distance flown. Consistent with this, distances flown were significantly greater on falling and low tides than on rising tides (Section 5.7).

5.5.10 Arrivals and Departures of Whole Flocks

As was to be expected, a number of arrivals of new flocks were recorded in the falling and low tide periods when the rocks become exposed (Table 5.13). These tended to be movements of flocks onto newly exposed areas rather than arrivals of birds at Redcar from high water roosts or feeding areas as the initial arrival of birds at Redcar was only partially covered by the observation periods.

On a rising tide there are very few arrivals and departures of complete flocks. Therefore, while there is a considerable amount of exchange between flocks there are very few new flocks formed (unless by splitting of flocks on the ground) and few flocks take flight. Thus the retreat of birds from the rocks as the tide advances is brought about in a much less coordinated way than is the advance of birds as the tide retreats.

The lesser tendency for birds to move as flocks on rising tides as opposed to falling tides reflects the lower arrival and departure group sizes on the rise (see above).

Birds were more likely to form new flocks when landing on sand (having previously been on either sand or rock) than when landing on rocky areas. Table 5.13 shows that about 50% of birds landing on sand formed new flocks rather than joining existing ones.

5.6 Successive Movements

Sanderling flocks appear to be dynamic, continually gaining and losing birds. This

raises the possibility of there being a balance between arrivals and departures. Do flocks have an equilibrium level about which they fluctuate?

In each of four tidal stages (falling tide, low water, early rising tide and late rising tide) arrivals tended to be followed by more birds joining the same flock, and departures by more departures (Table 5.15). This was particularly marked early on a rising tide when successive events were six times as likely to be the same as they were to be different. Movements were less directional over low-water.

It is clear that, far from there being a balance between arrivals and departures to and from a flock, flocks tend to be either building up or breaking down. This can be understood in terms of the constantly changing feeding conditions: as one area becomes less profitable with respect to another, birds will tend to move from the first to the second. Feeding conditions change most markedly on a rising tide as areas are flooded, and this is when movements are most directional. Whether changing feeding conditions can explain the gradual build-up and break-down of flocks at low water is less clear. It would need to be shown that birds were changing flock sizes or substrate types.

5.7 Choice of Flocks

What choices are birds making when they move between different flocks? Do they choose the largest or the smallest of available flocks, the nearest or the furthest? How are these choices related to movements between habitats? In what circumstances do birds tend to form new flocks? The aim of this section is to address these questions by looking at which of a range of flocks birds tend to join.

Movements between habitats were classified as: (1) no change, predominantly rock-rock ($n = 45$); (2) movement between different types of rocky substrate ($n = 24$), e.g. from ribs of rock to slabs; (3) movement from rock to sand ($n = 40$); and (4) movement from sand to rock ($n = 17$). The following analyses were restricted to undisturbed birds moving within the Redcar site. Because the data tended not to fit normal distributions, medians are given along with means and non-parametric statistics are used. In most cases, differences between tidal stages are looked for and then cases for rising tides are broken down in order to look for

Tidal Stage	Current Event	Last event	
		Arrivals	Departures
Fall	Arrival	9	5
	Departure	6	6
Low	Arrival	14	6
	Departure	8	23
Rise	Arrival	135	18
	Departure	25	156
Late rise	Arrival	18	3
	Departure	9	35

Table 5.15 — Successive Movements

Figures give the number of times that the row movement types were preceded by the column movement types. Only successive movements to or from the same flock are included. Sample sizes for the different tidal stages reflect not only a difference in the numbers of events taking place but also a difference in sampling effort. Comparisons should therefore be restricted to within a tidal stage.

effects of the type of habitat switch. Sample sizes were not sufficient to control for habitat switch when looking for effects of tidal stage.

5.7.1 Flock Size

Four measures were used in assessing choice of flock size. These were: (1) the sizes of the flocks joined; (2) the difference in size between the flock left and that joined; (3) the size of the flock joined ranked among the sizes of all flocks present and divided by the number of flocks; and (4) the tendency to form new flocks as opposed to joining existing ones. For simplicity, cases were not weighted by group size: analysis is therefore at the level of the group.

Table 5.16 shows that the sizes of flocks joined did not differ significantly between tidal stages (see also Section 5.5). However, there were differences in terms of whether birds tended to move to flocks which were smaller than the ones they had left and in terms of the sizes of flocks joined ranked among those flocks present. On both of these measures (Tables 5.17 and 5.18) groups tended to move to smaller flocks on falling and low tides than on rising tides.

Looking at rising tide cases only, the three different measures indicate that the tendency to join larger flocks was strongest when moving between similar rocky substrates or from sand onto rocks and was weakest when moving from rocks onto sand (Tables 5.19, 5.20 and 5.21).

The tendency to form new flocks rather than joining existing ones was not affected by tidal stage (Table 5.22) but was greatest when moving from rocky areas to sandy areas (Table 5.23).

5.7.2 Distance Flown

The distance flown to join a flock was greatest on falling and low tides and was lowest on rising tides (Table 5.24). When this was expressed as a rank of the flocks available, the tendency to join the nearest flock was similar in these two tidal stages and was weakest towards high tide (Table 5.25).

Groups moving from sand onto rocks tended to fly the furthest and showed the weakest tendency to join the nearest available flocks. Among the other cases,

Tidal stage	Mean	S.E.	median	<i>n</i>
Rising tide	42.2	3.7	26	126
Towards high tide	40.5	4.9	42	15
Falling and low tide	34.0	7.3	15.5	22

Table 5.16 — Flock Sizes Joined in Relation to Tidal Stage

Kruskal-Wallis ANOVA, $\chi^2 = 2.73, p = 0.255$.

Tidal stage	Mean	S.E.	median	<i>n</i>
Rising tide	-1.5	6.0	-2.0	120
Falling and low tide	-19.0	9.4	-6.0	14

Table 5.17 — Differences Between Initial and Final Flock Sizes in Relation to Tidal Stage

Kruskal-Wallis ANOVA, $\chi^2 = 1.17, p = 0.556$.

Tidal stage	Mean	S.E.	median	<i>n</i>
Rising tide	0.755	0.027	1.000	123
Towards high tide	0.950	0.050	1.000	10
Falling and low tide	0.550	0.064	0.500	20

Table 5.18 — Flock Sizes Joined (Ranked) in Relation to Tidal Stage

Kruskal-Wallis ANOVA, $\chi^2 = 12.83, p = 0.0016$.

Habitat switch	Mean	S.E.	median	<i>n</i>
Rocky-similar rocky	69.7	6.9	85	40
Rocky-different rocky	17.1	1.9	16	22
Rocky-sandy	16.4	2.5	10	34
Sandy-rocky	56.6	9.4	45	25

Table 5.19 — Flock Sizes Joined in Relation to Switches between Different Habitats on Rising Tides

Kruskal-Wallis ANOVA, $\chi^2 = 35.12, p < 0.00005$.

Habitat Switch	Mean	S.E.	Median	<i>n</i>
Rocky-similar rocky	44.6	9.2	63.0	39
Rocky-different rocky	-6.7	5.6	-4.0	22
Rocky-sandy	-46.9	6.7	-56.0	34
Sandy-rocky	-7.5	17.1	12.0	25

Table 5.20 — Differences between Initial and Final Flock Sizes in Relation to Switches between Different Habitats on Rising Tides

Kruskal-Wallis ANOVA, $\chi^2 = 35.39, p < 0.00005$.

Habitat Switch	Mean	S.E.	Median	<i>n</i>
Rocky-similar rocky	0.860	0.038	1.000	40
Rocky-different rocky	0.609	0.036	0.667	22
Rocky-sandy	0.572	0.067	0.333	33
Sandy-rocky	0.927	0.035	1.000	25

Table 5.21 — Flock Sizes Joined (Ranked) in Relation to Switches between Different Habitats on Rising Tides

Kruskal-Wallis ANOVA, $\chi^2 = 32.56, p < 0.00005$.

Tidal stage	Joined existing flock (<i>n</i>)	Formed new flock (<i>n</i>)
Rising tide	126	25
Towards high tide	15	3
Falling and low tide	22	9

Table 5.22 — Tendency to Form New Flocks in Relation to Tidal Stage

$\chi^2 = 2.70, df = 2, p = 0.259.$

Habitat switch	Joined existing flock (<i>n</i>)	Formed new flock (<i>n</i>)
rocky-similar rocky	52	6
rocky-different rocky	25	2
rocky-sandy	39	22
sandy-rocky	35	3

Table 5.23 — Tendency to Form New Flocks in Relation to Switches between Habitat Types

In this case, all tidal stages were included due to the sample size for rising tide cases alone being small. $\chi^2 = 20.53, df = 3, p = 0.0001.$

Tidal stage	Mean	S.E.	median	<i>n</i>
Rising tide	46.4	5.2	20	126
Towards high tide	89.7	21.0	40	15
Falling and low tide	110.0	22.0	45	22

Table 5.24 — Distances to Flocks Joined in Relation to Tidal Stage

Distances are in metres. Kruskal-Wallis ANOVA, $\chi^2 = 12.78, p = 0.0017$.

Tidal stage	Mean	S.E.	median	<i>n</i>
Rising tide	0.623	0.028	0.500	121
Towards high tide	0.900	0.067	1.000	10
Falling and low tide	0.562	0.078	0.500	20

Table 5.25 — Distances Flown to Flocks Joined (Ranked) in Relation to Tidal Stage

Kruskal-Wallis ANOVA, $\chi^2 = 8.17, p = 0.016$.

Habitat Switch	Mean	S.E.	Median	<i>n</i>
Rocky-similar rocky	25.6	2.3	15	40
Rocky-different rocky	51.4	6.4	65	22
Rocky-sandy	18.1	1.4	15	34
Sandy-rocky	73.8	7.2	60	25

Table 5.26 — Distances to Flocks Joined in Relation to Switches between Different Habitats on Rising Tides

Distances are in metres. Kruskal-Wallis ANOVA, $\chi^2 = 67.9, p = < 0.00005$

Habitat Switch	Mean	S.E.	Median	<i>n</i>
Rocky-similar rocky	0.642	0.042	0.500	40
Rocky-different rocky	0.435	0.032	0.367	22
Rocky-sandy	0.587	0.068	0.667	33
Sandy-rocky	0.809	0.052	1.000	25

Table 5.27 — Distances Flown to Flocks Joined (Ranked) in Relation to Switches between Different Habitats on Rising Tides

Kruskal-Wallis ANOVA, $\chi^2 = 18.20, p = 0.0004$.

Tidal stage	r_s	n	p
Rising tide	0.027	126	0.383
Towards high tide	-0.363	15	0.092
Falling and low tide	0.631	22	0.001

Table 5.28 — Correlations between Distances Flown and Flock Sizes Joined in Relation to Tidal Stage

r_s represents the Spearman rank correlation coefficient.

Tidal stage	r_s	n	p
Rising tide	0.624	121	< 0.0005
Towards high tide	0.667	10	0.018
Falling and low tide	0.564	20	0.005

Table 5.29 — Correlations between Distances Flown (Ranked) and Flock Sizes Joined (Ranked) in Relation to Tidal Stage

r_s represents the Spearman rank correlation coefficient.

Habitat Switch	r_s	n	p
Rocky-similar rocky	-0.395	40	0.006
Rocky-different rocky	0.170	22	0.225
Rocky-sandy	-0.221	34	0.105
Sandy-rocky	0.498	25	0.006

Table 5.30 — Correlations between Distances Flown and Flock Sizes Joined in Relation to Switches between Different Habitats on Rising Tides

Habitat Switch	r_s	n	p
Rocky-similar rocky	0.158	40	0.165
Rocky-different rocky	0.479	22	0.012
Rocky-sandy	0.933	33	< 0.0005
Sandy-rocky	0.151	25	0.235

Table 5.31 — Correlations between Distances Flown (Ranked) and Flock Sizes Joined (Ranked) in Relation to Habitat Switches on Rising Tides

groups moving between different rocky substrates showed the strongest tendency to choose the nearest of available flocks but actually flew the furthest.

5.7.3 Distances Flown and Flock Sizes Joined

When the actual distances flown and flock sizes joined are considered a significant positive correlation is obtained for groups moving on falling and low tides (Table 5.28). However, when ranked values are considered there are significant positive correlations for each period (Table 5.29).

Whether flock size and distance flown correlated varied with the habitat shift (Tables 5.30 and 5.31). In terms of actual distances flown and flock sizes joined, the strongest correlation was obtained for movements from rocky areas onto sandy areas.

5.7.4 Conclusion

In this section it has been shown that choices of substrate type moved to, of distance flown and of flock size joined were all interrelated and that these relationships depended on the tidal cycle. I have concentrated on providing a quantitative description of these relationships as a first step towards understanding them. The next step might be to test specific hypotheses arising from these results under conditions with fewer variables.

5.8 Group Sizes and Distances Flown

Birds which fly singly or in small groups between foraging flocks are presumably taking a risk in exposing themselves to aerial predators. The 'safety in numbers' hypothesis predicts that as a bird's risk increases it should group together more with other birds since individual risk is less in flocks where a predator takes only one (see Chapter 1). If risk increases with distance flown, which determines the time exposed to predators, then birds flying further should fly in larger flocks. It may also be that birds flying further are more at risk because they may be further from the nearest large group.

The following analyses, unless otherwise stated, refer to undisturbed birds moving within the Redcar site. Attempts to transform the data to fit normal distributions

failed and so non-parametric tests are used. Records were weighted by group size such that each individual was considered as one record.

5.8.1 Tidal Stage

Table 5.32 shows that there were similar correlations between group size and distance flown at different stages of the tidal cycle, the exception being late on a rising tide where the correlation was weak. Distances flown were significantly greater on falling and low tides (grouped together) than on rising tides (Mann-Whitney U-test, $U = 2486, n = 262, p = 0.001$).

5.8.2 Habitat Switches

It might be that the relationship between group size and distance flown arises from a relationship between habitat switch and group size (i.e. group sizes being greater for birds moving from sand onto rocks than for any other habitat switches) and between habitat switch and distance flown (i.e. distances flown being greater for sand to rock movements). However, Table 5.33 shows that the relationship applies to different habitat switches. The exception was that no relationship was found for movements between different types of rocky habitats, but this result may be due to the spread of cases across different distances flown being poor.

The data are not sufficient to allow break-down by both habitat switch and tidal stage, but the distribution of the data is such that the correlations given above for each level of one variable are unlikely to have been greatly influenced by confounding effects of the other.

5.8.3 Whole-Flock and Part-Flock Flights

Departures of complete flocks tend to represent larger groups than departures of part of a flock (Section 5.5.10). If whole-flock departure groups flew further than part-flock departures then this would result in a correlation between group size and distance flown. However, there was no difference between the distance flown when a whole flock flew and the distance flown by departing groups (means 217.1 ± 86.8 and 210.0 ± 20.2 respectively; medians 25 and 50; sample sizes 18 and 252; $U = 2292.5, p = 0.359$). Moreover, the correlation between group size and distance

Tidal stage	r_s	n	p
Falling	0.47	15	0.04
Low	0.43	26	0.01
Rising	0.34	188	< 0.005
Late rising	0.25	33	0.08
Overall	0.38	262	< 0.005

Table 5.32 — Correlations Between Group Size and Distance Flown in Different Tidal Stages

Habitat switch	r_s	n	p
Rocky-similar rocky	0.34	60	< 0.005
Rocky-different rocky	0.09	27	0.32
Rocky-sandy	0.35	61	< 0.005
Sandy-rocky	0.33	38	0.02

Table 5.33 — Correlations Between Group Size and Distance Flown for Switches Between Different Habitat Types

flown applies both to part-flock departures ($r_s = 0.36, n = 246, p < 0.0005$) and to whole-flock departures ($r_s = 0.36, n = 17, p = 0.078$).

5.8.4 Between-Site and Within-Site Flights

The number of departures where birds left the Redcar site completely, rather than simply moving within it, was 48 out of a total of 311 departures where the distance flown was recorded. The group sizes in which birds flew to a new site were not significantly different from those in which they moved within a site (means 6.58 ± 1.18 and 6.90 ± 0.91 respectively; medians 3.5 and 2; sample sizes 48 and 262; $U = 5227, p = 0.055$).

If the relationship between group size and distance flown were due to birds choosing to fly with more other birds when they were flying further then this raises the question of how the birds make such a choice. The simplest explanation might be that birds flying short distances make decisions independently, but birds flying longer distances are more likely to wait until another bird makes a move. This nevertheless requires some means by which a follower can determine how far a leader is likely to fly, otherwise birds making only short hops would be followed. It may be that there are cues which can be used in order to determine the distance for which a bird is likely to fly. The direction of take-off may provide some clue as to where the bird is going, and the angle of take-off may be less steep when the bird is making only a short hop. Also it may be that birds flying further are more likely to call when they fly up and so are more likely to be followed. When birds are disturbed, the numbers flying off and the distance flown, are likely to be determined by the immediate risks involved, and so the reasoning given above would not apply and there is no correlation between group size and distance flown.

5.9 The Influence of Disturbance on Flock Dynamics

5.9.1 Introduction

Many flights were initiated by people or dogs approaching the birds. As the following results show, such cases are very different from flights when no disturbance was apparent and so are analysed separately. How sanderlings respond to different types of disturbance will be considered in chapter 7.

	Undisturbed flocks			Disturbed flocks		
	Whole	Part	Propn.	Whole	Part	Propn.
Departures	49	339	0.13	43	38	0.53
Arrivals	93	277	0.25	40	31	0.56

Table 5.34 — Numbers of Part Flock and Whole Flock Movements in Relation to Disturbance

Propn. refers to the number of movements of whole flocks as a proportion of the total numbers of movements.

Groups/Flocks	Undisturbed		Disturbed		<i>U</i>	<i>p</i>
	median	<i>n</i>	median	<i>n</i>		
Part-flock departure group	2	339	10	38	2080	< 0.005
Flock left	34	339	58	38	5015	0.03
Whole-flock departure group	10	49	40	43	565	< 0.005
Part-flock arrival group	2	277	15	31	1406	< 0.005
Flock joined	28	277	30	31	3868	0.36
Founding flock	2	93	30	40	617	< 0.005

Table 5.35 — Comparisons Between Disturbed and Undisturbed Group and Flock Sizes

5.9.2 Departures

When no noticed disturbance was involved the proportion of departures where the whole flock left was less than when disturbance was involved (Table 5.34).

Departure group size was larger after a disturbance, both in the case of part-flock departures and in the case of whole-flock departures (where departure group size equals original flock size). It was found in Section 5.5 that departure group size was larger when the flock left was larger. Consistent with this, flocks left were greater when there was a disturbance than when undisturbed (Table 5.35). This may be a consequence of (a) a bias towards recording departures of or from large flocks when there is a disturbance, or (b) large flocks actually being disturbed more frequently. I suspect that the latter is the case and that dogs, which were the cause of many disturbances, were attracted by large flocks. It may also be that nearby small flocks, chased off by the same disturbances, went unnoticed in the resulting confusion, and so (a) may also be true. However, in these part-flock departure cases, the proportion of the flock taking flight is greater for disturbed birds than for undisturbed birds (medians 0.359 and 0.096 respectively; $U = 6641, p < 0.00005$) Therefore the greater departure group size of disturbed birds is due to a combination of larger flock size and a larger proportion taking flight.

5.9.3 Arrivals

Since departure group sizes were greater following disturbance, arrival group size should also have been greater (unless more flock splits occurred in flight). This is the case (Table 5.35).

On the basis of the hypothesis that individual risk of being taken by a predator decreases with increasing flock size (see Chapter 1), it might be supposed that arrival groups would join larger groups when they had just been subject to disturbance and that they would be less likely to form new flocks. However, the group sizes joined were non-significantly different and the proportion of times that a new flock was formed was in fact greater after disturbance than without disturbance (Table 5.35).

This tendency of groups landing after a disturbance to form new flocks rather than

join existing ones might be a product of their greater group size. That group size may affect the tendency to form a new flock or join an existing one is shown by the fact that groups forming new flocks after a disturbance are significantly larger than those joining other flocks (medians 30 and 15 respectively; sample sizes 40 and 31; $U = 411, p = 0.0149$). This trend was not apparent where there was no disturbance (medians both 2; sample sizes 93 and 277 respectively; $U = 11385, p = 0.0824$).

If disturbance itself caused groups of a given size to be more likely to form new flocks rather than joining existing ones, then part-flock arrival group sizes should be lower after disturbance. In fact they were found to be much larger (see above), and so the finding that birds after disturbance are more likely to form new flocks is attributable to their greater group size at take-off, which counteracts the lower tendency of disturbed birds to form a new flock (for any given group size).

The tendency of large groups to form new flocks may arise: (1) because large groups involve more of the local population leaving less choice, if any, of groups to join; or (2) because if group size is already large it may be disadvantageous, in terms of access to food resources, to join other birds in spite of any advantage in terms of reduced individual risk.

The effect of disturbance is to act against this trend. This may support the safety in numbers hypothesis. However, the finding that the flock sizes joined did not differ significantly between disturbance and non-disturbance cases does not support the hypothesis.

5.9.4 Group Size and Distance Flown

Where birds were disturbed there was no correlation between group size and distance flown ($r_s = 0.02, n = 21, p = 0.46$). Although the sample size was small, the ranges of values were great and so it is reasonable to conclude that there really is no correlation here. Thus, whatever causes undisturbed birds to fly in larger groups when flying further (perhaps the risk from aerial predators) does not affect the group sizes of disturbed birds. This is as expected since disturbed birds do not have the same choices in terms of when and in what group size to fly: whole flocks tend to take flight together.

5.9.5 Distance Flown

Considering movements within the Redcar site only, disturbed birds tended to fly further than undisturbed birds (medians 150m and 40m respectively; sample sizes 262 and 21; $U = 974, p < 0.000005$). It is clear that disturbances were causing birds to move much greater distances between flocks than they would normally fly.

5.10 Summary

Sanderlings tended to take flight either as whole flocks or as singles or groups representing only a small proportion of the flock.

That birds often moved in small groups meant that flock sizes were flexible: decisions to join and leave may have been made by few birds at a time.

As flock size increased, the proportion of the flock which left without the whole flock taking flight increased.

The cohesiveness of flocks varied with the tidal cycle. Flocks at low water, especially those preening and roosting, were best described as static flocks while those on rising tides underwent rapid fluctuations in size.

The sizes of the groups in which birds moved around did not necessarily reflect flock size. Departure group size correlated to a variable degree with the size of the flock left. Arrival group size correlated with flock size joined on the sands.

The relationship between flock size and the ratio of arrivals to departures depended on substrate and tidal range. On the rocks on rising tides the size of the flock did not affect whether it tended to grow or shrink. In contrast, on the rocks on falling and low tides, and on the sands, small flocks were more likely to be joined than left while large flocks were more likely to be left.

As the tide fell and the rocks were exposed, birds tended to move out in relatively large groups, often founding new flocks, but they moved back inland as the tide rose in smaller groups which flew shorter distances and which less often founded new flocks.

In all tidal stages flocks tended to be either building up or breaking down, rather than fluctuating around an equilibrium level. This was most marked on rising tides when feeding conditions were changing most rapidly, and least marked on falling tides.

Movements by groups between habitats often involved changes in flock size. Whether groups chose the largest or the smallest of the available flocks, the nearest or the furthest, was related to the type of habitat moved to and to the tidal stage.

Birds flying further tended to fly in larger groups.

Flock cohesion was greater when flocks were disturbed than at other times.

5.11 Discussion

In this chapter I have concentrated on providing quantitative descriptions of a number of aspects of flock dynamics. Although some interpretations are offered, little is known about how individual behaviour relates to flock dynamics. How does the decision of one bird to fly relate to the decisions of others? Why do birds

sometimes fly singly and sometimes in groups? What determines which flock an individual or group joins or leaves?

Interpretation can be attempted at the level of the particular situation being studied, or generalizations which might apply to other situations and other species might be sought. In this study, tides had a very strong influence on behaviour, affecting the flock sizes joined and left and the group sizes in which sanderlings moved. Choices of flock size can be made only within the constraints imposed by the tides in terms of exposing and flooding feeding areas and changing the profitability of those exposed. The fact that few movements occurred on falling tides and at low tide suggests that birds rarely faced a situation where there would be a net advantage in moving to a different flock.

The influence of the tidal cycle on flock dynamics is illustrated by the finding that birds tended to move out onto the rocks as they were exposed in relatively large groups, often founding new flocks, but moved back inland as the tide rose in smaller groups which flew shorter distances and which less often founded new flocks.

Although the group sizes in which birds moved around varied according to a number of factors, they were often very small. This indicates that flock sizes were very flexible: decisions to join and to leave may have been made by only one or a few birds at a time. It would be interesting to compare levels of flock cohesion in other species. Observations of knot, *Calidris canutus*, suggested a higher level of flock cohesion in this species, but this was not quantified.

If flock cohesion is low then particular individual birds are unlikely to remain with particular other individuals for the whole time that they are present at a feeding site. But individual associations would nevertheless be possible if certain individuals had a greater tendency than others to occur in the same flocks. A study of flock cohesion in a species in which individuals do associate non-randomly, e.g. turnstone, *Arenaria interpres* would be interesting.

It was originally hypothesized that the high levels of disturbance at the study site might be a reason for the low levels of associations between birds (Chapter 4), the reasoning being that as flocks are continually put to flight they will be fragmented

and the local population will be mixed up. The results of this study show that on disturbance flocks tended to fly off either as a whole or as large groups. In contrast most movements where disturbance was not involved tended to be highly independent (in that they involved very small group sizes), and as such were much more likely to be responsible for low levels of association between individuals.

