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Roosting and associated feeding behaviour of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in north-east England.

by

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Abstract.

Roosting and associated feeding behaviour of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in north-east England.

Both individual Turnstones and Purple Sandpipers were largely site-faithful during winter; after the breeding season, however, fewer surviving Purple Sandpipers than Turnstones returned to the study area. Both species were sedentary on small low water home ranges and were faithful to a small number of roost and high water sites.

Numbers of Turnstones and Purple Sandpipers flying to the main high water roost, Hartlepool West Harbour, were greatest on spring high tides, but were reduced in high winds. Numbers at other high water sites at nearby Hartlepool Headland were greatest on neap tides. Maximum Purple Sandpiper numbers at West Harbour showed a steady decline over the period from 1986/87 to 1993/94; maximum numbers of Turnstones dropped sharply in 1993/94 after redevelopment of the harbour in 1991/92. Overall disturbance rates to roosting shorebirds at West Harbour, and those from boats and man, increased over the study period and were probably responsible for the decline in Turnstone numbers and those of two other species. An artificial island, built in 1991/92, is now the main roost site for all species.

Intraspecific aggression on the feeding grounds was primarily a result of encounters over food; infringements of individual distance were relatively infrequent. Dominance hierarchies on low water feeding grounds were stable for both species; adult Turnstones dominated first-winter birds; Purple Sandpiper dominance was positively correlated with size. Survival was not related to dominance for either species.

Both species were segregated at the West Harbour roost into groups from different low water feeding areas; Purple Sandpipers also into groups of different (bill-length) size class. Aggression at the roost resulted from encounters over roosting sites or infringements of individual distance. As wind speed increased, encounters over roosting sites became more frequent and intensity of aggression increased. Dominance hierarchies at the roost were stable for both species; individual roosting dominance was positively correlated, though not always significantly so, to low water feeding dominance. Adult Turnstones dominated first-winter birds; Purple Sandpiper dominance was positively correlated with size. Roosting flocks were structured in accordance with dominance relationships: adults and dominants occupying denser, middle positions and first-winters and subordinates less dense, peripheral sites. Individuals (of both species) that were subordinate at the West Harbour roost frequented it less often than dominants (at least in some seasons), probably because they could not obtain good roosting positions there. Other sites allowed these birds to feed over high water.

Turnstones and Purple Sandpipers associated together frequently at the West Harbour roost in comparison to other species. There was no evidence that either species roosted with the other in order to exchange information concerning food resources or to save energy through the roost's microclimate. Both species shared vigilance with each other and probably roosted together in order to decrease the risk of being taken by a predator.

CONTENTS

CHAPTER ONE INTRODUCTION AND GENERAL METHODS

CHAPTER TWO SITE FIDELITY AND SURVIVAL

CHAPTER THREE SPECIES USE OF ROOST SITES

CHAPTER FOUR LOW WATER FEEDING BEHAVIOUR

CHAPTER FIVE INDIVIDUAL ROOSTING BEHAVIOUR

CHAPTER SIX MIXED-SPECIES ROOSTING

CHAPTER SEVEN GENERAL DISCUSSION

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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To my parents

and to Karen

Hyland had one bad little bit of news for me, for the turnstone had escaped and the waiter had died.

A. Trevor-Battye, *Ice-bound on Kolguev*

Male Purple Sandpiper, Spitsbergen, summer 1957 (Philip Burton).

Chapter 1.

Introduction and General Methods.

1.1. Introduction.

Communal roosting is a common phenomenon amongst birds and has been increasingly studied over the last thirty years (see Eiserer 1984). Most research has focused on the functions of nocturnal roosts, though amongst coastal waterbirds, roosting also occurs over high tide periods when low water feeding areas become flooded and unavailable. The present study examined aspects of the tidal roosting behaviour of two shorebirds, the Turnstone *Arenaria interpres* and the Purple Sandpiper *Calidris maritima* during the non-breeding season. Previous studies of roosting behaviour have concentrated upon its adaptive function and the possible advantages to individuals (see Ydenburg and Prins 1984); few have considered how roosting relates to and integrates with other aspects of daily behaviour, notably feeding. In the present study, the social behaviour of Turnstones and Purple Sandpipers on their intertidal feeding grounds formed the background to studies on the roosts; colour-ringed individuals could be followed between the sites.

Four main advantages of communal roosting behaviour have been suggested:

1). The 'information-centre' theory, whereby individuals come to the roost in order to obtain information from others concerning the location of food resources (Ward and Zahavi 1973).

2). The 'roost micro-climate' theory, which suggests that roost sites and / or roosting itself confer energetic advantages upon the individual (*e.g.* Francis 1976, Tast and Rassi 1973, Ormerod and Tyler 1990).

3). Roosting is a form of anti-predator behaviour (Lack 1966, 1968): the formation of large flocks at roosts may decrease an individual's risk of being taken by a predator by a dilution effect (*e.g.* Hamilton 1971, Cresswell 1994, Fox *et al.* 1994), an increase in total vigilance levels (*e.g.* Powell 1974, Siegfried and Underhill 1975) and / or an increase in predator confusion (*e.g.* Neill and Cullen 1974, Cresswell 1994, Fox *et al.* 1994).