Of the relationships found which may apply to other species and other situations, that between group size and distance flown may be one of the more general. Further tests of this relationship would be interesting.

There is considerable discussion in the literature about optimal flock sizes (e.g. Pulliam and Caraco, 1984). A problem with such models is that individuals may do better by joining a flock which has already reached the optimum level than by joining sub-optimal flocks. Flocks will therefore tend to be larger than the optimum level. Little attention has been given to the question of the group sizes in which birds move between flocks. The models tend to assume that individuals arrive consecutively and that each chooses the best flock to join at the time. The models may be complicated if birds move in groups, as often found in this study. The models are also based on the assumption that flocks will build up until they come to an equilibrium level, whether at the optimum flock size or where the net benefits of joining the flock are equivalent to those of joining other flocks. The concept would seem to have little relevance to a situation such as that on rising tides where flocks are always either building up or breaking down. Under such conditions flocks would be unlikely to be of the same size for significant time periods. It may be more relevant to flocks over low-water.

Chapter VI

Reactions to Disturbance

6.1 Introduction

Foraging flocks of sanderlings are readily put to flight, allowing a quantitative study to be made of those factors affecting their behaviour when they are disturbed, including in particular the presence and behaviour of other birds. Sanderlings often took flight in response to disturbances such as people walking along the beach. It is assumed that birds took flight because of a perceived risk. Behaviour on disturbance is therefore considered as anti-predatory.

A central theme of this chapter is the hypothesis that birds should adjust their behaviour in response to predators according to the costs and benefits involved rather than simply taking flight as soon as a predator is detected. A number of authors have implicitly assumed that the latter is the case (e.g. Siegfried and Underhill, 1975; Kenward, 1978; Barnard, 1980a), and so have taken the finding that birds in larger flocks take off at a greater distance from a predator as evidence for earlier predator detection. As pointed out by Ydenberg and Dill (1986), this reasoning confuses **detection** and **response**. That detection may precede response by a significant length of time has been recognized by some authors (e.g. Lazarus, 1979a; Grieg-Smith, 1981) and has been demonstrated at a neurophysiological level (e.g. Gabrielsen *et al.*, 1977).

Following Ydenberg and Dill (*op. cit.*), two hypotheses may be distinguished: the **perceptual limit hypothesis**, which proposes that the constraint of sighting the predator determines the flight response; and the **economic hypothesis**, which proposes that the flight response is varied according to the costs and benefits of different courses of action. These authors presented a simple graphical model to predict, on the basis of economic considerations, the distance from a predator at which the prey should take flight. This is termed the **flight distance**, (e.g. Altmann, 1958).

The model (Figure 6.1) assumed that at any distance the prey should choose that behaviour with the lowest costs. The cost of flight was modelled as increasing with the distance from the predator, while the cost of remaining decreased. The distance at which the prey should take flight was given by the crossover point of these two curves.

The cost of fleeing was taken to be in terms of lost feeding opportunity. The justification for this cost increasing with distance from the predator was that prey would have longer to wait in hiding before the predator passed. Sanderlings move on to a new feeding site rather than taking cover. Nevertheless, costs might increase with distance if birds flying up at a greater distance from a predator also tended to fly further. That is, there might be higher energetic costs. However, there is no reason to suppose that this is generally true. A more generally applicable reason, given by Ydenberg and Dill, is that birds flying earlier are more likely to fly unnecessarily and will thereby incur extra costs.

The cost of remaining, in terms of capture risk, was taken as increasing exponentially with decreasing distance from the predator. There might also be costs in terms of the time devoted to vigilance, rather than feeding, which would be expected to increase similarly. Another possibility is that there is a critical distance within which the prey is at high risk and outside of which it is at low risk.

Ydenberg and Dill reviewed the evidence for the predictions of the economic hypothesis as it relates to flight distance. I will confine discussion to those aspects most relevant to the situations I studied.

(1) Flight distance should increase with the risk of capture. Risk of capture is likely to increase with an increase in the predator's approach velocity. (It might also increase with the distance to a refuge, e.g. Dill and Houtman, 1989, but it was not clear in my study which, if any, features of the habitat provided such cover). Flight distance has been found to increase with predator approach velocity in a number of species (e.g. Zebra danio, *Brachydanio rerio*, Dill, 1974a), although there are exceptions (e.g. merino sheep, Hutson, 1982). The risk perceived by the prey is likely to vary with its experience. Other things being equal, Dill (1974b) found an increase in flight distance with experience. The fact that other authors have found the opposite effect of experience

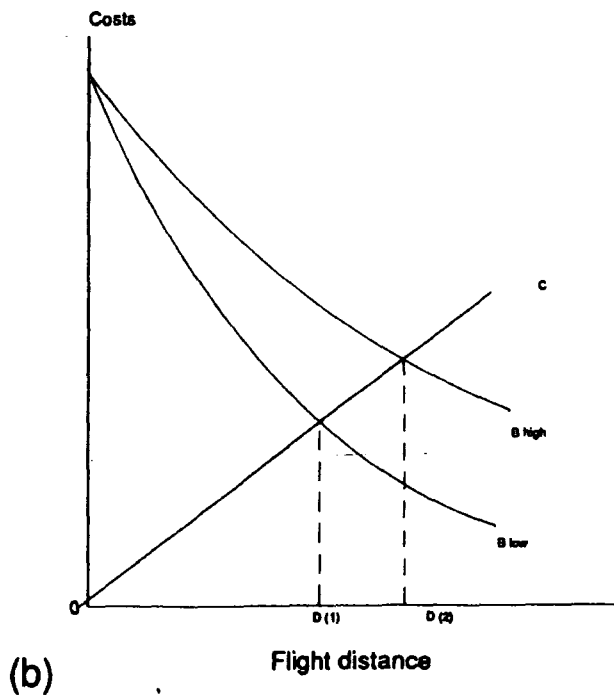
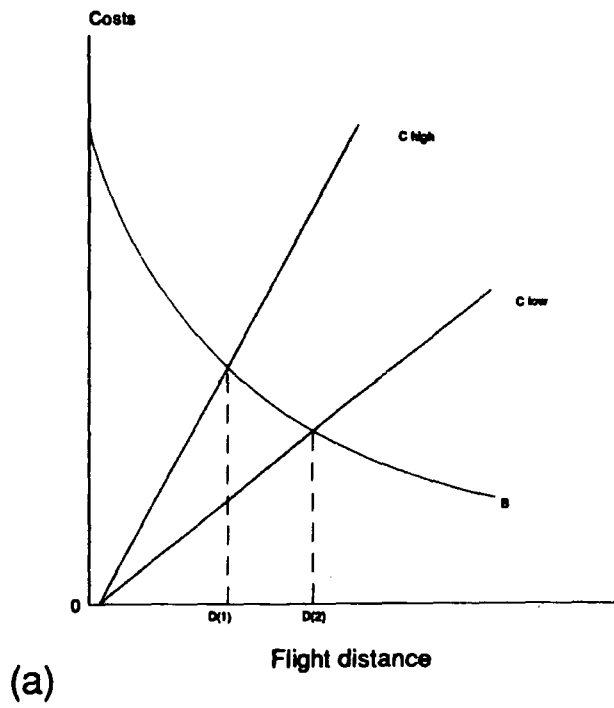


Figure 6.1 — Optimal Flight Distance

(a) As the costs of fleeing increase, the prey should fly at a shorter distance from the predator. (b) An increase in the cost of remaining means that prey should fly earlier. Follows Ydenberg & Dill (1986). Fig. 1. See also (c) (f) overleaf.

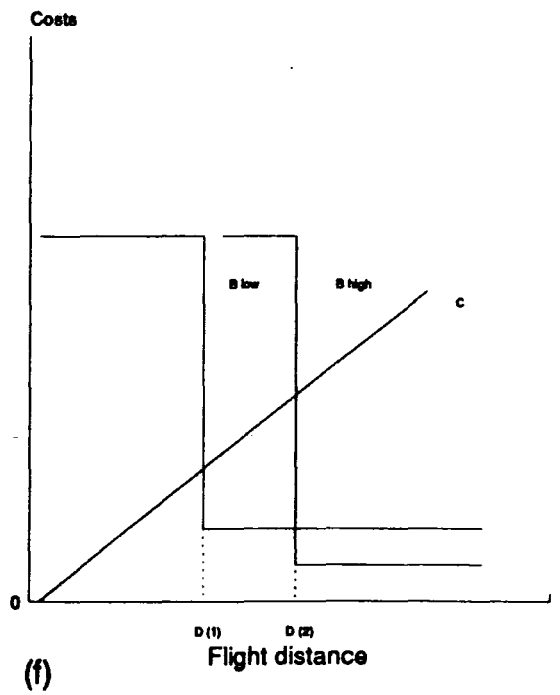
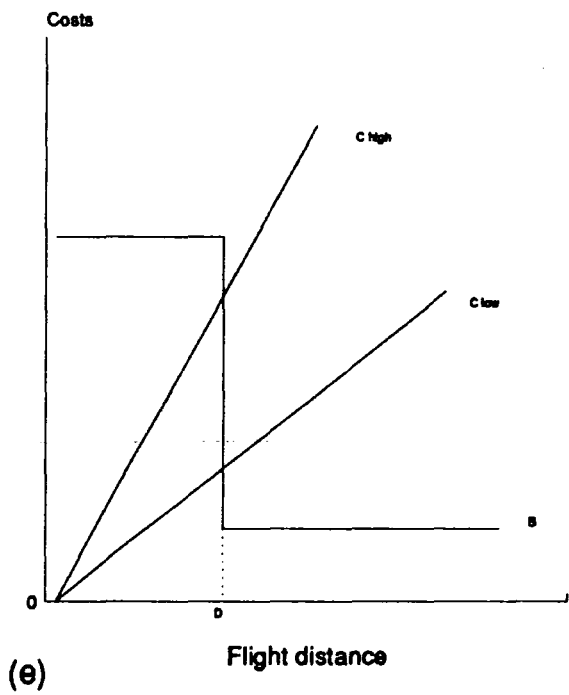
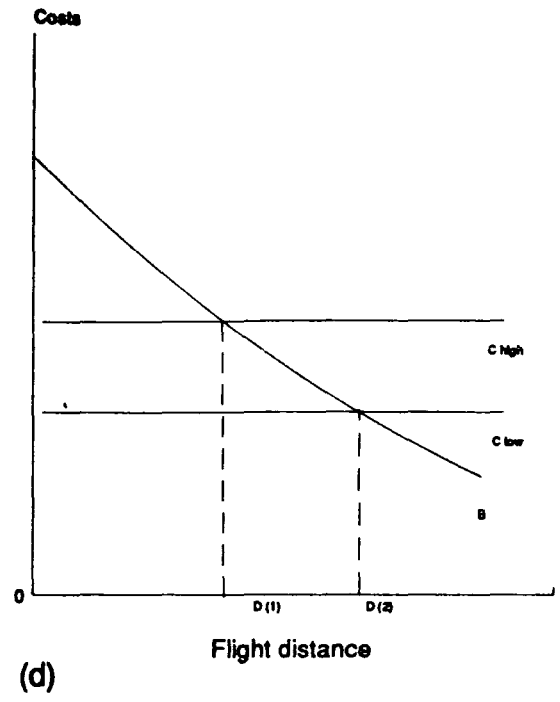
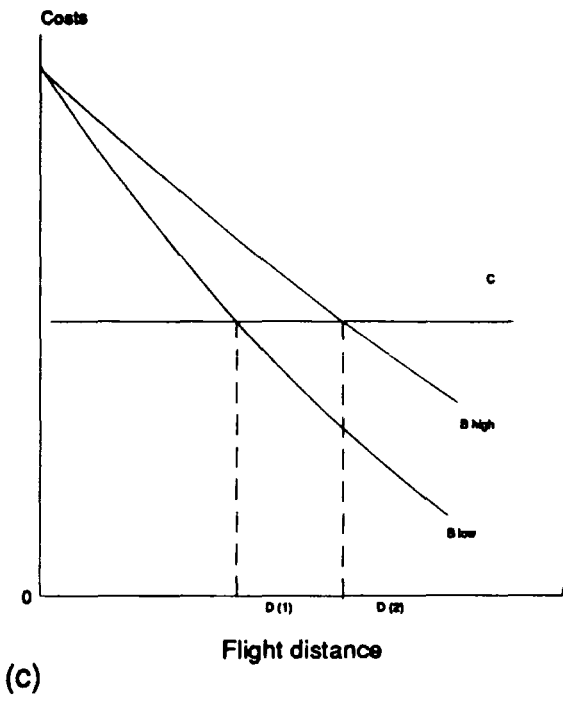


Figure 6.1 cont. (c), (d) Whether costs increase with distance or not does not qualitatively affect the predictions of the model. (e) If the costs of staying approximate more closely to a step function than to an exponential, then flight distance should not vary over a wide range of costs of fleeing but would be determined by the critical distance (f).

only strengthens the case for an economic interpretation: a range of effects is inconsistent with the perceptual limit hypothesis.

(2) Flight distance should decrease with increasing cost of fleeing. The cost of fleeing may be determined by the loss of feeding time. Barnard (1980a) found that house sparrows, *Passer domesticus*, with generally lower feeding rates tended to be the last to fly, continuing feeding for longer than more dominant birds. The birds which were last to fly were therefore the ones with the most to lose. Barnard (1980a, as interpreted by Ydenberg and Dill) also found that flight distance decreased with temperature. Since there was no relationship between temperature and vigilance, the decrease in flight distance could not be accounted for in terms of different levels of awareness.

In sanderlings, costs of flight may vary not only with current foraging profitability and the state of the tide (which is important in determining the latter) but also with the amount the bird has eaten; the amount it is likely to be able to eat over the subsequent few hours; and the amount of energy it will require over this period. Sanderlings would be expected to feed more towards dusk, after which feeding is likely to be reduced. The costs of fleeing may therefore be high at this time.

(3) Flight distance should vary with flock size. Flock size may act in a number of different ways, making predictions difficult. Greater numbers may be found on more profitable patches (e.g. Krebs, 1974) which, according to prediction (2), they should be less-ready to leave. Corporate vigilance increases with group size (e.g. Caraco, 1979a,b), so predators should be sighted earlier (although this should not necessarily affect the flight distance, according to the economic hypothesis). If individual risk is diluted as flock size increases (Hamilton 1971) then by prediction (1) birds should take flight later.

A range of different relationships has been found between flight distance and group size. Owens (1977) found that larger flocks of brent geese, *Branta bernicla*, had greater flight distances. Grieg-Smith (1981), working on ground doves, *Geopelia striata*, found that flight distance increased significantly with flock size for flock sizes of more than three. He suggested that this might be due to the increased chance of there being a particularly nervous individual present.

However, in flocks of up to three the trend was in the opposite direction. It might be, therefore, that the net benefits of foraging in a flock for ground doves reach an optimum at flock sizes of about three. The fact that intervals between departures increased up to flock sizes of four is consistent with the idea that birds are less ready to leave flocks of this size.

The perceptual limit hypothesis, which predicts that birds should take flight as soon as a predator is sighted, predicts that risk of capture and cost of fleeing should have no effect on flight distance. But flight distance should increase with vigilance and the factor most widely thought to affect vigilance is group size (see Chapter 5). Barnard (1980a) calculated the corporate vigilance of a flock as the product of the number of birds in a flock and individual vigilance. Corporate vigilance did not increase with flock size, and so the prediction of the perceptual limit hypothesis that there should consequently be no effect of flock size on flight distance was upheld.

Several studies on mixed-species flocks have also considered the effects of vigilance levels on flight distances. The presence of heterospecifics may have a marked effect on flight distances. Byrkjedal and Kalas (1983) found that dunlin, *Calidris alpina*, took flight more readily when in flocks with golden plovers, *Pluvialis aprinaria*, than when alone, while Thompson and Thompson (1985; see also Barnard and Thompson, 1985) found that both species had longer flight distances when together. Dunlin always took off after golden plovers. This was interpreted as evidence for golden plovers being more vigilant.

While acknowledging that flight responses should not necessarily be equated with predator detection, Barnard and Thompson (1985) used the assumption that birds would take flight as soon as a predator was sighted in order to predict the 'responsiveness' of flocks of lapwings and golden plovers from their levels of corporate vigilance in flocks or subflocks of different sizes, a subflock being the number of birds of a particular species in a mixed flock. They employed a standard alarm (the brief appearance of a person at 40m from the nearest bird) and measured individual responsiveness as the probability of an individual of a species responding to an alarm. Aspects of flock composition which influenced subflock vigilance also influenced individual responsiveness to the alarm. The implication seems to

be that birds make their own decisions about whether to fly based on their own levels of vigilance: if they flew in response to other birds flying, however small the number of such birds, then the relationship between vigilance levels and numbers flying would be much less clear. It might be that some birds which had missed the alarm stimulus flew up with those that had, but if so this effect was not great enough to obscure the relationship.

Barnard and Thompson (1985) also concluded that gulls had an 'early warning' effect. In mixed flocks of lapwings, golden plovers and gulls the latter responded first to the alarm stimulus and the other species followed, their response times being significantly shorter in the presence of the gulls.

It may be that in these cases the perceptual constraints hypothesis is indeed a better predictor of response times than is the economic hypothesis. But the findings might be interpreted in economic terms by arguing that the alarm signal was always first detected inside the maximum distance at which flight is better than remaining. Therefore the economic hypothesis is not necessarily contradicted. Furthermore, it remains a possibility that the different responses result not from different vigilance levels in the presence of other species, but from changes in the costs of fleeing as opposed to remaining. As Stinson (1988) points out, in the dunlin-golden plover case **both** species fly more readily when in mixed species flocks, whereas the vigilance hypothesis predicts only that dunlin should fly earlier because they are taking advantage of the vigilance of the other species. Implicitly using an economic argument, Stinson suggested that golden plovers may be more ready to give up feeding when in the presence of dunlin, perhaps because of reduced profitability. If associating with individuals of the more 'flighty' species has advantages (whether to do with predator detection or not), then following their movements may be favoured. Dunlin may gain from being with golden plovers and so may leave when they do.

A complicating factor is that birds flying up late may be responding not to an alarm stimulus but to the flight of others. Where the costs of mistakes are high, it may be beneficial to fly when others do. The theoretical basis for reducing individual vigilance in flocks assumes that birds can rely on the responses of others which might have seen a predator first as being appropriate. Thus birds may be selected

to fly when others do, even if this involves paying the costs of a few unnecessary flights.

Barnard and Thompson (1985) found good evidence to suggest that plovers used the flights of gulls in deciding whether or not to take flight, and further evidence for the 'early warning' hypothesis comes from the increased flight distances of plovers in flocks with gulls. But again the situation may be more complex than a simple consideration of vigilance levels would suggest.

Among the response parameters which might be measured, flight distance and Barnard and Thompson's (1985) 'responsiveness' have been mentioned. In some species flight responses are preceded by signs that a predator has been detected. The ground doves studied by Grieg-Smith (1981) 'froze' as approached. Lazarus (1979a) found different levels of response in caged birds alarmed by the appearance of a light. An increase in flock size resulted in a relative increase in orientation to the light as opposed to flight responses, as predicted by the hypothesised dilution of risk in large flocks (Hamilton, 1971).

Economic reasoning might also be applied in predicting how far birds should fly before resettling. That birds should weigh up the costs and benefits of flying further can be contrasted with the hypothesis that birds should simply fly until they judge the risks to be small. The latter hypothesis could be seen as the counterpart of the hypothesis that birds should fly as soon as they become aware of danger. Variance in distances flown which cannot be accounted for in terms of risk might be interpretable in economic terms.

If the costs and benefits of fleeing are such that a bird decides to flee earlier (i.e. the flight distance is large), then the same factors may favour prolonged flight before settling. Grieg-Smith (1981) found a positive correlation between flight distance and distance flown before settling for doves disturbed when alone.

Natural avian predators were uncommon at the study site. Only one peregrine and one merlin were seen at Redcar, although a kestrel was sometimes present at the north end of Coatham Sands. The reactions of the birds make it obvious when an aerial predator is present even if it is not seen, so it is unlikely that any were

missed. All birds present fly up together in one dense flock and gain height rapidly in an apparent attempt to rise above the predator.

Disturbances by people walking along the beach, by dogs, and by horses and motorbikes being ridden along the beach were common. These caused birds to fly up and re-land further away.

Clearly the response to such disturbances is qualitatively very different from that to aerial predators, but the question remains as to whether the birds are responding to the disturbances as threats, or whether they are simply moving out of the way of something which is taking over their foraging area. The hypotheses considered in this study are relevant to only the first possibility. Although aerial predation is likely to be a more significant selective pressure on sanderlings than terrestrial predation, the birds may nevertheless have been selected to fly away from ground predators, such as foxes, which may be particularly important at roost sites and on their breeding grounds. Therefore we would expect dogs to be treated as threats, and they may in fact represent a real threat as they may repeatedly chase sanderlings and have on occasions been close to catching them. It is difficult to say how humans are perceived. We would need to know the 'rules of thumb' by which the birds identify threats and how much discrimination between different kinds of threats is made.

There are a number of studies of reactions to predators in which humans have been used as the 'predator' (e.g. Barnard, 1980a; Rand, 1964; Kitchen, 1974; Greig-Smith, 1981; Barnard and Thompson, 1985).

In this chapter I investigate the dependence of behaviour in response to disturbance on a number of factors including the presence and behaviour of other birds. Two approaches were taken. Of these, carrying out experimental disturbances proved to be more fruitful than observing disturbances caused by the activities of others. Hypotheses based on the assumption that reactions are varied according to the costs and benefits of different courses of action were more successful than those based on the assumption that birds should take flight as soon as a predator is sighted.

6.2 Observed Disturbances

6.2.1 Methods

In the following the term 'disturbance' will be used to refer to a person, animal or vehicle causing birds to take flight. When a disturbance was seen to approach a flock, the following variables were recorded.

- (1) The number of people, dogs, horses, or vehicles involved.
- (2) The speed of approach of the disturbance (ranked on a scale of 1–3).
- (3) The substrate and the feeding methods or other activities being performed by the flock.
- (4) Flock size.
- (5) Distances to nearest neighbours for each bird in the flock (allowing computation of the mean and standard deviation).
- (6) The reaction of the flock. Where the flock split on flying, the largest group of sanderlings was followed.
 - (i) Alert distance, i.e. the distance at which the first birds became alert.
 - (ii) Run reaction distance, i.e. the distance at which the first birds started to run along.
 - (iii) Flight reaction distance, i.e. the distance at which the first birds started to fly.
 - (iv) Distance run, i.e. the distance run before stopping.
 - (v) Distance flown, i.e. the distance flown before settling.

The time of day, the site, and the tidal conditions were also noted.

The alert distance, the run reaction distance and the distance run proved difficult to record accurately by direct observation, and so the analysis concentrates on the flight reaction distance and on the distance flown. The following analyses are based on a sample of 155 disturbances. Because of the difficulty of recording all variables in very short time periods there may be a bias towards recording less complex events. The low sample sizes reflect both this difficulty and the fact that few disturbances were observed on each day.

6.2.2 Differences Between Sites

Observations were made at three sites: Redcar (including rocky and sandy habitats), Coatham Sands, and Seaton Sands. Significant differences in behaviour were found between sites (Table 6.1). Distances run were lowest at Redcar perhaps simply reflecting the difficulty of running over rocks. When birds at this site moved more than a very short distance they moved off an area completely by flying. The distance at which birds started to fly was lowest at Coatham. The distance for which birds flew was markedly greater at Redcar than at the other sites, and this may reflect the importance of the distance to the nearest suitable rocky feeding site as opposed to simply keeping out of range of a predator. There may be confounding factors, notably flock size, but sample sizes and the distribution of the data ruled out multivariate analyses.

6.2.3 Effects of Flock Size

Flock size does not seem to have a marked effect on responses (Table 6.2). The only significant result obtained was that the distance flown declined with increasing flock size at Coatham and at Seaton. The result could be interpreted as being consistent with the hypothesis that individual risk is reduced in flocks (Hamilton, 1971). Again, it may be that habitat constraints had an over-riding effect at Redcar.

6.2.4 Approach Speed

The speed with which a disturbance approached had no significant effect on either flight reaction distance or distance flown (Table 6.3). The responses therefore did not provide any evidence for the birds having perceived the risk to be any greater when they were approached more rapidly.

It might be that approach speed is important only in the case of aerial predation. Once a sanderling is in flight then it is no longer in danger from a terrestrial predator, whatever the speed of approach of the threat. The decision to take off may be a response to the distance of the threat and not of the perceived time that the bird has in which to escape.

Site	Flock size	Distance run	Flight reaction distance	Distance flown	<i>n</i>
Redcar	59.5	20	20	93	64
Coatham	24.0	40	11	30	33
Seaton	13.0	35	25	40	37
χ^2	14.27	9.63	17.40	12.13	
<i>p</i>	0.0008	0.008	0.0002	0.003	

Table 6.1 — Differences Between Sites

Figures give medians for each site. Distances are in metres. Probabilities were obtained using Kruskal-Wallis Analyses of Variance.

Response	Site	r_s	<i>n</i>	<i>p</i>
Flight Reaction Distance	Redcar	0.061	46	0.345
	Seaton & Coatham	-0.131	24	0.270
Distance flown	Redcar	-0.094	41	0.281
	Seaton & Coatham	-0.360	23	0.046

Table 6.2 — Effects of Flock Size

The table gives Spearman rank correlation coefficients of the response parameters with flock sizes at different sites.

Response	Site	<i>n</i>	χ^2	<i>p</i>
Flight reaction distance	Redcar	49	0.775	0.679
	Coatham & Seaton	24	3.584	0.167
Distance flown	Redcar	44	2.171	0.338
	Coatham & Seaton	21	1.458	0.482

Table 6.3 — Effects of Approach Speed

χ^2 values and probabilities were obtained using Kruskal-Wallis Analysis of Variance with three categories of approach speeds.

6.2.5 Conclusion

It proved more difficult than anticipated to collect sufficient detailed data in order to carry out the multivariate analyses necessary to address properly the factors affecting responses to disturbances. Only a few tentative inferences could be drawn and these do not allow a proper discussion at this stage.

6.3 Experimental Disturbances

6.3.1 Methods

Because of the large number of variables involved, an attempt was made to standardize the conditions under which data were recorded by carrying out experimental disturbances.

There were a number of reasons for choosing to carry out these experiments on Coatham Sands.

- (1) It is a linear habitat: birds are often found along the tide edge and so distances flown can be recorded more accurately.
- (2) Distances at which birds see approaching danger and react to it will not be affected by obstacles such as rocky promontories.
- (3) Distances to which birds fly should not be affected as much by habitat variability as they were at Redcar (Section 6.2).

I walked along Coatham Sands at a constant speed keeping about 2m in from the wave front and recording the following.

- (1) The distance between myself and the nearest sanderling.
- (2) The numbers of birds in each of five approximately judged 10m bands stretching along the tide edge beyond, but including, the nearest bird.
- (3) The distance between myself and the nearest bird at which the birds first reacted by (i) standing alert; (ii) running away; and (iii) flying away.
- (4) The numbers of birds from each of the 10m bands which flew.
- (5) The distance flown by the majority of birds from each of the 10m bands.
- (6) The direction flown by the majority of birds from each of the 10m bands.
- (7) The distances to the nearest birds in front of and behind me after birds had settled.

I also noted the time; tidal conditions; site; weather; angle and height of the sun; the time since the birds had last been disturbed; the direction of my approach; my speed of approach; and the feeding methods of the birds.

It was decided to record the numbers of birds in 10m bands rather than to try to record flock sizes because birds were often spread irregularly along Coatham Sands making it difficult to define flocks: small movements of individuals often caused what had been defined as a flock to split or for what had been defined as two flocks to merge. Dividing the birds according to their distances beyond the nearest bird meant that the behaviour of birds at different distances was recorded separately.

It was often difficult to judge how far a bird had run in response to disturbance as opposed to how far it had run in the course of foraging, so priority was given to recording distances flown.

Because other species were avoided where possible and were present only infrequently and in small numbers, this factor did not need to be considered.

Approaches were standardized as much as possible, approach speed being kept constant. The main variable was the number of birds approached.

My ability to estimate distance was regularly checked by pacing out the distance between marks in the sand. A continuous time record was made of each approach. Knowing my pace length and the number of paces per second, the distance moved in a certain time interval could be calculated and checked against my estimates of the distance to the nearest bird made at intervals during the approach.

In an attempt to make detailed and accurate records of the behaviour of individuals, use of a video camera was tried. However, with a field of view large enough to follow all movements, the resolution became inadequate.

In view of the frequency with which people walk along this stretch of beach, the disturbance caused by these experiments should not have had a significant effect on the birds' opportunity to feed.

Most variables were distance measurements. These were necessarily approximations so distance classes were used. This meant that measurement scales tended to be ordinal and that non-parametric tests were used.

6.3.2 Flight Reaction Distances and Numbers of Birds Present

There were no relationships of any appreciable magnitude between the flight reaction distance of birds in the first 10m band and either the numbers of birds in each of the other bands or the total numbers of birds (Table 6.4).

As with the birds in the first 10m band, there was no correlation between the numbers of birds in the second 10m band and the flight reaction distance ($r_s = -0.13, n = 70, p = 0.14$). A similar analysis of the behaviour of birds from the third band could not be carried out because of the much smaller number of cases where birds from this band flew.

These results do not provide any evidence for there being a relationship between the numbers of birds present and the distance from a disturbance at which the nearest birds take flight. Therefore, there is no evidence for the prediction of the economic hypothesis that variation in the numbers of other birds present affects responses through changing the costs and benefits of staying as opposed to flying. A proper test of the perceptual limit hypothesis would require the relationship between flock size and vigilance to be known. This was difficult to study for birds feeding on sandy areas (see Chapter 7).

6.3.3 Numbers Flying and the Distance Beyond the Nearest Bird

Table 6.5 shows that as the distance beyond the nearest bird to a disturbance increased, fewer birds flew. This represents a decrease in the number of cases where flying occurred rather than a decrease in group size of those flying. The latter was not examined because the birds in a band were frequently recorded as either all flying or as not flying at all and this was often an approximation. Only in 6 out of 198 cases (where 1 or more birds flew) did birds from the first band not fly while birds from further back did. Birds from the second 10m band were as likely to fly as not to, but birds further back were twice as likely to stay as to fly. So although the number of times that birds flew, as opposed to staying, decreased rapidly with distance from the front of the flock, the lack of a significant difference between bands three, four and five in the numbers flying and staying shows that if birds from the third band flew then birds from the fourth and fifth also tended to fly. It may be that the costs and benefits of staying as opposed to leaving were

Band <i>n</i>	Correlation with nos. in band <i>n</i>		Correlation with nos. up to band <i>n</i>		<i>n</i>
	<i>r_s</i>	<i>p</i>	<i>r_s</i>	<i>p</i>	
1	-0.03	0.33	-0.03	0.33	192
2	-0.03	0.33	-0.02	0.40	191
3	-0.02	0.41	-0.04	0.29	189
4	-0.11	0.08	-0.06	0.20	177
5	-0.16	0.02	-0.09	0.13	174

Table 6.4 — Reaction Distances of Birds in the First Band in Relation to Numbers Present

The table gives Spearman rank correlations between reaction distances and (i) the numbers of birds in each other band, and (ii) the total numbers of birds up to and including each band in turn. Only the responses of birds from the first 10m band are considered.

Band	<i>n</i> staying	<i>n</i> flying
1	6	192
2	76	70
3	83	43
4	56	22
5	31	16

Table 6.5 — Numbers Flying in Relation to Distance Back from Nearest Bird

The table includes cases where at least one bird from any band flew. Each figure represents the number of times that birds in a given band stayed or flew. Birds from a band are considered as flying if at least one bird in that band flies. $\chi^2 = 197.99, 4df, p < 0.0005$. There is no significant difference between bands 3 to 5: $\chi^2 = 0.86, 2df, p = 0.652$.

similar for these birds. Or it may be that there are disadvantages to not flying when all other birds in the area are leaving.

6.3.4 Flights of Birds in Relation to Numbers in Other Bands

Tables 6.6–6.8 compare cases where birds from a particular band flew with cases where they did not fly. The comparisons show that when birds in a given band flew rather than stayed, the number of birds flying from other bands, whether nearer to or further away from the disturbance, was greater (Table 6.7). That the relationship is not due to total numbers (whether staying or flying) is shown by Table 6.6, and that it is due to differences in the numbers of birds flying from other bands, rather than just to whether any flew at all, is shown by Table 6.8.

It is impossible to separate cause and effect: it can only be stated that an association exists between the likelihood of flight in one band and numbers of birds flying in others. Whether this is due to independent responses or whether the sight of other birds flying causes birds to take flight, either because this indicates a risk or because they are trying to stay with the flock, is unclear.

6.3.5 Responses in Relation to Flight Reaction Distance

Comparing cases where birds in the second 10m band flew with those cases where they did not fly shows that there is no significant difference in the reaction distances of the birds in the first 10m band (Table 6.9). The same was true for the third and fourth 10m bands. So there is no relationship between the readiness of the nearest birds to fly and the likelihood of birds further back flying.

6.3.6 Direction of Flight

This was looked at in relation to (1) the distance beyond the first bird; (2) the distance from the disturbance; and (3) the number of birds present. In each case, the nearest birds tended to fly in behind an approaching disturbance, whereas birds further away tended to fly away ahead of the disturbance. Figure 6.2 shows that birds flying ahead tend to be from bands further back than those flying in behind; and Figure 6.3 shows that they tend to be from greater distances in front of the disturbance. In order to find whether distance from the disturbance had an

Band A	Band B	Band A stay		Band A fly		<i>U</i>	<i>p</i>
		median in B	<i>n</i>	median in B	<i>n</i>		
2	1	2	76	4	70	1700	< 0.005
	3	2	56	3.5	54	1102	0.01
	4	2	32	2	32	495	0.81
	5	4	16	4	23	153	0.36
3	1	3	83	4	43	1476	0.11
	2	2	75	4	35	1109	0.18
	4	2	39	2	23	388	0.36
	5	4	18	4	14	111	0.56
4	1	2	56	4	22	347	< 0.005
	2	3	43	4	21	343	0.11
	3	3	43	3	19	368	0.53
	5	4	21	4	13	116	0.44
5	1	2	31	4	16	161	0.05
	2	3	24	5	15	156	0.47
	3	4	21	5	11	114	0.95
	4	3.5	22	4	12	121	0.67

Table 6.6 — Flights in Relation to Numbers in Other Bands

The tables compare cases where birds in band A flew with those where they did not fly. Only cases where at least one bird was present in each of the relevant bands were considered. Median values refer to the numbers of birds present in band B, whether subsequently flying or not. Probabilities were obtained from Mann-Whitney U-tests. (No comparison between cases where birds in the first band flew and cases where they did not fly could be made since they almost always flew).

Band A	Band B	Band A stay		Band A fly		<i>U</i>	<i>p</i>
		median in B	<i>n</i>	median in B	<i>n</i>		
2	1	1	76	4	70	1255	< 0.005
	3	0	56	2	54	532	< 0.005
	4	0	32	2	32	176	< 0.005
	5	0	16	2	23	64	< 0.005
3	1	2	83	3	43	1132	< 0.005
	2	0	75	4	35	237	< 0.005
	4	0	39	2	23	78	< 0.005
	5	0	18	3.5	14	27	< 0.005
4	1	1	56	4	22	223	< 0.005
	2	0	43	4	21	53	< 0.005
	3	0	43	3	19	30	< 0.005
	5	0	21	4	13	11	< 0.005
5	1	1	31	4	16	108	< 0.005
	2	0	24	5	15	29	< 0.005
	3	0	21	5	11	18	< 0.005
	4	0	22	4	12	2.5	< 0.005

**Table 6.7 — Flights in Relation to Numbers Flying from Other Bands
(1)**

As Table 6.6 but with median values referring to the numbers of birds in Band B which flew.

Band A	Band B	Band A stay		Band A fly		<i>U</i>	<i>p</i>
		median in B	<i>n</i>	median in B	<i>n</i>		
2	1	1	73	4	67	1031	< 0.005
3	1	2	79	3	43	1132	< 0.005
3	2	2	19	4	35	237	0.08
4	1	1	53	4	22	223	< 0.005
4	2	1	11	4	21	53	0.01
5	1	1	28	4	16	108	< 0.005
5	2	1	8	5	5	15	0.04

**Table 6.8 — Flights in Relation to Numbers Flying from Other Bands
(2)**

As Table 6.7 but with the median values of birds flying from Band B excluding cases where none flew.

Band A	Band A birds stay		Band A birds fly		<i>U</i>	<i>p</i>
	median	<i>n</i>	median	<i>n</i>		
2	12	76	13.5	70	2532	0.61
3	15	83	12	43	1656	0.50
4	12	56	10	22	495	0.17

Table 6.9 — Reaction Distances in Relation to Whether Birds Fly

The table compares cases where birds from band *n* did not fly with cases where they did fly. Medians and tests refer to reaction distances, i.e. the distances in metres from a disturbance at which birds from the first band took flight.

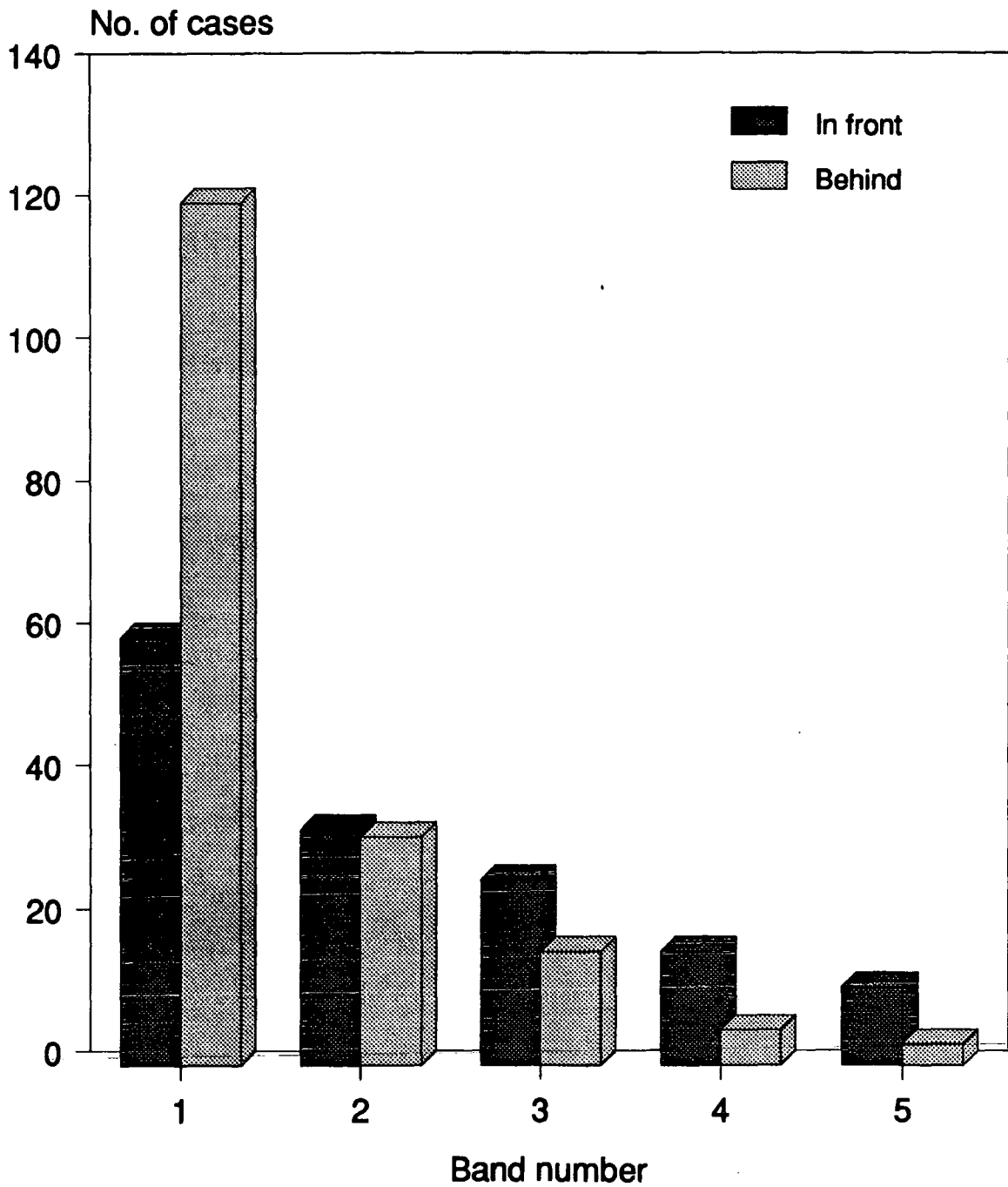


Figure 6.2 — Directions of Flight in Relation to Band Number

The number of cases (a case corresponding to a group of birds in a particular 10m band) where birds flew in front, as opposed to flying in behind, grouped by distance beyond the nearest bird in terms of 10m bands. Mann-Whitney U -test on band number by flight direction: $U = 8831, p < 0.00005$.

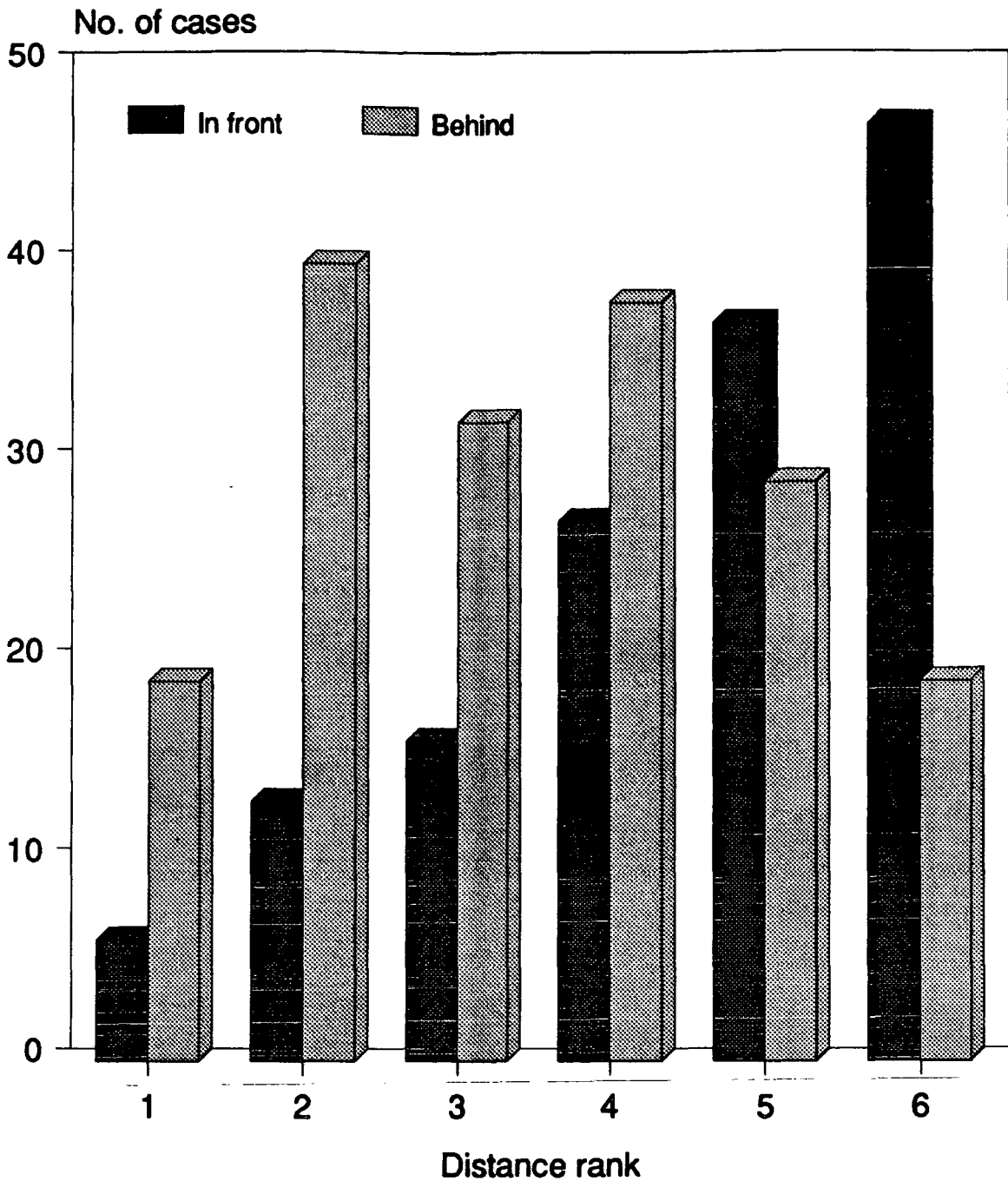


Figure 6.3 — Direction of Flight in Relation to Distance from Disturbance

As Figure 6.2 but with cases grouped according to the distance of birds from the disturbance. This was taken as the distance from the disturbance to the nearest bird plus the distance beyond this bird in terms of the 10m bands. Mann-Whitney U-test on distance from disturbance by flight direction: $U = 7926, p < 0.00005$.

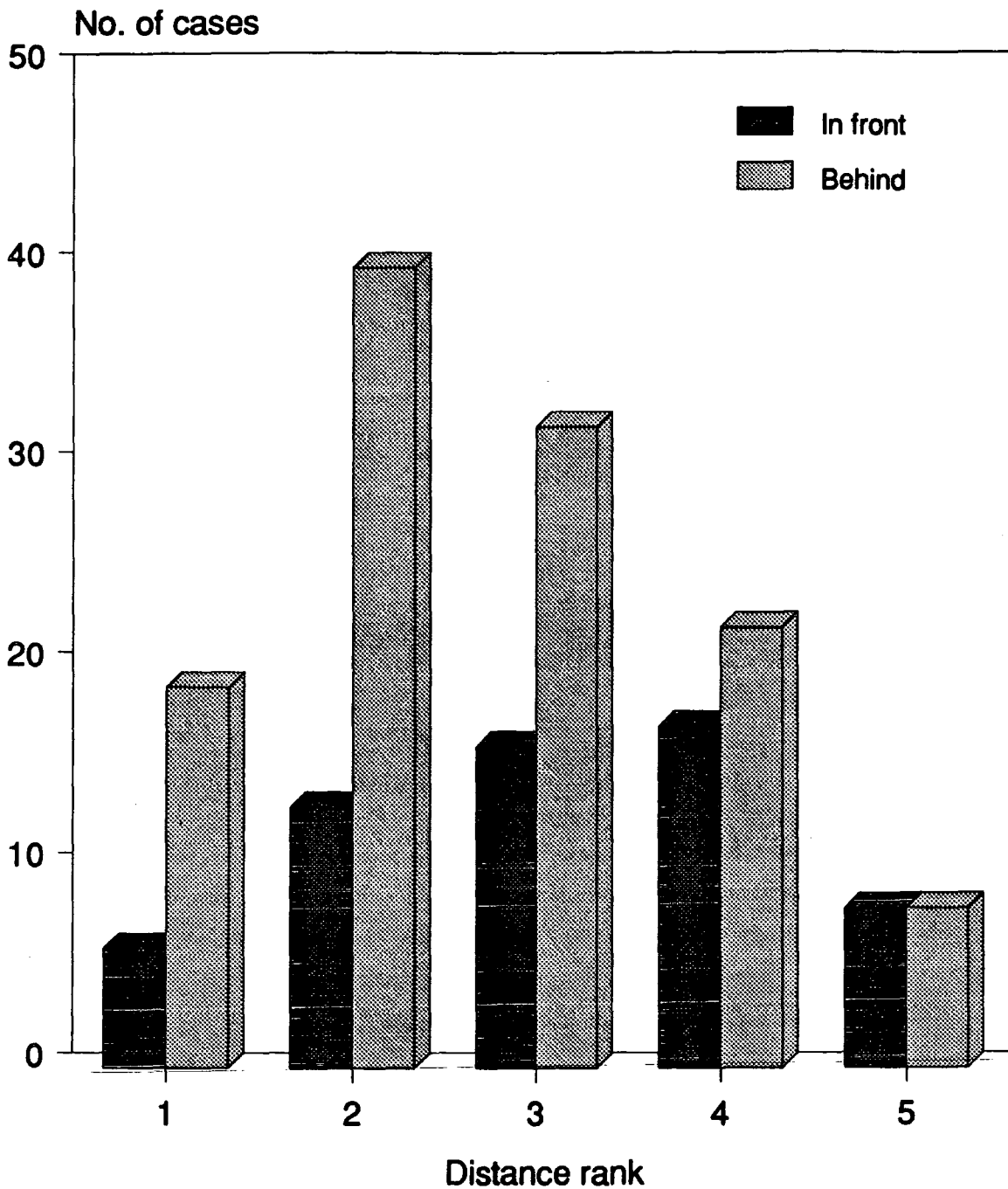


Figure 6.4 — Direction of Flight of Birds from First Band

As Figure 6.2 but considering only birds from the first band. Mann-Whitney U-test on band number by flight direction: $U = 2826, p = 0.01$.

effect independent of position in the flock, the directions of flight of the birds in the nearest 10m band only were analysed (Figure 6.4). Birds from the first band that flew ahead were significantly further in front of the disturbance when they took flight than were birds that flew in behind.

An analysis of the flight directions of birds in particular bands by the numbers of birds present in those bands (Table 6.10) showed no evidence of an effect of numbers except in the case of band 3 where flying forwards was associated with there being more birds present (although the medians do not show this).

Two types of explanation for the tendency of birds near to a disturbance to fly in behind and of birds further away to fly ahead can be imagined. First, birds may be responding to the perceived risks and may move so as to increase their safety or reduce their likelihood of being disturbed again. Secondly, they may be reacting to the numbers and positions of other birds. For example, it might be beneficial to move to an unoccupied area and whether this is achieved by flying in front or behind may depend on flock position. The first type of explanation is favoured by (1) the finding that the relationship between flight direction and distance from the disturbance holds when the position in the flock is controlled for; and (2) by the failure to find a consistent effect of the number of birds present on flight direction.

6.3.7 Distance Flown in Relation to Position

Distances flown were considered separately according to the direction of flight. If birds fly in behind, the total distance actually flown includes the flight distance. Because these two measures would therefore be correlated, the distance flown behind was instead taken as the distance behind the disturbance at which the bird landed.

In a number of cases birds from more than one 10m band flew up and landed together. When it was unclear which birds had landed at the front or rear the position moved to was taken as that of the nearest birds.

Each of the analyses presented in Tables 6.11 and 6.12 was initially carried out on each day's data separately. The results were found to be consistent and so the analyses presented are of grouped data.

Band	Front		Behind		<i>U</i>	<i>p</i>
	Median	Cases	Median	Cases		
1	3	60	2	121	3293	0.30
2	4	33	3	32	494	0.65
3	2	26	2	16	122	0.02

Table 6.10 — Direction of Flight in Relation to the Number of Birds Present

The table gives the median numbers of birds present in each band broken down by the direction of flight. Differences between the numbers present where birds fly in front as opposed to behind are tested using Mann-Whitney U-tests.

Birds included	Variable	r_s	n	p
All	Reaction distance	0.23	140	0.003
All	Reaction distance of nearest birds	-0.13	140	0.060
All	Band no.	0.31	140	0.001
First band	Reaction distance	0.01	57	0.476

Table 6.11 — Correlations with Distance Flown in Front

The table gives Spearman rank correlation coefficients for various response measures with distances flown in front of a disturbance either by all birds or by those from the first band only.

Distance flown by	Variable	r_s	n	p
All	Reaction distance	0.22	168	0.002
All	Reaction distance of nearest birds	0.06	168	0.220
All	Band no.	0.23	168	0.001
First band	Reaction distance	0.07	113	0.219

Table 6.12 — Correlations with Distances Flown Behind

As Table 6.11 but for birds flying in behind a disturbance.

Distances flown increased with the distance from the disturbance at which birds flew, both for birds flying forwards and for birds flying in behind. The distance of birds from the disturbance when they flew is made up of (1) the distance from the disturbance to the nearest birds to fly, and (2) the distance beyond these first birds. Measure (1) had no significant effect on distance flown, but distances flown both forward and back increased with distance beyond the first bird (measured in terms of 10m bands).

The relationships with distance from the disturbance can therefore not be explained as being a product of (a) a relationship between reaction distance and distance flown for the nearest birds, and (b) birds further back flying for a distance correlated with that flown by the nearest birds. This would suggest that birds are adjusting the distances to which they fly to their own distances, either back from the first birds or back from the disturbance.

The relationships between distance from disturbance and distance flown appear to be products of flock position. If they were due to distance from the disturbance *per se* then the relationships should be apparent when birds from only one band are considered. But the relationships do not hold for birds from the first 10m band only.

This conclusion is supported by the observation that when birds flew in behind, those birds which were initially nearer sometimes also landed closer behind so that birds flying from further away also had to fly further behind. In other words the flock may form a kind of 'mirror image' behind the approacher. However, in most cases the distances flown by birds in different bands were so similar that statistical tests were unnecessary.

Even if birds flying up at the same time from different bands fly similar distances, a correlation between band number and distance flown could arise if there were cases where birds in the nearer bands flew without birds from bands further back and if such flights tended to be short. In support of this, the distance flown behind by birds from the first 10m band was greater for cases where birds from the 20m band also flew ($U = 1058, p = 0.0099$). But there was no evidence for such a trend where birds flew forwards ($U = 344, p = 0.4409$).

So the relationship between the initial and final distances from the disturbance for birds flying in behind appears to be due to the finding that when birds from only the nearer bands fly they do not tend to fly as far. This suggests that there is some factor which causes only near birds to fly and also causes these birds to fly in only a short distance behind. It is unclear how the relationship for birds flying forwards can be explained.

6.3.8 Distances Flown in Relation to Numbers of Birds Present

There was a weak correlation between the number of birds in the first 10m and the distance ahead to which these birds flew (Table 6.13). There was a good correlation between the distance flown in behind a disturbance and the number of birds in the first 10m, but any correlations with the numbers of birds in bands beyond were weak (Table 6.14).

There was a correlation between the numbers of birds in the second 10m band and the distance flown in behind ($r_s = 0.30, n = 32, p = 0.046$). However, unlike the results for the 10m birds, there was no correlation with the distance flown ahead ($r_s = -0.02, n = 30, p = 0.46$). A similar analysis of the behaviour of birds from the third band could not be carried out because of the much smaller number of cases where birds from this band flew.

The strong tendency for birds in larger groups to fly in further behind and the weaker correlation with distance flown ahead contradict the hypothesis that birds in larger groups should behave as if at lesser risk than those in smaller groups. The reason for the correlations is unclear, but the fact that these responses varied points towards an economic interpretation.

6.3.9 Do Birds Habituate to the Experimental Disturbances?

Different relationships between responses and the time elapsed from the start of the experimental session were found on different days. It was therefore not possible to make a general comment about whether habituation occurs.

6.4 Summary

There was no evidence for an effect of the numbers of birds present on reaction distances.

Band <i>n</i>	Correlation with nos. in band <i>n</i>		Correlation with nos. up to band <i>n</i>		<i>n</i>
	<i>r_s</i>	<i>p</i>	<i>r_s</i>	<i>p</i>	
1	0.26	0.03	0.26	0.03	57
2	-0.12	0.18	0.07	0.29	57
3	-0.22	0.05	-0.06	0.33	57
4	0.03	0.41	0.01	0.48	53
5	0.03	0.43	-0.09	0.26	52

Table 6.13 — Correlations Between Distances Flown Ahead and Numbers Present

The table gives Spearman rank correlations between distances flown ahead and (i) the numbers of birds in each other band, and (ii) the total numbers of birds up to and including each band in turn. Only the responses of birds from the first 10m band are considered.

Band <i>n</i>	Correlation with nos. in band <i>n</i>		Correlation with nos. up to band <i>n</i>		<i>n</i>
	<i>r_s</i>	<i>p</i>	<i>r_s</i>	<i>p</i>	
1	0.53	< 0.005	0.53	< 0.005	113
2	0.12	0.11	0.50	< 0.005	112
3	0.09	0.17	0.48	< 0.005	111
4	0.05	0.32	0.45	< 0.005	105
5	0.18	0.04	0.47	< 0.005	104

Table 6.14 — Correlations Between Distances Flown Behind and Numbers Present

As Table 6.13 but for distances flown in behind a disturbance rather than for distances flown ahead.

Fewer birds took flight from further back in the flock, but when birds from 20m beyond the first bird took flight then those up to 60m away followed.

There was no relationship between the readiness of the nearest birds to fly and the likelihood of birds further away flying.

Birds near to the disturbance tended to fly in behind; those further away flew ahead. Position in the flock and numbers of birds present appeared unimportant in determining the direction of flight.

There were positive correlations between position in the flock and distance flown both for birds flying ahead and those flying in behind. The latter relationship was due to the fact that when only birds from the first bands flew they flew only a short distance.

There were positive correlations between the numbers of birds nearest to the disturbance and the distances flown by these birds, especially in the case of birds flying in behind.

6.5 Discussion

Are the responses observed consistent with the view that birds reacted to the presence of humans as if they were predators? This question is complicated by the fact that a bird's perception of an approaching disturbance may depend on its distance from it. Thus birds nearby often did not fly until closely approached and then flew in only a short distance behind. Such behaviour suggests that the birds did not perceive a great risk. Birds further away from the disturbance apparently reacted to the numbers of other birds flying up, rather than to the approacher as such, and may have been unaware of the cause of the disturbance.

If birds made a decision about the direction in which to flee solely on the basis of risk, then, in the situation studied, it would appear that all birds should choose to fly in the same direction. That the directions in which birds fled depended on their distances from the disturbance suggests that birds balanced the advantage of flying in behind the disturbance with the costs of flying in that direction. Their response can only be understood in economic terms.

The number of birds present had no effect on the distance at which birds reacted and so there was no evidence for the perceptual limit hypothesis. However, it is not clear how the alternative economic arguments can explain (1) the failure to find an effect of numbers on reaction distance or (2) the increase in the distance flown behind an approacher with increasing numbers. There was no evidence for the hypothesis that individuals would be at less risk when there were more present and so should behave accordingly.

The number of birds flying up decreased with distance from the disturbance. This might be explained in three ways: (1) that birds further back always fly when they are aware of the disturbance or of other birds flying but that they often miss both; (2) that birds would not be put to flight by nearer birds flying but would fly only when they saw the actual cause of the disturbance, which they often miss; or (3) that birds further away may be aware of the disturbance and/or that others are flying but make an economic decision about when to fly which frequently results in their not flying while nearer birds do. Other results demonstrate that flights of birds closer to the disturbance are important, so explanations (1) and (2) are both unlikely.

Some interrelationships between responses measured are apparent. For example, when only near birds fly, they fly only a short distance in behind. Such findings are of interest because they suggest that both are products of a common factor, such as the perceived level of risk.

Although the distances at which birds started to run could not be reliably quantified, it can be noted that birds normally ran along at a speed such that they maintained an approximately constant distance from the approacher (walking at a constant speed). It is possible that this was the maximum speed that they could sustain. This might be tested by approaching birds at different speeds, as observations suggest that birds will first run along and if the speed of approach is too fast will then take off.

The responses made by running fit the model given in the introduction better than do the responses made by flying. The problem with the model is that if the prey starts to flee at the optimal flight distance, as soon as it increases its distance from the predator the costs of fleeing overtake the costs of remaining. Thus the prey should maintain its distance from the predator. This prediction may not hold if costs of vigilance are incorporated into the model. While running behaviour may fit this model, flight behaviour does not. This might be because of the costs of take-off: numerous short flights would be uneconomic. A model of the distance to which prey should retreat would need to incorporate this factor.

Further studies could examine some of the factors which were not considered in this study. Approach speed could be varied in order to vary the apparent risk

involved in remaining (see Section 6.1, prediction 1). The costs of leaving in terms of lost feeding opportunity (prediction 2) could be looked at by disturbing birds feeding in areas of different prey density or on prey of different profitabilities.

In order to describe the situation more fully it would be necessary to record the distance for which birds ran along before flying, and also the time for which the disturbance was within certain distances from the nearest birds. These variables may have a marked effect on responses.

Further studies are clearly needed in order to assess the importance of perceptual constraints and the degree to which behaviour responds to economic factors. The latter tend to be given brief, if any, consideration (e.g. Barnard and Thompson 1985). There is clearly a need for more widespread recognition of the fact that the relationship between perception and response may be far from simple. Studies of disturbance provide a means by which the nature of this relationship can be investigated.

Chapter VII

Vigilance

7.1 Introduction

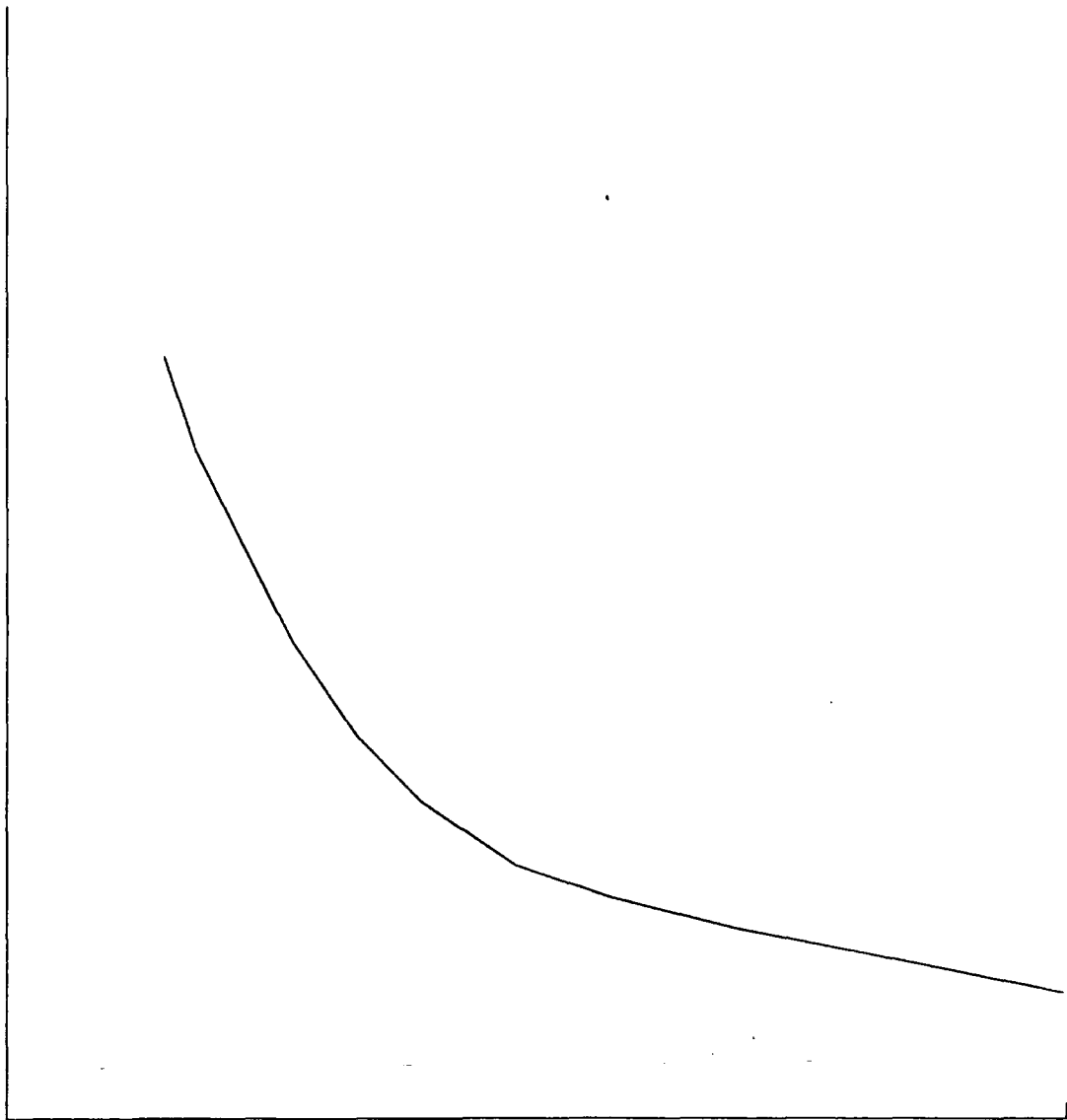
Many species of birds and mammals typically feed with their heads down, raising them occasionally to scan the environment, probably to detect predators but perhaps also for other reasons. The literature on such vigilance behaviour is considerable, but no thorough critical review has been made. I briefly review the literature, concentrating on birds, in order to identify those areas requiring further study and to introduce those which are addressed in this chapter. In particular, I examine the widely accepted negative relationship between flock size and the vigilance of individual flock members and point out that many factors other than flock size may affect vigilance.

7.1.1 Models of Scanning Behaviour

A central tenet of the work on vigilance behaviour has been that energy intake and predator detection are mutually exclusive activities requiring a trade-off in terms of time-budgeting (e.g. Pulliam, 1973; Caraco, 1979a, b). Pulliam (1973; Figure 7.1) showed that an individual in a flock could decrease its allocation of time to vigilance while maintaining or actually increasing its probability of detecting a predator because the combined, or 'corporate', vigilance of a flock increases with flock size. Furthermore, individual risk is likely to be diluted as flock size increases (Hamilton, 1971). Pulliam's model assumed (1) that scans were instantaneous; (2) that they occurred randomly; (3) that individuals scanned independently of each other; and (4) that when one bird detected a predator this information could be used by others.

Although a decrease in scan rate (the number of scans made by an individual in a given time) with increasing flock size has frequently been found (see Barnard and Thompson, 1985, and below), a number of violations of the assumptions of the

Individual
scan rate



Flock size

Figure 7.1 — Vigilance and Flock Size: Pulliam's Model

For a given level of corporate vigilance, an individual's scan rate falls with increasing flock size.

model have been reported. Scan duration has been found to be important. For example, Gluck (1987a) found that increased scan rate correlated with reduced scan duration. The basis for the assumption that scans should be given randomly is that if animals were to scan non-randomly a predator might be able to predict the timing of the next scan and time its final attack so that it would be invisible to the prey. This may be of more relevance to some predator-prey interactions than to others, but a number of studies have found distributions of inter-scan intervals which differ from the negative exponential distributions expected on the basis of random scanning. Lendrem (1983a, b), Hart and Lendrem (1984) and Sullivan (1985) found that very long and very short time intervals tended to be avoided. Poysa (1987b) found that interval lengths were non-random but were too short to be exploited by a predator.

If the risk of being unaware of an attack increases as the time since the last scan increases, then scanning should be a time-dependent process (Lendrem *et al.*, 1986). Incorporating minimum time intervals representing the physical constraints on inter-scan intervals, they found that a random but time-dependent model gave a better fit to data for three species than did a random, time-independent model.

Desportes *et al.* (1989) have pointed out that a fit between the observed frequency distribution of inter-scan interval durations and the distribution expected for a random process does not preclude the possibility that the sequence of inter-scan interval durations is non-random. They examined four vigilance sequences for two species and found non-random patterns.

Scanning behaviour should be dependent on the behaviour of other individuals. Pulliam *et al.* (1982) tested a model based on 'cooperation' in which individual scan rates maximise survival for all but in which individuals might 'cheat' by scanning less, against one based on 'selfishness' giving lower survival but being evolutionarily stable (in the sense of Maynard Smith, 1972). Data for yellow-eyed juncos, *Junco phaeonotus*, showed a better fit to the former, but the extent to which individuals cooperate in scanning is largely unknown. McGowan and Woolfenden (1989) describe an extreme case of cooperation, a sentinel system in scrub jays. But, for example, Bertram (1980) found no cooperation in ostriches, and Poysa

(1987b) found it unlikely in teals, *Anas crecca*, given the brevity of feeding and scanning bouts.

Further developments of models of scanning behaviour have been made in order to calculate the probabilities of detecting predators (e.g. Hart and Lendrem, 1984; Lendrem, 1986).

7.1.2 Ways in which Vigilance may be Varied

Increasing the total time devoted to vigilance is not a simple matter of increasing scan rate. Different strategies may be used. For example, Metcalfe (1984a) found that while purple sandpipers, *Calidris maritima*, increased vigilance by increasing their scan rate, turnstones, *Arenaria interpres*, increased vigilance by increasing the durations of their scans. McVean and Haddlesey (1980) proposed four ways in which vigilance might be increased.

- (1) Shorten inter-scan intervals; keep scan durations constant; scan rate increases.
- (2) Keep inter-scan intervals constant; increase scan durations; scan rate decreases.
- (3) Shorten inter-scan intervals while lengthening scan durations; the effect on scan rate depends on which is most significant.
- (4) Shorten inter-scan intervals and shorten scan durations to a lesser extent; scan rate increases.

7.1.3 Flock Size

Individual levels of vigilance usually decline as flock size increases (Table 7.1). There are exceptions to this rule. For example, Barnard and Stephens (1983) found no effect of flock size on redwing vigilance and Poysa (1987b) obtained similar results (see Section 7.1.6).

Nevertheless, much of the evidence is consistent with the hypothesis that flocking can be seen as a strategy for increasing the time available for feeding. In most of the studies cited in Table 7.1, feeding time increased with decreasing time spent vigilant. However, the relationship between vigilance and feeding rate is often unclear. While scan rate usually correlates negatively with flock size, peck rate

often correlates positively (e.g. Caraco, 1979b; Barnard, 1980a). Elgar *et al.* (1986) demonstrated that the latter correlation could not be accounted for in terms of confounding factors such as food density and argued that it was consistent with the hypothesis that decreased scanning allows greater food intake. However, Fleischer (1983), for example, found no increase in intake rate with decreased vigilance.

The ranges of flock sizes studied vary widely. Where the range is large, the decline in vigilance with increasing flock size is most marked over the lower part of the flock size range (as predicted by Pulliam, 1973). For example, in Brent geese there was little effect of flock size where this was above about 300 birds (Inglis and Lazarus, 1981). Nevertheless, there are considerable differences between species in terms of the flock size range over which individual vigilance declines appreciably.

While it is generally accepted that birds reduce vigilance with increasing flock size, few studies have examined the cues to which birds respond in modifying their vigilance. Metcalfe (1984a) found that vigilance was shared only with those neighbours which were in view and that the presence of individuals of other species could have a similar effect to the presence of conspecifics. Elgar *et al.* (1984) found that house sparrows responded to the number of other individuals in view rather than to the total number at a feeding station. They also found that whether vigilance declined with increasing numbers of birds present depended on the distance to those birds: vigilance was unaffected by the numbers of birds at a feeder 1.2m away.

In my study the aim was to examine whether the vigilance of individual sanderlings declined with increasing flock size and, if so, to look in more detail at what the birds were actually responding to. It might be that flock members cannot readily monitor flock size. Instead, birds may need to rely on cues which indicate flock size, such as the number of birds in a more restricted area around them. Alternatively, it may be that flock size itself is not an important factor determining the need for vigilance but simply correlates with another factor which is important: the distance to the nearest neighbour, perhaps, or flock density. The object was therefore to find which variables showed the strongest relationships with vigilance rates.

One way in which flock size may indirectly affect vigilance was suggested by Inglis and Lazarus (1981). These authors found support for the hypothesis that the relationship between vigilance and flock size resulted from birds on the edge of a

flock being more vigilant: as flock size increases, a lower proportion of birds will be on the edge and so average vigilance will decline. This 'edge effect' was also described by Jennings and Evans (1980).

Exploiting the vigilance of other flock members may have advantages, but there may also be advantages in maintaining individual vigilance. Elgar *et al.* (1986) showed that birds with their heads raised when a predator appeared took flight more rapidly.

7.1.4 Predation

Vigilance in relation to predation risk has been examined in a number of different ways (Table 7.2). The studies range from those in which predation risk is directly manipulated to those in which changes in predation risk are inferred. The studies of the effect of being near the edge of a flock (Section 7.1.3) could also be classed as studies of predation risk. While most studies report increases in vigilance with increased risk, Lima (1985; 1987*a, b*) shows, in theory and in practice, that vigilance may decrease so that the total period of exposure while feeding and being vigilant, and thereby the predation risk, is reduced.

7.1.5 Motivational State

McNamara and Houston (1986) modelled the dependence of vigilance on the state of the animal and the consequent changing relative values of performing different activities. They concluded that vigilance should be low when the need to feed is great, such as immediately before and after the over-night fast. In shorebirds such as sanderlings, the same may apply to the periods before and after the high-water roosting period. In support of the theory that state is important, Metcalfe and Furness (1984) found that vigilance declined with the need for enhanced food intake to permit pre-migratory fattening in turnstones. Time of year may have an important effect on vigilance. It could be hypothesized that the low temperatures of mid-winter might cause birds to spend more time foraging at the expense of vigilance.

Species	Flock size	Parameter	Effect	Reference
Ostrich <i>Struthio camelus</i>	4	vig. time	-	Bertram (1980)
White-fronted goose <i>Anser albifrons</i>	1000	vig. time	-	Dimond & Lazarus (1974)
	>1000	propn.	-	Lazarus (1978)
Brent Goose <i>Branta bernicla</i>	2000	propn.	-	Inglis & Lazarus (1981)
Teal <i>Anas crecca</i>	22	scan durn. feed time	= =	Poysa (1987b)
Bald eagle <i>Haliaeetus leucocephalus</i>	14	scan rate	=	Knight & Knight (1986)
Curlew <i>Numenius arquata</i>	28	vig. time	-	Abramson (1979)
Dunlin (feeding) <i>Calidris alpina</i> (preening)	>7	scan rate vig. time scan rate vig. time	- - = -	Redpath (1988)
Purple sandpiper <i>Calidris maritima</i>	40	scan rate	-	Metcalfe (1984a)
Turnstone <i>Arenaria interpres</i>	30	scan rate	-	Metcalfe (1984a)
Barbary dove (sleeping) <i>Streptopelia risoria</i> (feeding)	6	sleep int. sleep time feed time	+ + +	Lendrem (1984a) Lendrem (1984b)
Downy woodpecker <i>Picoides pubescens</i>	>3	scan rate	-	Sullivan (1985)
Fieldfare <i>Turdus pilaris</i>	129	scan rate	-	Barnard & Stephens (1983)
Redwing <i>Turdus iliacus</i>	55	scan rate	=	Barnard & Stephens (1983)

Species	Flock size	Parameter	Effect	Reference
Willow tit <i>Parus montanus</i>	6	p. of acts.	-	Ekman (1987)
	11	vig. time	-	Hogstad (1988a)
Yellow-eyed junco <i>Junco phaeonotus</i>	10	scan rate	-	Caraco (1979b); Caraco <i>et al.</i> (1980a, b)
House sparrow <i>Passer domesticus</i>	50	scan rate	-	Barnard (1980a)
	>50	scan int.	+	Elgar & Catterall (1981)
	4	vig. time	-	Studd <i>et al.</i> (1983)
	6	scan durn.	+	Elcavage
		inter-scan	=	& Caraco (1983)
	>4	inter-scan	+	Elgar <i>et al.</i> (1984)
Red-billed weaverbird <i>Quelea quelea</i>	32	scan rate	-	Lazarus (1979b)
Chaffinch <i>Fringilla coelebs</i>	12	vig. time	-	Beveridge & Deag (1987)
Goldfinch <i>Carduelis carduelis</i>	6	scan rate	-	Gluck (1987a)
Starling <i>Sturnus vulgaris</i>	250	vig. time	-	Jennings & Evans (1980)
		scan rate	-	Beveridge & Deag (1987)

Table 7.1 — Studies of Flock Size and Vigilance in Birds

The table gives the maximum flock size studied; the vigilance parameters measured; and the relationships between flock size and these measures. The lists of parameters measured are not comprehensive: other parameters may have been recorded or inferred; e.g. a decrease in vigilance time usually implies an increase in feeding time. Scan rate = number of scans in a given time period; vig. time = total time spent scanning in a given time period; feed time = total time spent feeding in a given time period; scan durn. = scan duration; inter-scan = inter-scan interval duration; propn. = proportion of birds scanning; and p. of acts. = proportion of instantaneously recorded activities which were scans. Unless otherwise stated, studies were of feeding birds. All were field studies except for Lendrem (1984a, b) and Lazarus (1979b).

Factor	Species	Parameter	Effect	Reference
Trained hawk	Yellow-eyed junco <i>Junco phaeonotus</i>	scan rate	+	Caraco <i>et al.</i> (1980a)
Model predator	Downy woodpecker <i>Picoides pubescens</i>	scan rate	+	Sullivan (1984)
	Goldfinch <i>Carduelis carduelis</i>	scan durn.	+	Gluck (1987b)
Wild predator	Teal <i>Anas crecca</i>	scan rate	+	Poysa (1987b)
		vig. time	-	
Predator (ferret)	Barbary dove <i>Streptopelia visoria</i>	feed rate	-	Lendrem (1984b)
Distance to cover	House sparrow <i>Passer domesticus</i>	scan rate	+	Barnard (1980a)
		scan rate	=	Elgar (1986)
		scan rate	-	Lima (1987a)
	Yellow-eyed junco	scan rate	+	Caraco <i>et al.</i> (1980b)
	Willow tit <i>Parus montanus</i>	vig. time	+	Hogstad (1988b)
	Blue tit <i>Parus caeruleus</i>	scan rate	+	Lendrem (1983b)
Visual obstructions	House sparrow	scan time	-	Lima (1987a)
		scan rate	-	
	Turnstone <i>Arenaria interpres</i>	scan durn.	+	Metcalfe (1984a)
	Purple sandpiper <i>Calidris maritima</i>	scan rate	+	Metcalfe (1984a)
Predator activity	Dark-eyed junco <i>Junco hyemalis</i>	vig. time	+	Lima (1988)
Disturbance	Bald eagle <i>Haliaeetus leucocephalus</i>	scan rate	+	Knight &
		vig. time	+	Knight (1986)

Table 7.2 — Studies of Predation Risk and Vigilance in Birds

7.1.6 Why Scan?

Vigilance is usually considered to be associated with predator detection. The validity of this assumption is supported by the increase in vigilance with increasing predation risk (Section 7.1.4). But this does not preclude the possibility that scanning has additional functions. Indeed, the hypothesis that flock members make use of the anti-predatory vigilance of others implicitly requires birds to maintain some degree of vigilance in order to monitor others and so perceive when others have detected a predator.

Scanning has occasionally been considered to have other functions. For example, Poysa (1987b) suggested that the failure to find the strong relationships between teal flock size and time spent scanning predicted by the Pulliam (1973) model might have been due to an increase in scanning associated with observing other group members in order to maintain flock cohesion. Alados (1985) and Caine and Marra (1988) proposed that individuals may scan in order to observe other group members while Caro (1987) found that vigilance may relate to looking for prey.

The function of scanning may depend on flock size. Whereas the vigilance patterns of bald eagles feeding in groups of 1 to 7 were consistent with the anti-predator hypothesis, the hypothesis that birds look up to detect conspecifics and thereby avoid being kleptoparasitized or injured provided a better explanation for the vigilance of groups of 8 to 14 (Knight and Knight, 1986).

Sanderlings might scan for any of the following reasons.

- (1) Predator detection. Other potential threats such as the presence of other species (e.g. gulls may kleptoparasitize sanderlings) or disturbance caused by human activity can be included here.
- (2) To assess feeding opportunities in the area, particularly in circumstances where the tide is rapidly exposing or flooding potential feeding areas.
- (3) To assess the number of conspecifics present which, if large, may reduce their feeding success through interference.
- (4) To watch conspecifics and thereby obtain information about the location of food resources.
- (5) To ensure that they remain within the flock or to keep a check of the numbers of birds present and use this to decide whether to remain in the flock or perhaps

move to another of a different size.

- (6) To assess the level of corporate vigilance of the flock, in which case the vigilance levels of the other birds should also be monitored.
- (7) To watch for indications that other birds have detected the approach of a predator.
- (8) To monitor the distance to the nearest conspecifics. This may be important in that it may, according to the domain of danger hypothesis (Hamilton, 1971), determine risk.

It is more difficult to generate and test hypotheses based on the functions of scanning other than predator detection. For example, the relationship between scan rate and the number and position of neighbouring conspecifics will depend on which of the reasons for scanning are of most importance. If monitoring conspecifics is the major reason for scanning then it is not obvious that there should be any relationship, although it could be argued that monitoring would be most critical where the number of conspecifics is small since a slight change in the number present would have a more significant impact. Much more theoretical work is required in order to predict vigilance behaviour based on the above hypotheses, none of which have been tested as alternatives to the predator awareness hypothesis.

7.1.7 Constraints on Vigilance

Vigilance may suffer as other activities impose constraints. Metcalfe (1984a) suggested that the feeding techniques used by turnstones imposed constraints on their scanning behaviour such that they could not reduce their inter-scan intervals as readily as could purple sandpipers.

Lawrence (1985) found that blackbirds, *Turdus merula*, presented with cryptic prey as opposed to conspicuous prey spent longer feeding, spent only half as long being vigilant, and spent twice as long with their heads down between scans. In explanation it was suggested both that the higher feeding rate on conspicuous prey may have allowed more time to be devoted to vigilance and that the difficulty of feeding on the cryptic prey interfered with the birds' ability to maintain vigilance. Similarly, the scanning behaviour of blue tits, *Parus caeruleus*, feeding on peanuts was apparently constrained by the handling times necessary for different types of peanut (Lendrem, 1983b).

In teals, as the duration and depth of feeding bouts where the eyes were beneath the water surface increased, inter-scan bout length increased while scanning rate decreased (Poysa, 1987b). Although scan duration increased, overall vigilance was reduced. Observed average feeding bout lengths were well within the maxima recorded and so there was no evidence for physiological constraints affecting scanning behaviour. Teals have short inter-scan intervals and the costs of reducing these further may be great since transitions between feeding and scanning cost time and energy.

7.1.8 How Exclusive are Foraging and Scanning?

Some birds raise their heads to handle food items (notably granivorous birds, e.g. Lendrem, 1984b; Gluck, 1987b). Most birds do not, so foraging and scanning are normally exclusive activities (e.g. McVean and Haddlesey, 1980). Teals may (1) maintain a head-up scanning posture; (2) feed with the bill submerged and so potentially retain some vigilance; or (3) feed with the head submerged (Poysa, 1987b). Inglis and Lazarus (1981) distinguished between head-up, extreme head-up, and head-down postures in Brent geese. The question of how much birds see while feeding remains largely unanswered. In wading birds the eyes are placed on the sides of the head and so it may well be that some degree of vigilance can be maintained while feeding. In this chapter the vigilance of birds feeding with different head postures will be compared.

7.2 Order of Presentation of Data in this Chapter

The first approach taken (Section 7.3) was to study the scanning rates of sanderlings feeding by pecking on rocky areas. The main aims were (1) to examine the relationship between flock size and vigilance and in particular to look at the effects of flock density; and (2) to find which of a range of other factors affect vigilance.

Further data on sanderlings pecking on rocky areas were analysed in terms of inter-scan interval durations and are presented in Section 7.4. Particular attention was paid to whether scanning was a time-dependent or time-independent process. The relationship between changes in scan durations and inter-scan intervals was also examined.

In Section 7.5 observations of sanderlings using feeding methods other than pecking on rocky areas are presented in order to compare the ways in which the birds might maintain vigilance while performing activities which apparently differ in terms of the degree to which they allow vigilance to be maintained.

Flock sizes and densities explained variance in vigilance to only a limited extent. Studying the vigilance of preening birds (Section 7.6) meant that several of the factors potentially affecting the vigilance of feeding birds, such as food density, did not need to be considered. The effect of the type of flock on the vigilance of preening birds was examined. Data were analysed in terms of inter-scan intervals allowing further examination of scanning patterns and of the relationship between different vigilance parameters. The inter-scan intervals of preening birds were compared with those of feeding birds. Video-taping allowed analysis of inter-scan intervals in terms of the types of preening movement performed during those intervals (Section 7.7). The occurrence of prolonged scans was also related to movement types.

7.3 Vigilance of Sanderlings Pecking on Rocks

7.3.1 Introduction

In this study I examine the scanning rates of sanderlings feeding by pecking on rocky areas in terms of the following main points.

- (1) The relationship between vigilance and flock size and spacing (see Section 7.1.3).
- (2) The effects of other factors such as season, time and tidal stage. One way in which such factors might act is through their effects on the motivational state of the birds (see Section 7.1.5).
- (3) The purpose of scanning (see Section 7.1.6).

7.3.2 Methods

On rocky areas sanderlings usually fed rapidly with their heads down, giving intermittent upward movements of their heads such that the head was above the

level of the back. The head was usually lowered again immediately. Birds were considered to be vigilant when they gave such scans.

Data were collected throughout the 1987–88 winter. Focal birds (Altmann, 1974) were selected arbitrarily from those clearly in view and the following were noted when individual vigilance records were taken.

- (1) The size of the flock of which the individual was a member (SIZE);
- (2) the distance from the individual to its nearest-neighbour (INN);
- (3) the number of birds within a radius of an estimated 5m of the individual, recorded only from December onwards, (RAD);
- (4) the duration of the vigilance record;
- (5) the number of scans during this period;
- (6) the numbers of knot, *Calidris canutus*; gulls, *Larus* spp.; turnstone, *Arenaria interpres*; ringed plover, *Charadrius hiaticula*; oystercatcher, *Haematopus ostralegus*; redshank, *Tringa totanus*; and dunlin, *Calidris alpina*, present within approximately 5m; and
- (7) the percentage of the flock feeding (PFEED) as opposed to preening, roosting or bathing.

The date, time of day and state of the tide were also noted.

Records were made by speaking into a continuously running tape recorder. The tape was played back to determine scan rates. Checks on the reliability of the running speed of the tape were made by recording stopwatch bleeps separated by timed intervals.

The 5m radius is essentially arbitrary in that it is not based on any knowledge of the distance within which sanderlings can keep track of the number of conspecifics present. In theory, the numbers present within radii of 1m, 2m, etc. could be recorded, and the respective correlations with vigilance rate used to infer the distance at which other birds are monitored. However, it was impractical to record so many variables. It was therefore assumed that if the birds were adjusting their vigilance rates in accordance with the number of conspecifics in an area smaller than that occupied by the whole flock, then the number of birds within 5m should approximate to the cue actually used better than would the other variables recorded (i.e., flock size and individual nearest-neighbour distance).

The topography of the area (Section 2.2) was such that birds may not have been aware of the whole flock of which they were a member. Flocks were not always discrete units (Section 2.6). Given these factors, the number of birds within a 5m radius might be a more important cue than flock size.

The proximity of birds to the edge of the flock proved too difficult to record reliably because of the irregular shapes of the flocks and because of the problem of perspective.

7.3.3 Results

Plots against vigilance rate suggested that approximately linear relationships existed with SIZE, INN, PFEED, MINS, and RAD, but not with time of year or time in relation to the tidal cycle. The latter two were therefore treated as categorical variables. Time of year was classed as (1) September–November, (2) December–February, and (3) March–May, so that the mid-winter period was separated from the autumn and spring passage periods. Time in relation to the tidal cycle was classed as (1) falling and low tide, or (2) rising tide. Each of the following analyses were carried out in two parts: the first across all times of year, and the second including the variable RAD but confined to cases from December onwards when this variable was noted.

Vigilance rate (\log_{10} -transformed in order to satisfy the assumptions of the parametric statistics used) was subjected to an analysis of covariance by time of year and time of tide with SIZE, INN, PFEED and MINS as covariates. In a second analysis, there were only two time of year categories, and RAD was included as an additional covariate.

No evidence of any effects of time of year or of time in relation to the tidal cycle were found (Table 7.3) and so all cases were grouped together for the following analyses.

A stepwise multiple linear regression of \log_{10} -transformed scan rate with PFEED, INN, SIZE and MINS with a sample size of 197 cases yielded the following equation:

$$\log_{10}(RATE + 1) = 1.0033(\pm 0.0837) - 0.0036(\pm 0.0010)PFEED$$

Source of variation	SS	df	MS	F	p
Within cells	19.34	186	0.10		
Regression	2.27	4	0.57	5.46	< 0.005
Time of year	0.48	2	0.24	2.29	0.10
Time of tide	0.23	1	0.23	2.19	0.14
Interaction	0.03	2	0.02	0.17	0.85

(a) ANCOVA of \log_{10} -transformed scan rate by time of year (Sep–Nov; Dec–Feb; Mar–May) and time of tide (falling and low; rise), with SIZE, INN, PFEED, and MINS as covariates.

Source of variation	SS	df	MS	F	p
Within cells	10.33	91	0.11		
Regression	2.85	5	0.57	5.02	< 0.005
Time of year	0.20	1	0.20	1.76	0.19
Time of tide	0.01	1	0.01	0.07	0.79
Interaction	0.01	1	0.01	0.10	0.76

(b) ANCOVA of \log_{10} -transformed scan rate by time of year (Dec–Feb; Mar–May) and time of tide (falling and low; rise) with SIZE, RAD, INN, PFEED, and MINS as covariates.

Table 7.3 — ANCOVA of Scan Rate by Time of Year and Time of Tide

$$+0.0306(\pm 0.0121)INN,$$

where the T values of all terms in the equation were significant at the $p < 0.01$ level and where $F_{194,2} = 9.744$, $p = 0.0001$; Beta values -0.26 and 0.17 respectively.

Analysis of the 110 cases where RAD was recorded gave:

$$\log_{10}(RATE + 1) = 1.0328(\pm 0.1112) - 0.0035(\pm 0.0013)PFEED,$$

with $F_{108,1} = 7.076$, $p = 0.009$, Beta -0.25 .

Correlations between the independent variables complicate the interpretation of the regression equations. More instructive are the partial correlations given in Table 7.4.

The clearest result from both the regressions and the partial correlations is that as the proportion of a flock which was feeding (as opposed to preening or roosting) increased, the scan rate decreased. It may be that this is due to a factor which causes birds both to spend less time feeding and to spend more time being vigilant. For example, there may be times when foraging profitability is low and the costs of not feeding also low.

An ANCOVA of PFEED by time of year with flock size as a covariate reveals that time of year has a significant effect on the proportion of birds feeding. (Table 7.5). It was hypothesized that there will be most pressure on birds to feed in mid-winter, and that this may result in a decline in vigilance if time is limiting. Although no effect of time of year on vigilance was found, the proportions of birds feeding are highest in mid-winter (Table 7.6) and as a result of the relationship between the proportion feeding and vigilance, vigilance will tend to be greater in winter.

The finding of a negative correlation between scan rate and flock size is consistent with the large number of other studies which have examined this relationship (see introduction). However, this result was only apparent when the number of birds in a 5m radius was controlled for. The latter factor had an opposing effect to that of flock size when flock size was controlled for. This contradicts the hypothesis that birds might adjust their vigilance rates more in response to the numbers of birds in the immediate vicinity than to the numbers in the flock as a whole.

Variable	Partial corr.	<i>p</i>
SIZE	-0.03	0.32
INN	0.12	0.05
PFEED	-0.25	< 0.005
MINS	-0.04	0.30

(a) Partial correlations of the row variables with \log_{10} -transformed scan rate controlling for the three other row variables. Based on 191 cases.

Variable	Partial corr.	<i>p</i>
SIZE	-0.26	< 0.005
INN	0.13	0.09
PFEED	-0.27	< 0.005
MINS	-0.13	0.09
RAD	0.17	0.05

(b) Partial correlations of the row variables with \log_{10} -transformed scan rate controlling for the four other row variables. Based on 102 cases.

Table 7.4 — Partial Correlations With Scan Rate

Source of variation	SS	df	MS	F	p
Within cells	97854	208	470		
Regression	6810	1	6810	14.48	< 0.005
Time of year	22158	2	11079	23.55	< 0.005

Table 7.5 — ANCOVA of the Proportion of a Flock Feeding by Time of Year

The regression term refers to the covariate of flock size.

Season	Percentage feeding		
	Mean	S.E.	n of flocks
Autumn	84.37	2.01	104
Winter	98.57	1.00	56
Spring	69.87	4.70	52

Table 7.6 — Percentages of Flocks Feeding by Time of Year

The positive partial correlations between scan rate and nearest-neighbour distance support the hypothesis that vigilance should increase with Hamilton's (1971) 'domain of danger.' The finding is also consistent with the results of those studies which have looked at the effect on vigilance of being at the edge of a flock (see Section 7.1.3) since birds with larger nearest-neighbour distances are more likely to be at the edge.

A number of potentially important variables were not examined in this study. One was feeding rate. When birds were feeding by pecking on rocky areas, movements were too rapid and insufficiently discrete to allow feeding rate to be measured. The number of cases where birds of other species were present proved to be too small for the presence of other species to be brought in to the regression analysis. Finally, recording the numbers of scans in a given time does not provide a full description of a bird's vigilance. A better description is provided by the methods used in the next section.

7.4 Vigilance While Feeding: Analysis of Inter-Scan Intervals

7.4.1 Introduction

In this section, vigilance is considered in terms of the lengths of time between successive scans (inter-scan interval durations), rather than simply in terms of scan rates. Reasons why the frequency distribution of inter-scan interval durations might be of interest were discussed in Section 7.1.

7.4.2 Methods

Data were collected in autumn 1988. In addition to the variables given in Section 7.3.2, the following were recorded.

- (1) The numbers of birds feeding within 5m of the focal bird;
- (2) the number preening within 5m;
- (3) the number roosting within 5m;
- (4) the extent to which the bird moved (on a scale of 1 to 5, 5 representing the most movement);
- (5) the extent to which the bird's vision appeared to be hampered (on a scale of 1 to 5, 5 representing a clear view);

- (6) the manner in which the record ended (i.e. whether the bird started preening, flew away, walked away, or continued feeding while observations switched to a new focal individual);
- (7) the number of scans apparently associated with the following factors: (i) brief preening movements; (ii) a rising tide forcing a sanderling to take evasive action; (iii) other species causing sanderlings to take evasive action; and (iv) other birds coming in to land or flying off.

Records were made by speaking into a continuously running tape recorder. Initial analyses of the tapes from autumn 1988 were carried out both in terms of scan rates and in terms of inter-scan intervals. A computer program, MINKEY, then became available. This allowed more accurate analysis of inter-scan intervals through recording the times of key-presses corresponding to scans. For simplicity, only this more accurate analysis is presented.

The computer program gave the time of a key-press in hundredths of a second. In practice, accuracy is reduced because of (1) the times between a bird scanning and these events being recorded on tape; and (2) the times taken to make appropriate key-presses when playing back the tape. The latter error was tested by making repeat runs through the tape. Differences were usually of a few hundredths of a second and rarely more than a tenth of a second. However, this does not represent an independent check on accuracy.

Most of the following analyses are of mean inter-scan intervals. Since scan durations were typically very short, mean inter-scan interval will be approximately equal to the reciprocal of scan rate. However, accuracy should be greater, notably by avoiding the errors which may be introduced by including in an observation the times from the start to the first scan and from the last scan to the end. The sample sizes are small since many cassette tapes had been erased for re-use before this analysis was carried out.

The following events were recorded.

- (1) Scans.
- (2) Ends of scans. Scans were mostly recorded as being 'instantaneous' in that they were too brief to allow recording of the start and the end of the scan as

separate events. However, scans were occasionally 'extended.' When this was the case the ends of the scans were recorded.

(3) Starts of other activities (feeding or walking).

(4) Ends of other activities.

If the end of a record occurs randomly then the longer the inter-scan interval the more likely that interval is to be cut. Therefore, if records are short there will tend to be a bias towards short inter-scan intervals. In order to avoid this, only records of over 60s were included.

7.4.3 Frequency Distribution of Inter-Scan Interval Durations

When \log_{10} -transformed, the inter-scan interval durations fit a normal distribution (mean= 0.707, $n = 659$, Kolmogorov-Smirnov one-sample test $D_{max} = 0.037$, $p = 0.305$) so parametric statistics could be used.

In the following analysis only those records during which no extended scans were made were included (see below). This left a sample of 423 intervals with a mean of 10.01 ± 0.62 s (\log_{10} -transformed data, mean 0.776 ± 0.021).

The frequency distribution of inter-scan interval durations was tested against distributions expected if scanning were (1) a time-independent process, and (2) a time-dependent process (see Section 7.1.1). Following Lendrem *et al.* (1986) the probability density functions used were

$$f_t = \lambda t e^{-\lambda t}; t > 0$$

for the time independent process; and

$$f_t = \lambda t e^{-\lambda t^2/2}; t > 0$$

for the time-dependent process, where λ represents the rate of scanning (the mean number of scans per second) and t represents the inter-scan interval duration (in seconds). Therefore, the proportions of inter-scan intervals of up to t seconds are given by

$$1 - e^{-\lambda t}$$

and

$$1 - e^{-\lambda t^2/2}$$

respectively.

No attempt was made to make the functions dependent on variables such as flock size (e.g. Elcavage and Caraco, 1983). Minimum inter-scan intervals were incorporated into the models by substituting $t - m$ for t , where m was the minimum criterion. The justification for this is that there is likely to be a physical constraint on the time between scans (Lendrem *et al.*, 1986). The values of λ and m giving the best fit to the observed data were obtained by carrying out a non-linear regression using SPSS-X (SPSS Inc., 1988) for each of the two models.

Figure 7.2 shows that the distribution of inter-scan interval durations gave a better fit to the time-independent model (where $\lambda = 0.013$, $m = 0.67$ secs., Kolmogorov-Smirnov two-sample test, $D_{max} = 0.045$, $p \gg 0.05$) than to the time-dependent model (where $\lambda = 0.039$, $m = 0$, $D_{max} = 0.165$, $p < 0.001$).

7.4.4 Variance Within and Between Observations

Before looking at how particular factors (varying between but not within observations) affected the lengths of interscan intervals, I tested whether the variance between observations was greater than that within observations. Selecting only observations with at least 3 inter-scan intervals and where there were no extended scans, between observation effects were highly significant ($F_{60,10} = 4.1842$, $p = 0.0002$). Where there were 10 or more intervals per record a similar result was obtained ($F_{158,12} = 3.522$, $p = 0.0001$).

7.4.5 Extended Scans

The mean logged inter-scan interval duration for an observation (excluding those intervals preceded immediately by an extended scan) was greater where no extended scans were recorded than where one or more extended scans were recorded (means 0.845 ± 0.035 and 0.662 ± 0.075 ; t-test $p = 0.020$). That is, the occurrence of extended scans was associated with shorter inter-scan intervals: both measures of vigilance increased together.

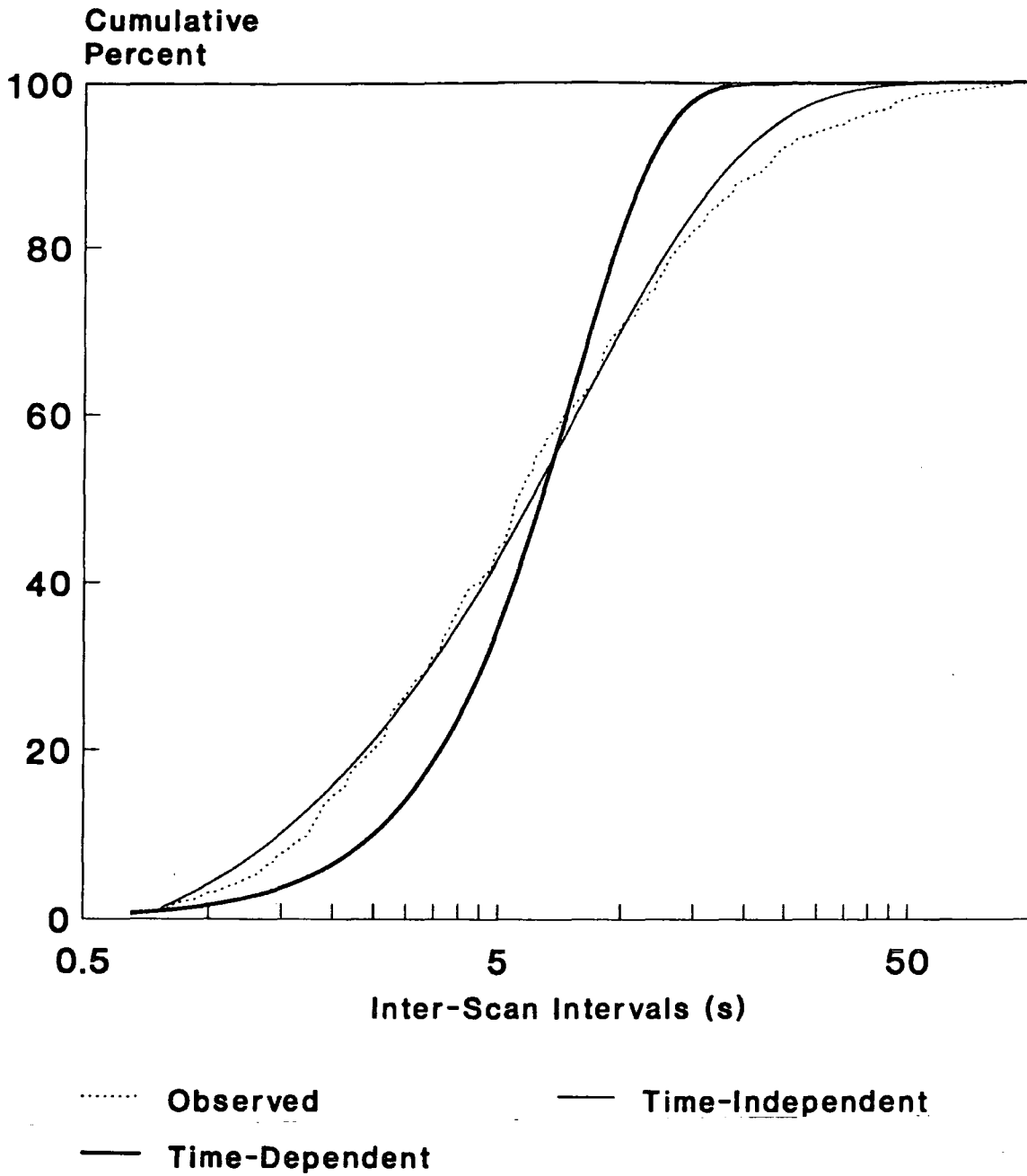


Figure 7.2 — Time-Independent and Time-Dependent Models of the Inter-Scan Intervals of Feeding Birds

However, inter-scan interval durations following extended scans were not significantly different from those following instantaneous scans (logged means 0.667 ± 0.068 , $n = 62$, and 0.711 ± 0.018 , $n = 597$, respectively; *t*-test, $t = -0.62$, $p = 0.54$).

Samples where any of the following were noted were selected (see Section 7.4.2). (1) Where a few brief preening movements were made; (2) where a rising tide caused sanderlings to take evasive action; (3) where other species caused sanderlings to take evasive action; and (4) where birds were seen to be flying off. Table 7.7 shows that extended scans tended to be associated with the occurrence of one or more such events during a record. The sample sizes were not sufficient to look more specifically at which factors tended to be associated with the occurrence of extended scans.

Movement score had no effect on the occurrence of extended scans (Table 7.8). However, vision score did have a significant effect on the occurrence of extended scans (Table 7.9): where vision was good there were fewer than expected extended scans. There was no relationship with tidal stage (Table 7.10).

7.4.6 Factors Affecting Durations of Inter-Scan Intervals

Since sample sizes were small and cases were not evenly distributed across all possible values of each variable, multivariate analyses could not be carried out. Instead, each factor was looked at in turn using *t*-tests (where the independent variable had only two categories) and one-way ANOVA (where there were more than two categories) on mean logged inter-scan interval durations. Cases where extended scans occurred were excluded.

The following factors had no significant effect on inter-scan interval duration. (1) The occurrence of the various events considered in section 7.4.5 ($t = 1.08$, $p = 0.29$); (2) visibility scores ($t = -0.67$, $p = 0.51$); (3) movement scores ($t = 1.92$, $p = 0.06$); (4) tidal stage ($F_{54,2} = 1.30$, $p = 0.28$); (5) presence or absence of preening birds ($t = 1.70$, $p = 0.10$); (6) flock size ($F_{34,3} = 1.49$, $p = 0.23$); (7) numbers of birds feeding within 5m ($F_{34,3} = 0.32$, $p = 0.81$); and (8) nearest neighbour distance ($t = 0.14$, $p = 0.89$).

These results show that although various events were found in Section 7.4.5 to

Extended scans	Events	
	none	≥ 1
none	37	20
≥ 1	5	11

Table 7.7 — Occurrence of Extended Scans in Relation to Occurrence of Various Events

$\chi^2 = 4.498, df = 1, p = 0.03$ with Yates correction.

Extended scans	Movement score	
	low	high
none	16	25
≥ 1	2	10

Table 7.8 — Occurrence of Extended Scans in Relation to Movement Scores

$\chi^2 = 1.192, df = 1, p = 0.28$ with Yates correction.

Extended scans	Vision score	
	low	high
none	19	27
≥ 1	27	8

Table 7.9 — Occurrence of Extended Scans in Relation to Vision Scores

$\chi^2 = 8.994, df = 1, p = 0.0027$ with Yates correction.

Extended scans	Tidal stage		
	fall	low	rise
none	25	18	14
≥ 1	5	7	4

Table 7.10 — Occurrence of Extended Scans in Relation to Tidal Stage

$\chi^2 = 1.025, df = 2, p = 0.60.$

be associated with the occurrence of extended scans, in cases where there were no extended scans the events were not associated with any decrease in inter-scan interval. That is, the events would only be associated with a decrease in inter-scan interval through their association with the occurrence of extended scans, which in turn are associated with shorter inter-scan intervals.

7.4.7 The Way in which Observations Ended

Observations on a focal bird ended in different ways: the bird walked away, flew away, started preening or continued feeding while observations were switched to another bird. An ANOVA shows that there is no relationship between the length of the last inter-scan interval and the way in which the record ended ($F_{83,4} = 1.23, p = 0.30$). Thus, there is no evidence for the length of inter-scan intervals varying according to the activity performed next.

7.5 Vigilance while Feeding by Different Methods

Sanderlings at Teesmouth feed by (1) pecking on rocky substrates; (2) pecking on sandy areas; (3) probing in sand; (4) 'stitch-feeding' in sand; and (5) water-column feeding (Section 2.3).

The ranges of feeding methods and of foraging substrates used by sanderlings raise the question of how vigilance is affected by whether foraging is visual or tactile; by the head position while foraging; and by constraints on the times at which a bird may raise its head.

Fewer observations were made of the vigilance of birds employing feeding methods other than pecking on rocky substrates. This was because the study of vigilance behaviour depends on the reliable recognition of scans which was only possible when birds were feeding by pecking with their heads down on rocky areas. When birds were using the other feeding methods, scans could be defined only subjectively as occasions when a bird appeared to look from side to side while walking; when it cocked its head to look upwards with one eye; or when it momentarily stopped feeding, apparently alarmed. Because of the difficulty in defining scans objectively, the results should be treated with some caution.

The extent of a feeding bird's vision is difficult to assess. When birds were probing, pecking on sand, or water-column feeding, their heads were generally held in a raised position, being lowered only to make the feeding movements. The difference between the head position while pecking on rocks and that while pecking on sand is apparently due to pecking actions on the former substrate being much more frequent and interspersed with much less movement. At other times birds may have their heads up for much of the time while feeding and so may have continuous good visibility.

Table 7.11 shows that mean scan rate differed considerably between feeding methods. The differences were significant (ANOVA, $F_{864,6} = 10.92, p < 0.005$). However, it proved difficult to compare the vigilance of birds using different feeding methods: where the head is normally in the down position, simple head-raises will be counted as scans whereas only more pronounced scans will be counted for birds feeding with their heads up.

When water-column feeding, the head is held in a characteristic position with the neck extended and the beak pointing vertically down. As it is apparently a visually-guided method (as opposed to stitch-feeding which is largely tactile), it might be hypothesized that birds would have to interrupt their concentration on feeding in order to look for predators. On the other hand, a bird feeding with its head up may be at an advantage with respect to one which is, for example, stitch-feeding.

These unknowns make it very difficult to draw conclusions about the levels of vigilance which birds might be able to maintain while feeding in different ways. The levels of vigilance possible while feeding may have implications for the sizes and spacing of flocks of birds using different feeding methods. If some feeding methods can be employed while maintaining higher vigilance levels than are possible while using other methods then, according to the hypothesis that one of the advantages of larger flocks is their greater corporate vigilance, there may be less pressure on birds to join large flocks when employing such methods.

Although there are difficulties in comparing methods, data for each feeding method can be analysed separately. Taking each feeding method in turn, analyses of covariance of \log_{10} -transformed scan rate were carried out by categories of time of

Feeding method	Mean scan rate	S.E.	<i>n</i>
Probing	3.74	0.73	38
Stitching	7.05	0.59	124
Water	3.95	0.73	39
Pecking (sand)	6.41	0.41	257
Pecking (rocks)	6.23	0.26	344

Table 7.11 — Mean Scan Rates for Birds Using Different Feeding Methods

Feeding method	<i>n</i>	Flock size		N. n. dist.		No. in 5m	
		corr.	<i>p</i>	corr.	<i>p</i>	corr.	<i>p</i>
Probing	26	-0.48	0.01	0.04	0.42	-0.06	0.38
Stitching	49	0.17	0.12	0.23	0.05	-0.23	0.05
Water	14	0.04	0.43	0.20	0.22	0.14	0.30
Pecking (sand)	149	0.05	0.25	0.03	0.38	0.06	0.23

Table 7.12 — Partial Correlations with Scan Rate for Different Feeding Methods

The table gives partial correlation coefficients and their significance levels for \log_{10} -transformed scan rate with each column variable, controlling for the other column variables.

year, time of day and time of tide with flock size, numbers within 5m, and nearest-neighbour distance as the covariates. These failed to find any significant effects on scan rate of the time variables, so cases were combined for computation of the partial correlations given in Table 7.12.

The findings of (1) a negative correlation between scan rate and flock size for probing birds, and (2) that the scan rate of stitching birds increased with the distance to the nearest neighbour while decreasing with the numbers of birds within 5m, are consistent with the hypothesis that individuals should decrease their vigilance with increasing flock size and density (Section 7.1.3). Flocks of probing birds tended to be more evenly dispersed than flocks of stitching birds (personal observations) which tended to consist of one or more dense aggregations of stitching birds, often with pecking birds more widely spaced around the periphery. This difference in flock spacing may explain why the vigilance of probing birds appears to respond to flock size while that of stitching birds responds to the numbers within a smaller radius.

There were too few data for conclusions to be drawn in the case of water-column feeding birds and, despite a large sample size, no flock size and spacing variables had significant effects in the case of birds pecking on sand.

Further work could include an analysis of the durations of stitch-feeding attempts, where the duration is the time for which the bill is moved through the sand. Between some stitch feeding attempts the bill is raised only briefly out of the sand. Thus, the duration of a stitch-feeding attempt may be shorter than what was taken above as the inter-scan interval duration: only more pronounced upward movements of the head between stitches were counted as scans. The fact that the stitch duration can be recorded more objectively than the inter-scan interval probably makes it the more reliable measure.

7.6 Vigilance While Preening

7.6.1 Introduction

In this section, the vigilance of preening sanderlings is examined so that comparisons can be drawn with that of feeding birds. Only one study of vigilance while

preening has been published (Redpath, 1988). Studying the vigilance of feeding birds is complicated by the large number of variables affecting feeding behaviour. The costs and benefits of feeding as opposed to being vigilant may be affected by prey density and availability and by the densities of other birds. Birds may scan for a number of reasons (Section 7.1.6). Watching birds which are preening rather than feeding means that fewer of these factors need to be considered. The vigilance of preening birds can therefore be used as a base-line against which to compare the more complicated feeding situations.

As when studying the vigilance of feeding birds, the effects of flock size on vigilance were investigated, together with nearest-neighbour distance, flock density and the numbers within a certain radius in order to find what birds are really responding to (Section 7.1.3). The hypothesis that birds need to spend more time feeding and therefore are less ready to break off from either feeding or preening in order to scan in mid-winter was also tested.

7.6.2 Methods

Data collection was carried out in October and November 1988 and in January and February 1989 at Redcar Rocks. The conditions under which observations were made were standardized as much as possible. Observations were mostly made between two hours before and two hours after low water of tides of medium range (approximately 3.8m) on rocky outcrops only exposed at these times. Variables of substrate type, tidal level and time of day were recorded so that they could be brought into the analysis if necessary.

The following were noted for each individual for which a vigilance record was taken.

- (1) The size of the flock of which the individual was a member;
- (2) the individual's nearest-neighbour distance;
- (3) the number of birds within 5m of the individual;
- (4) the number of these which were feeding;
- (5) the number of these which were preening; and
- (6) the number which were roosting.

Records were made by speaking into a continuously running tape recorder. On playing back the tape, the computer program MINKEY was used in order to

accurately time the lengths of inter-scan intervals (see Section 7.4.2). As in Section 7.4, scans were classified as (1) instantaneous, and (2) extended (where the scan lasted for a measurable length of time). Sample sizes are small since many cassette tapes were erased for re-use before this analysis was carried out.

The following analyses refer to a sample of approximately 200 records of preening birds, each record lasting a minimum of 20 seconds. This was sufficient to avoid a bias towards short inter-scan intervals (see Section 7.4.2).

7.6.3 Frequency Distribution of Interval Lengths

The mean inter-scan interval length was $2.688 \pm 0.035s$, $n = 2899$. (This excludes cases which differed significantly and appreciably, i.e. inter-scan intervals which followed extended scans and records during which the bird was rubbing, see Section 7.6.6). \log_{10} -transformation of inter-scan interval durations produced a good fit to a normal distribution allowing the use of parametric statistics.

As in Section 7.4.3, the frequency distribution of inter-scan intervals was tested against those expected on the basis of different models of scanning (Section 7.1.1; Figure 7.3). A time-dependent model gave a better fit (where $\lambda = 0.280$, $m = 0.12$ secs., Kolmogorov-Smirnov 2 sample test $D_{max} = 0.052$, $p \ll 0.05$) than a time-independent model (where $\lambda = 0.542$, $m = 0.85$ secs., $D_{max} = 0.212$, $p \ll 0.001$).

7.6.4 Intervals Following Extended Scans

\log_{10} -transformed inter-scan interval durations were significantly and appreciably shorter when preceded by extended scans than when preceded by instantaneous scans (means 0.115 ± 0.033 and 0.360 ± 0.240 respectively, t-test, $t = -7.25$, $p < 0.0005$.)

The following analyses are confined to intervals following instantaneous scans.

7.6.5 Ends of Records

Most records ended with the bird walking off to feed. Because there were few cases where the record ended differently, tests of the effect on vigilance of how the record ended and what the bird did next could not be carried out. It is assumed that,

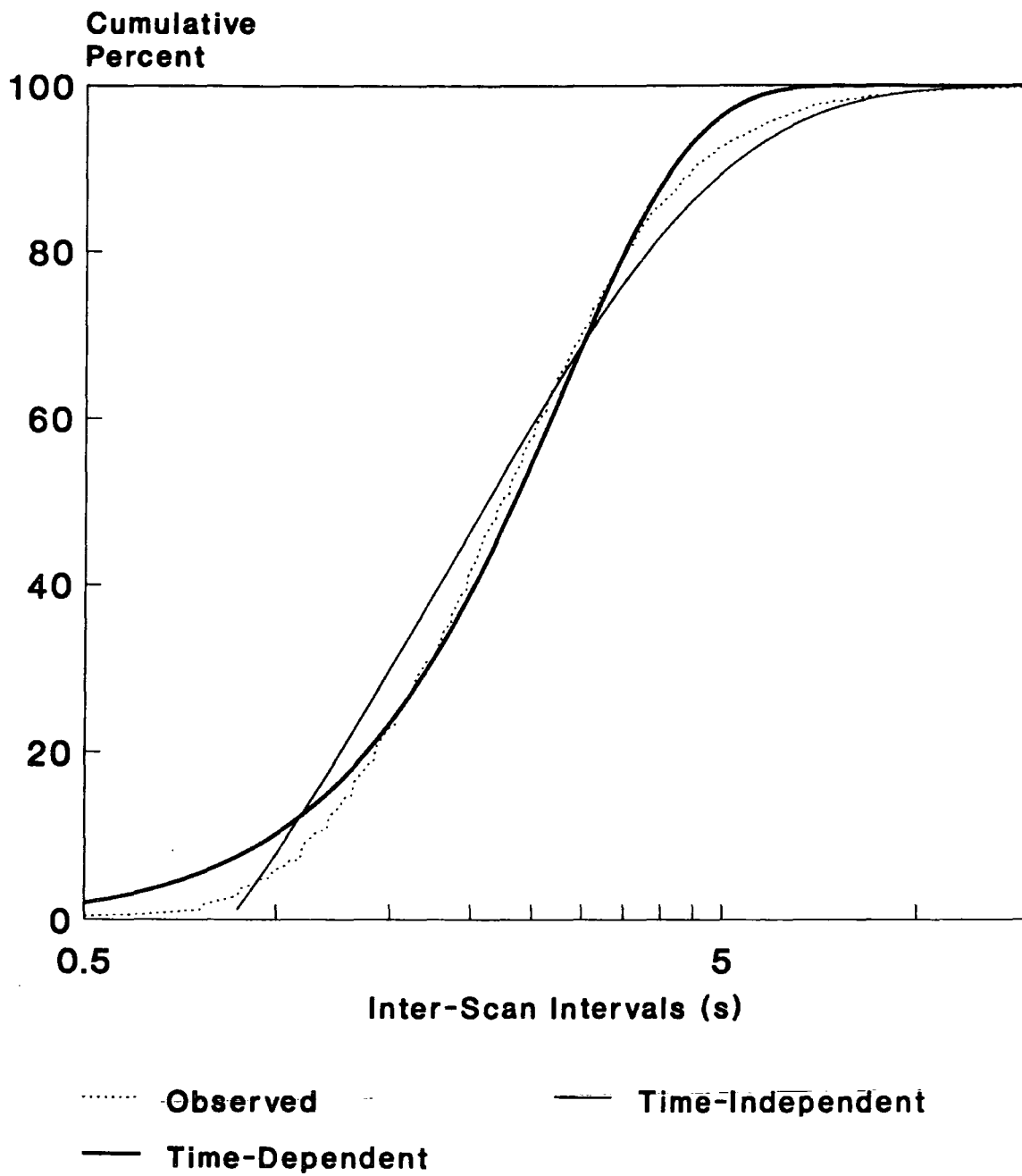


Figure 7.3 — Time-Dependent and Time-Independent Models of the Inter-Scan Intervals of Preening Birds (1)

as in the case of feeding birds (Section 7.4), vigilance and the way which a record ended were not related.

7.6.6 Type of Preening

It was apparent that birds rubbing oil from the preen gland over their bodies made much faster movements and scanned much more frequently than birds making other preening movements. Such birds were therefore distinguished from the others. For each observation where there were at least three inter-scan intervals (excluding those following extended scans) the mean \log_{10} -transformed inter-scan interval was computed. The mean of these values for birds 'rubbing' was 0.184 ± 0.021 . This was significantly shorter than that for other preeners: mean = 0.389 ± 0.011 , t-test, $t = -8.61$, $p < 0.0005$.

The following analyses exclude 'rubbing' birds.

7.6.7 Other Factors Affecting Inter-Scan Interval Durations

Mean logged inter-scan intervals were computed for each vigilance record as described in the previous section. Observations were divided according to whether they were made in October and November or January and February. An analysis of covariance of mean logged inter-scan interval by season was carried out with flock size; number of birds within 5m preening; number of birds within 5m feeding; distance to nearest-neighbour; and number of extended scans made during the observation as the covariates. Significant effects both of season and of the covariates were found (Table 7.13). The mean logged inter-scan interval length, adjusted by the covariates, for the autumn was smaller than that for the winter (Table 7.14). This result is consistent with the hypothesis that sanderlings should be less vigilant in mid-winter because of the higher pressure to feed (Section 7.1.5). The analysis was repeated with each inter-scan interval as one record (rather than each observation). The results were similar (Tables 7.15 and 7.16).

Because cases from autumn differed significantly from those in winter, the data were divided by season. The following analysis includes only those cases collected in the autumn. Sample sizes were insufficient to carry out a similar analysis on data for January and February.

Source of variation	SS	df	MS	F	p
Within cells	2.23	140	0.02		
Regression	0.17	5	0.03	2.18	0.059
Season	0.13	1	0.13	8.42	0.004

Table 7.13 — ANCOVA of Mean Log₁₀-Transformed Inter-Scan Interval Durations by Season (1)

Seasons: October–November and January–February. The regression term refers to the covariates of flock size; number preening within 5m; number feeding within 5m; nearest-neighbour distance; and number of extended scans.

Season	Mean	± S.E.	n
Oct–Nov	0.377	0.012	141
Jan–Feb	0.450	0.020	30

Table 7.14 — Effects of Season on the Vigilance of Preening Birds (1)

Mean log₁₀-transformed inter-scan interval durations for each record

Source of variation	SS	df	MS	F	p
Within cells	141.06	2622	0.05		
Regression	2.42	5	0.48	8.98	< 0.0005
Season	2.76	1	2.76	51.37	< 0.0005

Table 7.15 — ANCOVA of Log₁₀-Transformed Inter-Scan Interval Duration by Season (2)

Seasons: October-November and January-February. The regression term refers to the covariates of flock size; number preening within 5m; number feeding within 5m; nearest-neighbour distance; and number of extended scans.

Season	Mean	± S.E.	n
Oct–Nov	0.350	0.005	2521
Jan–Feb	0.422	0.012	378

Table 7.16 — Effects of Season on the Vigilance of Preening Birds (2)

Log₁₀-transformed inter-scan interval durations

Variable	All flocks		Flocks < 60		Flocks ≥ 60	
	corr.	<i>p</i>	corr.	<i>p</i>	corr.	<i>p</i>
Flock size	0.11	0.13	-0.12	0.18	0.45	< 0.005
No. preening in 5m	0.10	0.15	0.11	0.21	0.09	0.27
No. feeding in 5m	-0.12	0.12	-0.16	0.12	-0.03	0.42
Nearest neighbour dist.	-0.07	0.25	0.11	0.20	-0.35	0.01
No. of extended scans	-0.19	0.03	-0.27	0.02	-0.16	0.14

Table 7.17 — Partial Correlations With Inter-Scan Interval

The table gives partial correlations between the row variables and the mean logged inter-scan interval (see text) controlling for the other row variables. Sample sizes were 59 for flocks less than 60 and 49 for flocks of 60 or more.

A plot showed that inter-scan interval appeared to decrease with flock size up to flock sizes of around 60 and then increase. An attempt to bring flock size into the regression as a quadratic function failed so cases were divided according to whether flock sizes were less than or greater than 60.

Table 7.17 shows that inter-scan interval increased with flock size (as predicted) and decreased with nearest-neighbour distance (as predicted), but only where flock size was 60 or more. Inter-scan interval decreased as the number of extended scans increased, but this was only significant for smaller flocks.

7.7 Vigilance While Preening: Analysis of Video Tapes

7.7.1 Introduction

The main questions addressed in this section are:

- (1) How does vigilance in terms of (a) the lengths of time between scans and (b) the durations of scans vary with the sizes, densities, and predominant activities of flocks.
- (2) Do frequency distributions of inter-scan intervals give better fits to time-dependent or to time-independent (Lendrem *et al.*, 1986) models of scanning behaviour?
- (3) Are sequences of inter-scan interval durations non-random (Section 7.1.1; Desportes *et al.*, 1989)?
- (4) How do the durations of scans and of the intervals between scans vary with the type of preening movements performed during those intervals? It might be that different activities impose different constraints on scanning behaviour (see Section 7.1.7) or it may be that different activities have different associated costs and benefits. If, as is generally assumed, time is limiting then the lengths of time allocated to different activities may be varied in line with those costs and benefits. According to this line of reasoning, if there are different costs involved in delaying or not performing the various kinds of preening movements then the differences may lead to differences in vigilance. In other words, the way in which the balance

is struck between vigilance and other activities may vary according to the nature of those activities.

The interval between scans might depend on whether there are costs involved in switching activities, and if so how great these are. Take as an example a bird which is covering its feathers with oil secreted by the preen gland. This type of preening is associated with very rapid movements, perhaps necessary for efficient transfer of the oil. It could be argued that if a bird has completed the sequence of movements involved in spreading the oil over its feathers then the cost of breaking off to give a scan may be small. But the efficiency of more complex preening operations might be considerably reduced if they were interrupted frequently.

The hypothesized costs of breaking off from one activity in order to perform another are most readily imaginable in terms of time: a bird making one long preening movement might need less time than one which interrupts the movement because of (i) the time taken to move to a scanning posture; (ii) the time spent scanning, (iii) the time taken to return to preening, and perhaps also (iv) the time taken to regain the stage of preening reached before the interruption. The latter is based on the notion that in the case of a complex task the bird may not simply be able to pick up where it left off.

If interruptions do not have a cost then it can be predicted that there should be no differences between movement types in inter-scan interval durations. If there are costs in terms of reason (i) then intervals while preening the breast, for example, should be shorter than those while preening the tail. If there are costs in terms of reason (iv) then more complex movements should be associated with longer inter-scan intervals.

Differences in inter-scan intervals between movement types could also be predicted if different movement types were associated with different degrees of visibility (i.e. ability to see the surrounding area) while preening (see Redpath, 1988). Thus, a bird preening its breast may have better visibility than one preening its belly and so may not need to break off to scan as frequently.

Different types of movement may also be associated with differing degrees of risk: birds preening their wings may be less capable of taking flight rapidly and so may

need to be more vigilant.

7.7.2 Methods

Birds preening in flocks on the feeding areas at Redcar Rocks were video-taped on 3 days in late March and early April during the periods from 2 hours before low water to low water: little preening takes place on the feeding areas outside of these times. For each record the following variables were noted:

- (1) Flock size;
- (2) number of birds of other species present;
- (3) distance to the nearest-neighbour;
- (4) activity of nearest-neighbour;
- (5) percentage of flock preening;
- (6) tidal stage;
- (7) time since last disturbance; and
- (8) substrate type.

Data were transcribed from the video tapes using the MINKEY program to convert key presses into codes representing different behavioural events (see Section 7.4.2). Because events occurred in rapid succession, the times of events were first spoken into a cassette recorder and the tapes were then played back so that the keyboard could be kept in view while the keys were pressed and mistakes thereby minimised. A sequence of less rapid events was used to show that this indirect method did not produce differences of more than a few hundredths of a second in interval lengths.

Events were recorded as in Section 7.4.2. That is, the time of each scan was recorded, together with its duration if measurable, and the beginnings and endings of any other activities.

During preening movements the following different behaviours were recorded. The types of movement were used to describe the inter-scan interval, computed as the time between scans before and after the movement recorded.

- (1) BREAST AND NECK. The head is often raised during such movements so that it points vertically down.
- (2) BELLY: The head is normally lowered so that the bill points horizontally into the body.

- (3) WING.
- (4) UNDERWING.
- (5) BACK.
- (6) PREEN GLAND AND BASE OF TAIL AREA. As it was sometimes difficult to see where the tip of the bill was these movements were considered together.
- (7) RUBBING. This involved rubbing the back of the head over the body.
- (8) SCRATCHING. Usually of the face, using the foot.
- (9) BEHIND. Birds often preened the side of their body facing away from the camera. Although the general position of the head can be seen in such cases, the tip of the bill could not and so to avoid errors such movements were not assigned to any of the above categories.

Flock size, tidal stage, substrate type, nearest-neighbour distance and activity, and time since disturbance were recorded so that if significant effects of these variables were found, the data could be subdivided accordingly before analysis with respect to the factors of interest. It was not intended that analyses by all of these factors should be attempted.

7.7.3 Comparison Between Birds in Different Flock Types

Flocks on the feeding sites were classed as compact preening and roosting (CPR) flocks and scattered feeding (SF) flocks. Focal individuals in CPR flocks were members of larger, more compact flocks in which more birds were preening and roosting (Table 7.18).

Selecting those of the main interval types which did not differ significantly in duration (i.e. WING, UNDERWING, BREAST, BELLY, TAIL, and BACK; see Section 7.7.5), mean logged inter-scan interval durations were computed for each observation where there were at least four intervals of these types.

Mean \log_{10} -transformed inter-scan interval durations were significantly longer for birds in compact preening and roosting (CPR) flocks than for those in scattered feeding (SF) flocks (Table 7.19) and the number of extended scans was greater for birds in SF flocks than for birds in CPR flocks. Therefore, by both measures, individuals were less vigilant when in large, compact, preening and roosting flocks than when in smaller, more scattered, predominantly feeding flocks. Extended

scans were too short relative to the level of accuracy in timing for a useful comparison to be made between the durations of extended scans in the different flock types.

7.7.4 Comparison of Birds in Different Situations

All further analyses were confined to preening birds in compact preening and roosting flocks. All focal birds had nearest neighbours at distances of two bird lengths or less which were roosting or preening.

The following analysis is not intended to provide a rigorous test of whether any of the variables considered had a significant effect on vigilance: it is intended to show whether cases can be lumped together for further analysis. The following variables were considered: flock size, days through the winter, substrate and percentage of the flock preening. The number of birds within a 5m radius was not considered because it correlated strongly with total flock size. The activity of the nearest neighbour was not considered because it was strongly related to the percentage of birds preening. Each of the variables were given two or three categories. Because no data were obtained for several combinations of these categories, a multivariate analysis could not be carried out. Instead each combination of categories for which more than three mean interval duration values were obtained was taken as a category of the variable SITUATION. Thus, one value of SITUATION might refer to cases where the flock size was small; the proportion preening was small; the substrate was rock; and the day was the first day of filming.

To simplify the analysis, cases were divided according to the preening movement made. Each interval length was \log_{10} -transformed and the mean logged interval duration was computed for each observation. Because of the large variance of mean values when the sample size was small, this procedure was confined to observations where there were four or more intervals of the particular type.

This procedure drastically reduces the number of data points but has the advantage of not being subject to the problem of interval lengths within an observation being statistically dependent. On the other hand, it could be argued that the statistical methods used are conservative in reducing the samples to mean values

Flock type	Flock size		No. in 5m		Nearest-neighbour distance (m)		Nearest-neighbour activity			Percentage of flock feeding		n
	Mean ± S.E.		Mean ± S.E.		Mean	± S.E.	Feed	Preen	Roost	Mean ± S.E.		
SF	32.7	10.1	9.9	3.1	0.91	0.42	10	1	0	81.8	1.2	11
CPR	75.3	4.4	26.1	1.7	0.23	0.01	0	35	31	51.1	2.0	66
t_{75}	-3.71		-3.73		4.12					-6.17		
p	< 0.0005		< 0.0005		< 0.0005					< 0.0005		

Table 7.18 — A Comparison of Scattered Feeding Flocks with Compact Preening and Roosting Flocks

Flock type	Mean log ₁₀ -transformed ISI duration			No. of extended scans per min.		
	Mean ± S.E.		n	Mean ± S.E.		n
	SF	0.293	0.027	9	2.062	0.563
CPR	0.398	0.011	62	0.089	0.116	66

Table 7.19 — Vigilance of Birds in Flocks of Different Types

Mean log₁₀-transformed ISI durations were longer for birds in compact preening and roosting (CPR) flocks than for those in scattered feeding (SF) flocks: $t_{69} = -3.33, p = 0.001$. The number of extended scans was greater for birds in SF flocks than for birds in CPR flocks: $t_{75} = 3.35, p = 0.001$.

for each interval type and observation, i.e. that the methods may fail to uncover real differences.

No significant effects of situation were found. For example, for intervals during which the breast was preened in eight SITUATIONs, an ANOVA of mean logged inter-scan interval duration gave $F_{41,7} = 1.20, p = 0.33$.

Because no significant effects were apparent within the ranges of values of the variables in the data collected, the data were lumped for the following analyses.

7.7.5 Comparison of Intervals of Different Types

Mean interval durations for different interval types from the same observations were assumed to be statistically independent. (This is justified by the finding in Section 7.7.7 that correlations between the durations of successive intervals of different types were generally weak or non-significant).

There was a significant effect of movement type (i.e. WING, UNDERWING, BELLY, BREAST, TAIL, BACK, BEHIND, and RUBBING) on mean \log_{10} -transformed interval duration ($F_{167,7} = 7.51, p < 0.00005$). A Scheffe test showed that this was due to RUBBING intervals being significantly shorter than all others (see Table 7.20). No other pairings gave significant differences showing that, in general, the type of preening movement performed during inter-scan intervals does not affect the length of those intervals. Nevertheless, movement type can affect interval length, giving some support to the hypothesis discussed in Section 7.7.1 that vigilance might be affected by the costs and benefits of different activities or by constraints imposed by those activities.

Unless otherwise stated, RUBBING and BEHIND intervals are excluded from the following analyses: the former because they were significantly different in duration from other interval types; the latter because they were more difficult to record accurately. Exclusion of rubbing intervals results in a real change in the frequency distribution of interscan intervals, (rather than simply one caused by removing recording errors, as should be the case when BEHIND intervals are excluded). Therefore, when discussing the overall frequency distribution of interval durations, what is being discussed is that for birds which were not RUBBING.

Movement type	Inter-scan interval		
	Mean	± S.E.	<i>n</i>
Wing	0.373	0.016	20
Back	0.417	0.026	15
Tail	0.414	0.031	20
Breast	0.404	0.012	51
Belly	0.380	0.025	20
Underwing	0.411	0.025	10
Rubbing	0.169	0.030	7
Behind	0.472	0.023	32

Table 7.20 — Inter-Scan Interval Durations in Relation to Preening Movement Types

The data are based on mean \log_{10} -transformed values for each movement type for each observation. Means were only computed where there were 4 or more movements of the particular type during the observation.

7.7.6 Is Scanning a Time-Dependent Process?

Only intervals which commenced at the end of an instantaneous scan were included in this analysis because the occurrence of prolonged scans affects the lengths of those intervals which follow (Section 7.7.10). The analysis is therefore concerned with normal vigilance, while recognizing that this is not the full picture and that the shape of the distribution of inter-scan intervals may be influenced by other events such as prolonged scans.

The sample of 1458 intervals had a mean length of 2.79 ± 0.03 s. A Kolmogorov-Smirnov one-sample test showed a significant difference from a normal distribution ($D_{max} = 0.10, p < 0.00005$), but \log_{10} -transformation produced a good fit.

As in Sections 7.4.3 and 7.63, the frequency distribution of inter-scan intervals was tested against those expected on the basis of different models of scanning. A time-dependent model gave a better fit (where $\lambda = 0.282, m = 0.33$ secs., Kolmogorov-Smirnov 2 sample test $D_{max} = 0.031, p \gg 0.05$) than a time-independent model (where $\lambda = 0.536, m = 1.03$ secs., $D_{max} = 0.219, p < 0.001$).

7.7.7 Correlations Between the Lengths of Successive Intervals

Although the relationship explains little variance, there was a significant effect of the length of one interval on that of the next where both intervals were of the same type ($F_{1252,1} = 74.69, p < 0.00005, Beta = 0.237$). A regression gave:

$$\log INT = 0.2647(\pm 0.0122) + 0.2362(\pm 0.0273)\log LAST,$$

where INT was the length of the interval and LAST was the length of the previous interval. This relationship held within observations and so could not be accounted for in terms of between-observation differences. Where successive intervals were of different types there was no significant relationship.

Given that there was no overall significant difference between the lengths of intervals of different types, it is surprising that a factor affecting the lengths of intervals should only act where successive intervals are of the same types. One possibility is that the variance in interval lengths between bouts (where a bout is a series of movements of the same type) is greater than the variance within bouts, and that

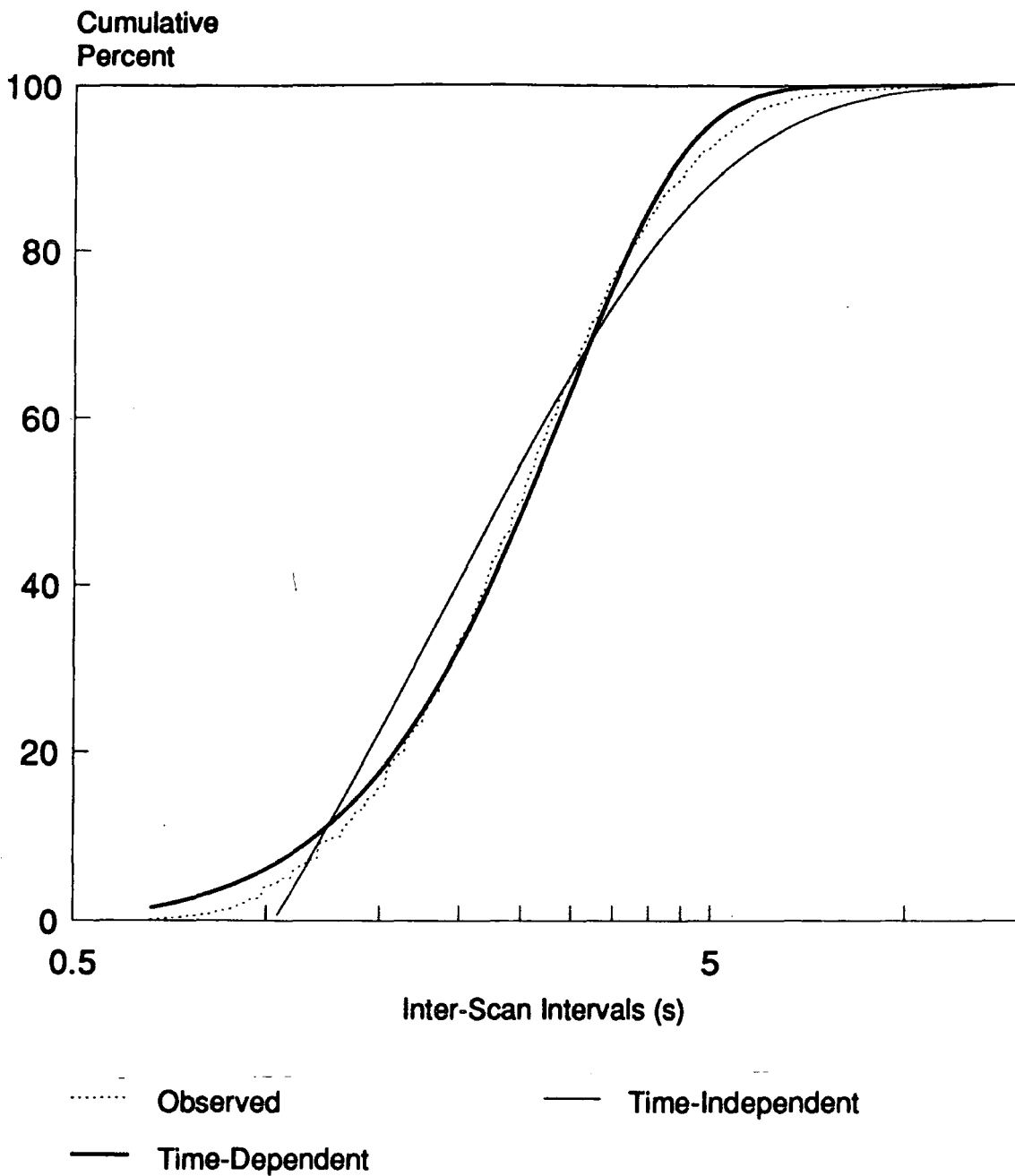


Figure 7.4 — Time-Dependent and Time-Independent Models of the Inter-Scan Intervals of Preening Birds (2)

this holds whether or not bouts are of the same type (since there is no overall difference between intervals of different types). A more profitable way of looking at the relationship between the length of one inter-scan interval and that of the next is to examine sequences of inter-scan intervals.

7.7.8 The Sequential Pattern of Inter-Scan Interval Durations

Desportes *et al.* (1989) have pointed out that the frequency distribution of inter-scan intervals may approximate to that expected if scanning were a random process while sequences of inter-scan intervals may be non-random.

Figures 7.5 and 7.6 give example sequences of inter-scan intervals and Table 7.21 shows that many were non-random. This non-randomness was due to there being more switches than expected from intervals being longer than previous ones to intervals being shorter than previous ones. That is, if one interval was longer than the previous one then the next will tend to be shorter. This is consistent with the results of Desportes *et al.* for data from a purple sandpiper, *Calidris maritima*, and barbary doves, *Streptopelia visoria*.

An inter-scan interval which is longer than both preceding and following intervals can be considered as a peak. Table 7.22 gives the frequencies of different gap lengths between peaks in terms of the numbers of inter-scan intervals. The results were very similar to those of Desportes *et al.* who found mean gaps between peaks of 2.79–3.14 intervals.

7.7.9 Sequences of Movements of the Same Type

There are differences between movement types in the lengths of bouts, i.e. the numbers of each type of movement performed before switching to a different movement type (Table 7.23; $\chi^2 = 60.89, p < 0.005$). Scratching movements occur in the shortest bouts; rubbing movements in the longest. The small median bout lengths make it difficult to look at between bout variance in relation to within bout variance, within observation variance, and between observation variance.

7.7.10 Extended Scans

The distribution of the numbers of extended scans per observation period was

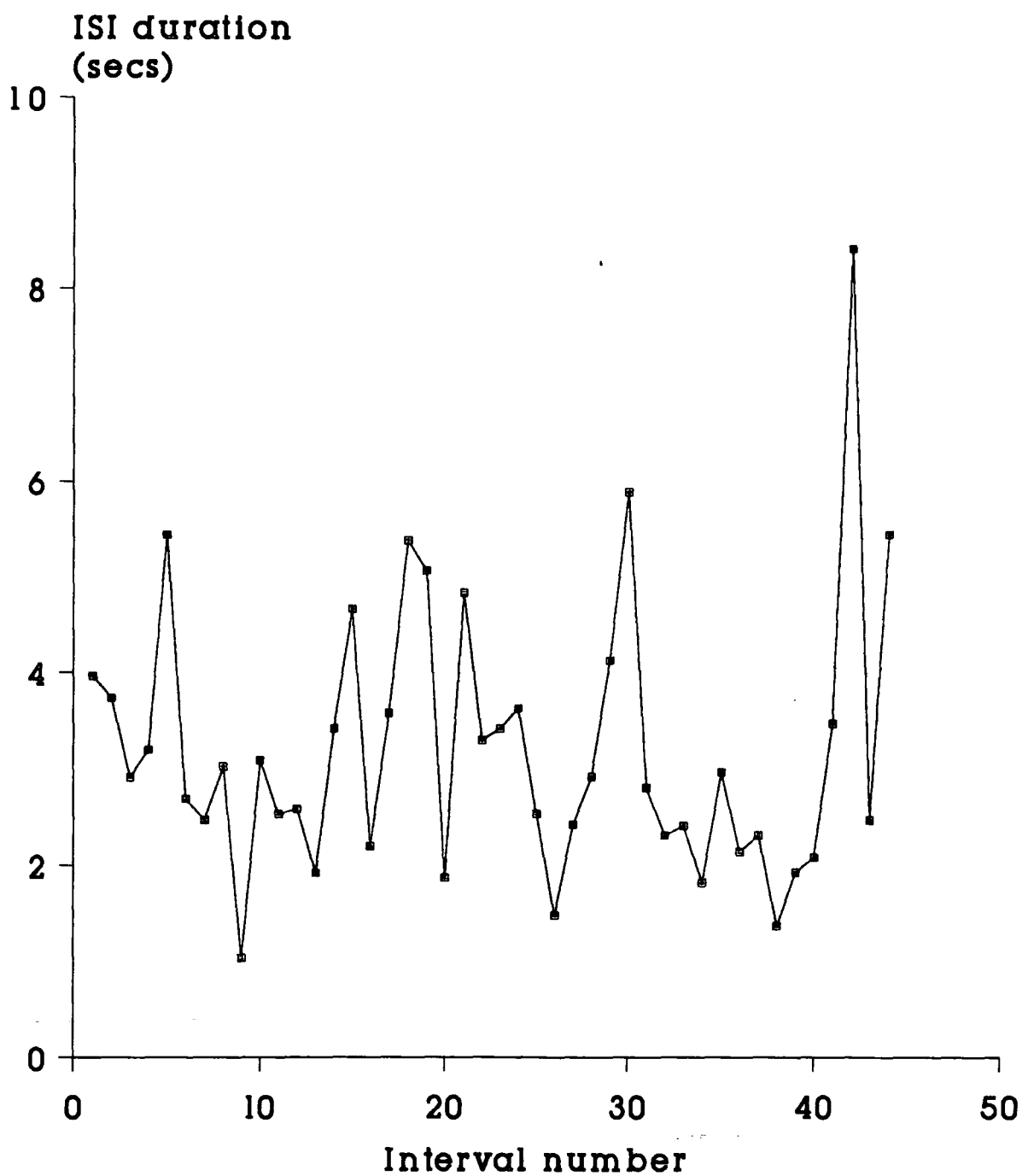


Figure 7.5 — An Example Sequence of Inter-Scan Interval Durations
(1)

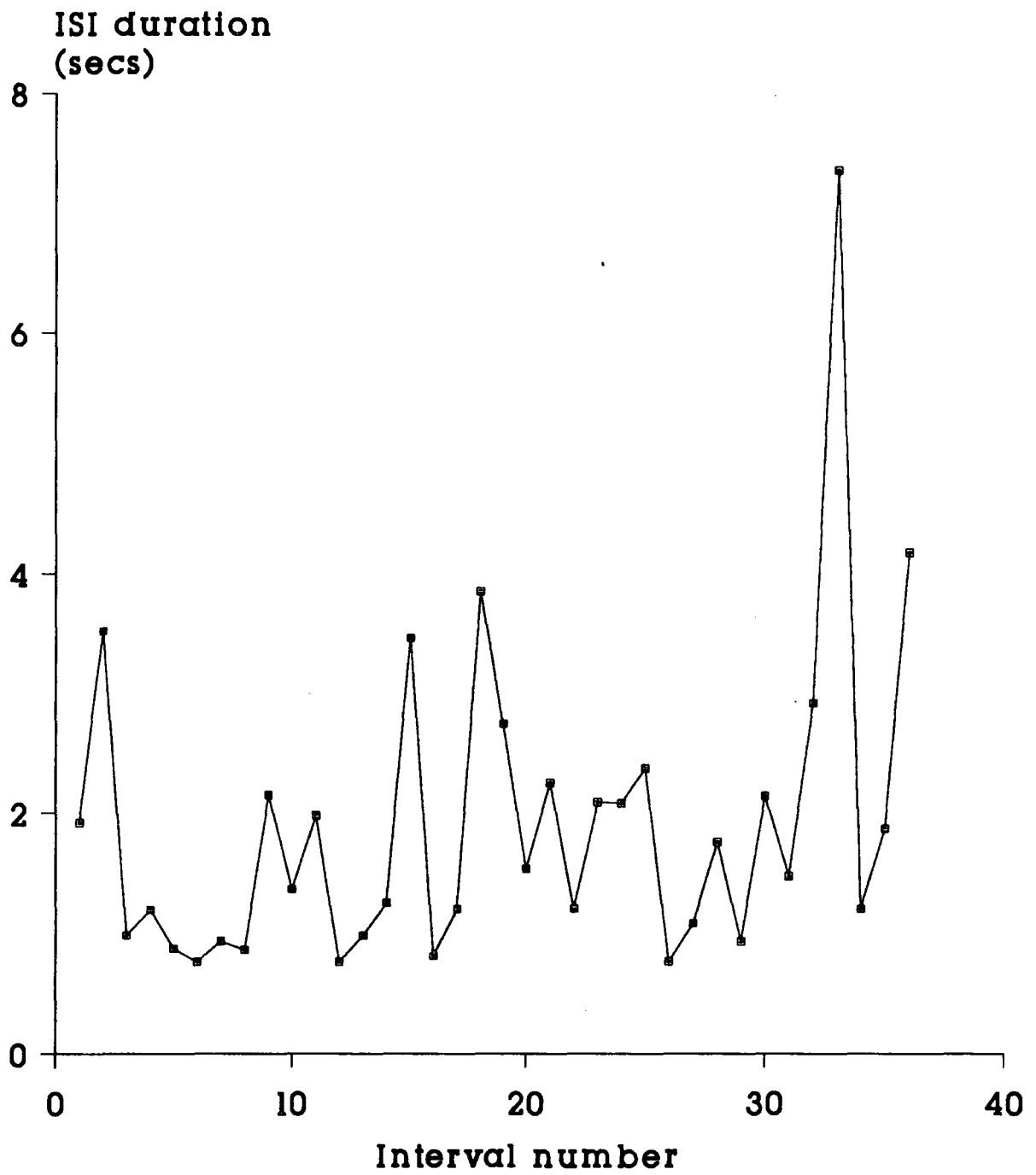


Figure 7.6 — An Example Sequence of Inter-Scan Interval Durations
(2)

No. of comparisons	No. of runs	Difference < 0	Difference ≥ 0	Z	p
30	22	14	16	2.07	0.038
30	17	11	19	0.63	0.530
30	19	16	14	0.96	0.338
31	21	16	15	1.47	0.142
33	18	16	17	0.01	0.996
34	26	15	19	2.73	0.006
36	24	16	20	1.62	0.106
36	23	17	19	1.21	0.228
36	26	21	15	2.44	0.015
37	26	17	20	2.06	0.040
39	24	18	21	1.02	0.309
40	25	21	19	1.14	0.254
43	28	20	23	1.58	0.113
43	28	19	24	1.66	0.098
50	35	25	27	2.57	0.010
52	35	29	23	2.37	0.018
52	35	25	27	2.26	0.024
54	33	26	28	1.39	0.166
68	45	33	35	2.45	0.014

Table 7.21 — Runs Tests on Differences Between Successive Inter-Scan Interval Durations

Of 19 samples, 8 sequences were significantly non-random at the $p < 0.05$ level.

No. of intervals between peaks	Frequency
2	210
3	166
4	73
5	34
6	7
7	4
8	2
Total	496

Table 7.22 — Numbers of Inter-Scan Intervals Between ‘Peaks’

Peaks are defined as inter-scan interval durations which are longer than those preceding and following. Mean = 2.956 ± 0.049 .

Movement type	Intervals <i>n</i>	Bouts <i>n</i>	Bout length	
			med.	max.
Wing	288	97	1	13
Back	287	75	1	19
Tail	295	74	1	11
Breast	370	161	2	16
Belly	250	108	1	7
Scratch	166	24	1	2
Underwing	317	49	2	12
Rubbing	429	24	4	23

Table 7.23 — Sequences of Preening Movements of the Same Type

skewed in that there were more records with large numbers than would be expected on the basis of a Poisson distribution (mean = 1.59, $\sigma = 2.11$, $n = 66$), though this is in part due to variation in observation length. The distribution of extended scan durations was also skewed: there were more long scans than expected on the basis of a Poisson distribution.

Types of Movement Preceding and Following Extended Scans

Using the observed frequencies of each type of interval in cases where the interval neither preceded nor followed an extended scan, the expected frequencies of each type of interval immediately preceding but not following extended scans were computed. Table 7.24 shows that some interval types were more likely to precede extended scans than were others. In particular, SCRATCHING movements tended to precede extended scans while RUBBING movements were much rarer than expected. The tendency for movements preceding extended scans to have themselves followed extended scans was greater than that for movements preceding instantaneous scans, illustrating the clumped distribution of extended scans in time.

A corresponding procedure to that above showed that some types of interval were more or less likely to occur after extended scans than would be expected on the basis of their numbers when neither preceding nor following extended scans (Table 7.24). There were markedly fewer RUBS than expected and more BELLY movements. However, there were no more SCRATCHES than expected, as would be predicted if the same factor determining the likelihood of different types of event occurring before an extended scan also determined events immediately after.

The Lengths of Intervals Before and After Extended Scans

Intervals were divided into (1) those preceding extended scans but not following them; (2) those following extended scans but not preceding them; and (3) those neither preceding nor following extended scans. An ANOVA of logged interval duration (Table 7.25) showed a significant effect of scan type (i.e. categories (1) to (3) above) with no effect of interval type (i.e. types of preening movement performed) and no significant interaction between the two. A Scheffe test showed that the

Movement type	Before			After		
	Observed	Expected	χ^2	Observed	Expected	χ^2
Wing	13	10	1.2	6	9	1.2
Back	5	8	1.4	9	8	0.1
Behind	18	15	0.6	7	15	4.0
Tail	7	8	0.0	3	7	2.5
Breast	20	27	1.6	36	26	3.9
Belly	13	8	3.5	18	8	14.3
Scratch	5	1	17.2	1	1	0.0
Underwing	7	5	0.6	5	5	0.0
Rubbing	0	7	7.1	1	7	5.1

Table 7.24 — Frequencies of Different Movement Types Before and After Extended Scans

(a) Before: $\chi^2 = 33.31$, $df = 8$, $p = 0.01$. (b) After: $\chi^2 = 30.95$, $df = 8$, $p < 0.01$.

Source of variation	Sum of squares	Degrees of freedom	Mean Square	<i>F</i>	<i>p</i>
Within cells	68.62	1447	0.05		
Scan type	1.37	2	0.69	14.48	< 0.005
Interval type	0.23	5	0.05	0.98	0.43
Interaction	0.29	10	0.03	0.62	0.80

Table 7.25 — Analysis of Variance of Interval Durations by Scan Type and Interval Type

Each interval was considered as an independent record (but see earlier analyses where independence was not assumed) and the analysis was confined to WING, UNDERWING, BACK, BREAST, BELLY and TAIL movements which were shown in other analyses not to differ significantly in duration.

effect was due to intervals following extended scans (mean \log_{10} -transformed inter-scan interval 0.244) being significantly ($p < 0.05$) shorter than intervals preceding extended scans (0.391) and intervals neither preceding nor following extended scans (0.392).

To find whether extended scans had an effect on interval lengths beyond those intervals which followed immediately, I divided intervals into (1) those immediately following an extended scan; (2) those following an instantaneous scan which was preceded by an extended scan; (3) those following an instantaneous scan which was not preceded by an extended scan. Class (1) intervals were significantly shorter than both class (2) and class (3), the latter two not being significantly different ($F_{1446,2} = 17.46, p < 0.005$). Thus, the effect of extended scans on interval lengths is limited to the first interval following the extended scan.

7.8 Summary

Vigilance Rates of Birds Pecking on Rocky Areas

No effects of time of year or tide were found. However, there was a strong negative relationship between the proportion of a flock feeding and scan rate. Vigilance was low in winter because the proportion feeding was highest at this time.

There was a small positive relationship between scan rate and nearest-neighbour distance. Relationships with flock size were unclear due to correlations with other variables. There was no evidence for the number of birds within 5m being more strongly related to vigilance rate than was flock size.

Inter-Scan Intervals of Birds Pecking on Rocky Areas

The frequency distribution of inter-scan interval durations gave a better fit to a time-independent model than to a time-dependent model.

Although the variance in interval length between observations exceeded that within observations, mean inter-scan interval showed no relationship with flock size; nearest neighbour distance; number feeding in 5m; whether any birds in 5m were preening; tidal stage; extent to which the focal bird moved; focal bird's visibility; or the occurrence of various events (preening movements, avoidance of waves, avoidance of other birds, other birds flying off).

The latter events were associated with an increase in the number of extended scans which were in turn associated with a decrease in mean inter-scan interval: an increase in vigilance through increasing scan duration was accompanied by an increase due to reducing inter-scan interval. Extended scans were rarer when birds had less obstructed vision.

Vigilance of Birds Using Feeding Methods Other Than Pecking on Rocky Areas

Birds using different feeding methods differed in terms of their head positions while foraging and in terms of their head raising frequencies. Different relationships were found between flock size and density and head raising frequency for different feeding methods.

Inter-Scan Intervals of Preening Birds

Inter-scan interval durations were markedly shorter when preening than when feeding.

The frequency distribution of inter-scan interval durations gave a better fit to a time-dependent model of scanning.

Inter-scan intervals were slightly and significantly shorter in October–November than in January–February.

There was evidence for the hypothesis that inter-scan intervals should increase with flock size and decrease with nearest-neighbour distance only for flocks of over 60 birds.

Inter-scan interval durations decreased as the number of extended scans increased.

Inter-Scan Intervals of Preening Birds: Analysis of Video Tapes

Preening birds in scattered predominantly feeding flocks were more vigilant than those in compact preening and roosting flocks: inter-scan intervals were shorter and the mean number of extended scans per minute was greater in the former.

The following applies only to compact preening and roosting flocks.

Situation (defined as a particular combination of flock size, substrate, day and percentage preening) had no effect on vigilance (measured as mean logged inter-scan interval).

The type of movement performed during an inter-scan interval had a significant effect on interval length: rubbing intervals were shorter than all others, but no other paired comparisons gave significant effects.

The frequency distribution of intervals gave a better fit to the distribution expected of a time-dependent process than that of a time-independent process.

Sequences of inter-scan interval durations were non-random in that they tended to cycle between long and short intervals.

Extended scans tended to be preceded by SCRATCH intervals and not by RUBBING intervals. They tended to be followed by BELLY movements and not by RUBBING intervals. Intervals immediately following extended scans were shorter than other intervals, but those preceding extended scans were not.

7.9 Discussion

7.9.1 Flock Size and Spacing

Overall, there was some support for the hypothesis that flock size and density affect vigilance but the variance explained by these factors was small. There was no evidence for the hypothesis that birds might adjust their vigilance rates according to the number of birds within 5m as opposed to total flock size.

In the case of feeding birds, the predictions of a negative correlation between scan rate and flock size and a positive correlation with nearest-neighbour distance were supported. However, the corresponding predictions of a positive correlation between inter-scan interval and flock size and of a negative correlation between

inter-scan interval and nearest-neighbour distance were only supported in the case of flocks of 60 or more. That effects should be found in large but not in small flocks is surprising given that both predictions and the findings of other studies (Section 7.1.2) suggest greater effects in small flocks.

The videos of preening birds provided evidence that the type of flock affected vigilance of preening birds in terms of both inter-scan intervals and scan durations. This result may have been due to differences in flock size, flock spacing or individual activities. Redpath (1988) found no effect of flock size (measured as the number of birds within 10m) on vigilance of preening birds, but the results are difficult to compare since he did not report the activities of the other birds in the flock.

How important are vigilance considerations in determining flock size and spacing? Sanderlings may avoid feeding in small flocks or at large distances from other birds in order to avoid the extra vigilance costs. The naturally occurring variance in flock sizes and nearest-neighbour distances would then be reduced. This would be difficult to test since the frequency distribution of flock sizes might be a consequence of a range of factors.

7.9.2 Time of Year

As the proportion of a flock which was feeding (as opposed to preening or roosting) increased, the scan rate of feeding birds decreased. Thus, although no direct effect of time of year was found, the reduced preening and roosting in mid-winter implies a reduction in vigilance. This finding could be interpreted as being consistent with the hypothesis that vigilance is determined by time-budgeting constraints: as birds become able to spend time roosting or preening they can also spend more time being vigilant. This situation may arise when the costs of not feeding are low. Birds spent less time roosting and preening in mid-winter and scanned less frequently.

The longer inter-scan intervals of preening birds in January and February than in October and November are consistent with the hypothesis that vigilance should decline in mid-winter because the greater pressure to feed results in less time for preening and, within that time, less time for vigilance.

7.9.3 Scanning Patterns

Although the intervals between scans of preening birds (both datasets) gave a better fit to a time-dependent model of scanning, feeding birds fit a time-independent model better. The results for preening sanderlings are therefore consistent with those of Lendrem *et al.* (1986) for a feeding purple sandpiper, but those for feeding sanderlings are not. The similarity between preening sanderlings and the feeding purple sandpiper may be related to the fact that the ranges of interval lengths are similar. The inter-scan intervals of preening sanderlings were almost all less than six seconds and those of the feeding purple sandpiper were almost all less than four seconds. Those of feeding sanderlings tended to be much longer. It seems that the tendency for scanning to be time-dependent is most apparent when the mean inter-scan interval is small. It could be hypothesized that an increase in the level of vigilance involves both a decrease in mean inter-scan interval and an increased tendency to avoid long inter-scan intervals.

Sequences of inter-scan interval durations of preening birds were non-random in that they tended to cycle between long and short intervals. The results were similar to those of Desportes *et al.* (1989). The existence of such patterns implies that vigilance behaviour may be varied in more subtle ways than previously suspected. It may be that descriptions of vigilance behaviour in terms of scan rates and inter-scan intervals are inadequate and that what should be measured are the parameters of the sequences of inter-scan intervals. The advantages of a cyclical pattern of inter-scan interval durations are far from clear. However, it is clear that there is some predictability in the sequences of inter-scan intervals. This may not be selected against in sanderlings if their predators do not make use of it in timing their attacks (Section 7.1.1).

Further work might try to relate the temporal pattern of scanning to the temporal pattern of preening (see van Rhijn, 1977, for an analysis of the sequence of movements made by a preening herring gull, *Larus argentatus*).

7.9.4 Extended Scans

Certain events (including neighbouring birds flying off and avoidance of waves or other birds) resulted in an increase in vigilance of feeding birds through an increase

in the number of extended scans.

In preening birds extended scans were found to be related to types of preening movement. Birds rubbing oil over their feathers rarely give extended scans, and this suggests that they become unnecessary as inter-scan intervals are shortened. That extended scans tend to be followed by birds preening the belly suggests a link between the type of movement and the need for vigilance: birds may need to make a particularly thorough scan before lowering their head to a position from which they might see little. The fact that inter-scan intervals were no shorter when preening the belly does not support the hypothesis that birds are at greater risk, though it could be argued that there are possibly higher movement costs involved which would act in the opposite direction. That scratches tend to be followed by extended scans might be explained in similar terms, but another reason might be that they mark the end of a bout of preening at which point the bird takes some time to look around and decide what to do next. Consistent with this, birds were often observed to stretch or scratch before pausing and then walking off to start feeding.

It may be that whatever causes scans to be extended also causes the following inter-scan interval to be shortened: an increase in risk acts on both. If this is the case then the risk must be short-lived because the second inter-scan interval after an extended scan is no shorter than other intervals. One possibility is that birds scan according to an internal timing mechanism based on the interval between the start of one scan and the next, so that if a scan is extended there is less time remaining before the start of the next scan.

The intervals preceding extended scans were no shorter than other intervals. In other words, there was no evidence to suggest that birds had broken off in the middle of an inter-scan interval in order to make an extended scan, as would be expected if birds were alarmed by particular events. This result might be due to most extended scans in this dataset being associated with particular movements rather than particular events, or it might be that events causing scans to be extended do not cause scans to be given any earlier: it might be that such events are only noticed once the bird has its head up.

The occurrence of extended scans in preening birds was not associated with a decrease in mean inter-scan interval. The difference may have been due to the extended scans being given for different reasons: when feeding they were associated with events which might have indicated risks lasting for more than a few seconds whereas when preening they tended to be associated with particular types of preening movement rather than with external factors.

7.9.5 Inter-Scan Interval Lengths in Relation to Activities

Most types of movement are associated with inter-scan intervals of similar length. It is not possible to distinguish between the hypotheses (1) that all intervals should be of the same length, and (2) that different intervals may involve different costs but that any differences in interval lengths which these might lead to are offset by advantages of maintaining a particular scanning pattern. The exceptions are intervals where birds are spreading oil over their feathers. It could be argued that the short inter-scan interval associated with this type of movement is due to it taking less time than any other to perform, or there being less cost involved in breaking off to scan. If so, this would imply that all other movement types are imposing constraints on scanning such that inter-scan intervals are longer than they would otherwise be. Alternatively birds might need to scan more frequently if they are at greater risk when spreading oil.

7.9.6 Variance in Vigilance

High levels of variance in vigilance were found in each study and there was only limited success in assigning this variance to particular factors.

Elgar *et al.* (1986) also noted that studies of vigilance typically found high levels of variation in scan rates for each flock size looked at. They found that such variation was accounted for mainly by between-flock rather than within-flock variance and suggested that differences in temperature, time of day, and the occurrence of loud noises and of predators might be among the causes. It is clear that a large number of variables need to be considered in field situations and that general relationships between vigilance and particular variables are difficult to distinguish in such conditions.

7.9.7 Vigilance While Feeding and While Preening

Why are inter-scan intervals so much shorter when birds are preening than when they are feeding?

In the only published study of the vigilance behaviour of preening birds, Redpath (1988) compares the decrease in the visual field caused by feathers covering the eyes while preening with the effect of obstacles. Metcalfe (1984a) found that foraging turnstones and purple sandpipers increased their vigilance when their visual field was obstructed by rocks. This apparent increase in perceived vulnerability might have been due to individuals being less able to see (1) their neighbours and/or (2) approaching predators. If they could not see their neighbours then the hypothesized decrease in vigilance rates in response to flock size (see Section 7.1.2) would not apply since in order to exploit the vigilance of others the detection of a predator by another bird must be perceived. In fact Metcalfe controlled for the effects of conspecific density by only considering cases where the density of birds (measured as the number of birds within a certain radius) visible to the focal bird was above that at which density affected vigilance, so it appeared to be the reduced ability to detect a predator which caused the increase in vigilance.

A distinction should be made between what can be seen while foraging and what can be seen when the head is actually raised: it might be that between scans the birds can still see something but that when this peripheral vision is impaired by obstacles the birds have to increase the rate or length of scans to compensate. Alternatively, and this is the explanation put forward by Metcalfe, the vigilance time or rate must be increased to compensate for the reduced effectiveness of each scan. According to this explanation, any vision between scans is unimportant. Since vision will be impaired only while preening and not while breaking off to scan, the question of scans having reduced effectiveness does not apply. Therefore, of the two explanations, the only applicable one is that vigilance must be increased in order to compensate for reduced peripheral vision.

To take another approach, it may be that sanderlings maintain higher vigilance levels when preening than when feeding because the costs of interrupting preening are less than those of interrupting feeding. According to this hypothesis, birds must make the most of good feeding opportunities as they arise and so are more

constrained by time than are preening birds since preening may be carried out when the costs of not feeding are low. As noted above, the increase in scan rate with increasing numbers of birds preening and roosting is consistent with this hypothesis.

7.9.8 Vision

It has been noted above that the ability of a bird to observe an approaching predator or its surroundings is likely to depend on its posture and activity. Work on vigilance behaviour assumes that birds with their heads raised can see more than those with their heads lowered. There is a need for more integration between studies of vigilance and studies of how vision depends on posture, on visual field and on the distribution of particularly sensitive areas in the retina. Research into how much animals can see can be hampered by the complex relationship between detection and response discussed in Chapter 6. Heart-rate telemetry may provide a useful way of measuring detection.

7.9.9 Energetics

The extent to which wintering sanderlings have difficulty in meeting their energy requirements, and consequently the extent to which time affects their behaviour, is unknown. Time-budgeting is of particular relevance to vigilance behaviour: if the costs of time spent not feeding are small then birds can spend longer being vigilant. Gudmundsson (1982) found no evidence for a change in the allocation of time to different activities in the pre-migration period and concluded that the build up of fat reserves at this time might be due to an increase in the length of time during each tidal cycle for which the birds were away from the high-water roost, although there was no evidence for a change in the allocation of time to different activities during this time. Maron and Myers (1985) found that sanderling weights declined through the winter, increasing again in spring. They related these weight changes to changes in prey capture rates and suggested that the birds were having difficulty balancing their energy budgets during the winter. In contrast, other studies of shorebirds (e.g. Evans and Smith, 1975) have found increased weights in winter.

Chapter VIII

General Discussion

A recurring theme throughout this thesis has been that of how the behaviour of individual sanderlings is affected by the presence and behaviour of conspecifics. A range of effects has been demonstrated but it has also been shown that individuals often appear to act with considerable independence.

The extent to which an individual's usage of different sites within a winter and its consistency of distribution between winters are affected by other birds is very difficult to determine (Chapter 3). What can be stated is that individual distribution patterns tended to be consistent in that they tended to change little between years and that these patterns of site usage were apparently independent in that no groups of birds within the population moving around together were found (Chapter 4). The lack of close inter-individual associations has important implications for the social organization of sanderlings (see also Myers, 1983, and Section 4.1). In short, it means that the benefits of flocking appear to be independent of the other particular individuals involved.

Flock cohesion was variable (Chapter 5). At times membership of flocks was constantly changing meaning that flocks could not be defined spatially or temporally. There were indications that the numbers of other birds present did affect decisions as to which flocks to leave and to join and how to move between flocks. Although many movements were of only ones and twos, flights of whole flocks were also common. Thus flock cohesion was apparent, particularly when flocks were disturbed.

Although the economic hypotheses tested had only limited success in explaining the variation in responses to disturbances, it was clear that the presence of other conspecifics did affect behaviour, both qualitatively and quantitatively (Chapter 6).

Flock sizes and densities explained only some of the variance in vigilance behaviour (Chapter 7). However, some effects of the presence and behaviour of other individ-

uals were apparent. A bird feeding near to a preening bird often stopped feeding and started preening alongside. This appears to be an example of social facilitation (e.g. Lazarus, 1979b): switches to preening appear to be far more synchronized than would be expected by chance, even given that different birds are likely to be subject to similar pressures and so are likely to decide to switch at a similar time. Why should the decision of one bird affect the decisions of others? Is there an advantage in behaving synchronously? This may well be the case: preening birds amongst other preeners were less vigilant than were those amongst feeding groups (Section 7.7.3). But there may be other examples where the reasons for individuals taking account of the behaviour of others are much more subtle.

More studies of how the activities of individuals affect those of others are clearly required in order to build up a framework in which an individual's behaviour, from its level of philopatry to the distance it maintains between itself and its nearest-neighbour, can be related to its interactions with other individuals.

How important are groups to sanderlings? Wilson (1975) defined groups as sets of individuals which "remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics." Foraging flocks of sanderlings were open in the sense that flock membership was continually changing, at least in some circumstances. They were difficult to define spatially and temporally. Thus, flocks are likely to be of less significance to sanderlings than they would be if they were discrete, cohesive units. The behaviour of individuals may be influenced by the presence and behaviour of other individuals but it is not clear that the flock itself is the important unit of structure. Thus, although flocks often fly up as units, groups of neighbouring individuals often leave flocks together or neighbouring flocks may depart together.

As far as the advantages of flocking are concerned, some evidence for the size and spacing of flocks relating to the food supply was found. The observation that flocks tended not to be either closed or discrete is consistent with flocking being a product of aggregation in profitable feeding areas. It was shown that birds may benefit from flocking by reducing their individual vigilance, particularly in the case of preening birds. They may also gain in terms of reduced individual risk. For

example, flock cohesion was high when birds were disturbed suggesting that there were advantages in remaining in a flock when risk was high.

Much remains to be learned about the reasons for inter- and intra-specific behavioural variation. The behaviour of sanderlings at Teesmouth may be contrasted with that of turnstones. The social organization of the two species is very different. Turnstones on rocky shores have lower levels of itinerancy, stronger inter-individual associations, and compete for food through stable dominance hierarchies (Metcalf, 1986; Whitfield, 1985). The nature of the food supply, including its predictability and its patchiness, is likely to be an important factor affecting behaviour. The stability of food resources may determine site tenacity (e.g. Whitfield, 1985) and territoriality has been linked to prey stability (e.g. Myers, 1984). Evans (1981) proposed that inter- and intra-specific differences in itinerancy might be accounted for in terms of the stability of prey distribution. However, no evidence was found in this study to link the type of food supply to levels of association between birds, to the nature of competitive interactions or to itinerancy.

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Appendix A

Sightings of Sanderlings

Colour-Ringing

Most colour-ringed birds present during my study period had been ringed before the start of my study by members of Durham University and of the South Cleveland Ringing Group. Darvic colour-rings of height 7mm and internal diameter 3mm of white, lime, green, blue, orange and red were used. Three or four colour-rings were used on each bird.

Table A.1(a) shows the numbers of sanderlings colour-ringed between 1976 and 1986, after which very few were ringed. Ringing was carried out during the months August to May, most being rung between September and November (Table A.1(b)). Table A.1(c) shows that almost three times as many birds were colour-ringed on the south side (Saltburn–Coatham Sands) as on the north side (North Gare Sands–Crimdon).

Reliability of Sighting Records

I excluded a number of sightings from my analyses on the basis of their type and reliability. Only 12 records were of dead birds: these were included in the analyses. Captures accounted for 710 records, but these were only included if the birds were colour-ringed on or before the day of capture since it is unreasonable to include a bird in the list of birds which can potentially be sighted at a given time if it can only be sighted when captured. The type and reliability of a record had not been noted for 1364 sightings, so on the grounds that the type would have been noted if unusual these sightings were grouped with the 9137 sightings made by Durham observers and noted as reliable. If this assumption is incorrect then (unless there is actually a bias towards these cases being unusual ones) ninety percent of them should be classified correctly by this grouping, and so any error should be small. Of the sightings made by Durham observers, 193 had been noted as being unreliable. I excluded these records from my analyses on the grounds that the advantages of greater sample sizes were more than offset by the dangers of drawing false conclusions. It was not stated why there were doubts about the birds' identities and whether these doubts arose in the field or when the identities were checked against those normally seen at the site. If the latter were the case then exclusion of these records would introduce a bias.

Numbers of sightings

Between the winter of 1975–76 and the early-autumn of 1986, 12201 sightings of colour-ringed sanderlings were made. These sightings were mainly along the coast of N.E. England from Saltburn in the south to Holy Island in the north (Figure 2.1), with some additional records from further afield. The observations varied in their geographical coverage and in their regularity. Table A.2 gives the total numbers of sightings in each year broken down by sites.

Numbers of Observation Days

Cooper (1988) presents a list of observation days for the winters 1982–83 to 1984–85. The number of observation days increased up to the winter of 1979–80 and then varied between 76 and 133. The number of days on which the south side of the Tees estuary was visited was generally greater than for the north side of the estuary, and this was particularly true of the winters 1983–84 and 1984–85.

The Number of Birds Seen per Day

This may reflect (1) the number actually present, which may in turn reflect (a) population variation; (b) the number of birds colour-ringed at the time; or (c) the general frequency of usage of that site by colour-ringed birds; and (2) the thoroughness of the check for colour-ringed birds.

Year	76	77	78	79	80	81	82	83	84	85	86
<i>n</i>	31	29	18	30	68	41	34	24	87	54	11
cumulative <i>n</i>	31	60	78	108	176	217	251	275	362	416	427

(a)

Month	1	2	3	4	5	6	7	8	9	10	11	12
<i>n</i>	28	28	18	13	20	0	0	35	101	64	93	27

(b)

Site	<i>n</i>
Saltburn to Redcar	93
Redcar	57
Coatham Sands	161
Seal Sands	2
North Gare Sands	45
Seaton	52
Crimdon	14

(c)

Table A.1 — Numbers of Birds Colour-Ringed

(a) Total numbers of sanderlings colour-ringed in each year. (b) Total numbers ringed in each month. (c) Total numbers ringed at each site.

Winter	Sites							n
	1	2	3	4	5	6	7	
76	+	+	78		+			58
77	+	+	79		21			24
78	+	+	20		56	+		378
79		33	43		22			533
80			25		30	18	+	1173
81	18	20	33	+	21	+	+	1700
82	16	28	26	+	20	+	+	1254
83	30	31	26	+	+	+	+	2154
84	22	+	+	+	26	27	+	931
85	+	43	22	+	18	+	+	1432

Table A.2 — The Distribution of Sightings Between Sites

The table gives the total numbers of sightings of colour-ringed birds made in each year and the percentages of these sightings which were made at each site. Percentages are given where these are greater than 10% ; '+' represents some sightings. Sites: 1=Saltburn to Redcar; 2=Redcar; 3=Coatham Sands; 4=Bran Sands; 5=Seaton; 6=Crimdon; 7=Whitburn.

Year	Mean	max.	<i>n</i>	single sightings
77	1.1	2	8	7
78	7.4	24	36	5
79	9.6	28	40	6
80	9.0	21	51	6
81	12.1	29	95	8
82	10.3	34	113	10
83	18.4	66	100	8
84	4.6	18	96	21
85	7.4	23	155	44

Table A.3 — Sighting Frequencies per Bird

The table gives the numbers of sightings of colour-ringed birds in each year in terms of the mean number per individual; the maximum number for an individual; the number of individuals; and the number of these seen only once.

Thoroughness varied markedly and there was no clear distinction between days when only one or a few birds were apparently noted 'in passing' and days when complete checks were made.

Distribution patterns can only be looked at where most birds are seen several times per year. Table A.3 gives the mean sighting frequencies of colour-ringed birds in different years. The dramatic increase in the number of birds seen only once seems disproportionate to the overall reduction in the number of sightings per bird and may be due to observer error; to differences between years in the manner of data collection; or to differences in the distribution patterns of birds present.