4). Roosting occurs to help in the regulation of populations, through epideictic displays (Wynne-Edwards 1962).

It is possible that roosting occurs for more than one of these reasons and possibly has different advantages for different individuals (see Weatherhead 1983, Ydenburg and Prins 1984). Gyllin *et al.* 1977, Yom-Tov *et al.* (1977) and Jenni (1991) have all found, for example, that although roosts do provide micro-climatic advantages for birds, these advantages do not fully explain the roosts' formation. Conclusive proof that roosting occurs primarily for any of these reasons is difficult to obtain and there is a particular lack of evidence in support of the information-centre hypothesis (Mock *et al.* 1988, Richner and Marclay 1991). As the present study covered the behaviour of birds in the non-breeding season, the fourth hypothesis may not be relevant here.

Roosting may also hold disadvantages, though these vary between individuals. Assuming that detection of successful foragers at roosts does occur, these successful birds may face increased competition when others follow them to food resources (Mock *et al.* 1988). At roost sites, subordinate birds may be forced into peripheral positions where they remain exposed to poor weather (*e.g.* Swingland 1977, Jenni 1993). The large concentrations of birds that occur at roosts may also attract predators (Ward and Zahavi 1973) and in these cases, peripheral birds will be at greater risk (Kus *et al.* 1984). In the present study, the use of roosts by different species and individuals was investigated in relation to the advantages and disadvantages that they may confer.

The first of five main chapters in this thesis (Chapter 2) reports the site-fidelity of the two species to the study area, within and between years. The degree of site-fidelity shown by different species is largely determined by the temporal stability of their food resources and varies amongst wintering waders according to their habitat preferences (Evans 1981, Myers 1984). Site-fidelity may allow stable dominance hierarchies to be established among groups of individuals, possibly through individual recognition (Collias 1943). As a basis to understanding dominance relationships and the use of the study area by the two species, individuals of both species were classified as 'residents' or 'visitants' to the study area and the 'home' feeding area of residents determined.

Chapter 3 summarizes how numbers at roosts varied according to the season, the tide and weather conditions and also the use of different sites within the main roost site (Hartlepool West Harbour, Co. Cleveland, north-east England). Disturbance to roosting shorebirds has become an increasing problem in recent times (*e.g.* Mitchell *et al.* 1988) and this chapter additionally includes data on the causes, rates and consequences of disturbance to shorebirds at the West Harbour roost.

The following chapter (Chapter 4) details the intertidal areas and habitats that were important for feeding Turnstones and Purple Sandpipers over the low water period and investigates how their feeding requirements may vary seasonally and according to the individual. The possibility exists that differences in the dominance of individuals on feeding grounds may determine where and how long they feed and may have consequences for their roosting behaviour. This chapter reports on the stability of dominance hierarchies on feeding grounds and relates this to the site-fidelity of the species, and examines how dominance varies between individuals of different age, sex and size (*e.g.* Ekman and Askenmo 1984, Ens and Goss-Custard 1984, Senar *et al.* 1992).

The description of individual dominance on feeding grounds precedes the chapter on individual roosting behaviour (Chapter 5). A number of studies have found that roosts are not homogeneously mixed but may be structured according to the age, sex or size of birds (Swingland 1977, Still *et al.* 1987, Summers *et al.* 1987, Jenni 1993). Such structuring is a consequence of the dominance of some individuals over others, dominants supplanting subordinates from preferred positions in the roost. Central positions in roost flocks are likely to be preferred to those at the edge, as they offer protection from predators (Kus *et al.* 1984) and are often microclimatically favourable

(Whitlock 1979). The structuring of roosts of Turnstones and Purple Sandpipers and the influence of weather conditions on the aggressive behaviour of individuals at the roost are reported in Chapter 5. In addition, this chapter documents the relationship between roosting dominance and feeding dominance. The two are likely to be correlated if dominance is based on physical determinants, such as size, sex or age, and is not overly site dependent. Analysis of the influence of both roosting and feeding dominance upon the choice of which 'roost' to use and whether to feed or roost over high water is also presented.

Many shorebird species commonly roost with others and although this may initially be a consequence of the limited availability of roost sites, much variation exists in the species' associations that result. Turnstones and Purple Sandpipers are commonly found to roost together (Cramp and Simmons 1983). The reasons for this high association and the varying degrees of association between these and other species were investigated and are presented in Chapter 6. Individuals of one species may roost together with individuals of another for the same reasons that they roost with conspecifics (see above), though the advantages of roosting together may differ between the two species concerned (Gadgil 1972).

Each main chapter is provided with a summary at the end.

1.2. The study species.

Turnstones and Purple Sandpipers are both primarily winter visitors to Britain, migrating each year from breeding quarters in the sub- and high arctic. The Turnstones that winter in Britain and north-western Europe originate from Greenland and Canada (Branson *et al.* 1978, Cramp and Simmons 1983), though in autumn and spring these are supplemented by birds of the Fenno-Scandian and Siberian populations passing through on their way to and from west and southern African wintering grounds (Branson *et al.* 1978, Cramp and Simmons 1983, Summers *et al.* 1989). The wintering population of Turnstones in Britain is estimated at 45,000 (Moser 1987).

The Purple Sandpipers that winter in Britain comprise primarily two populations: a 'short-billed' population from Norway and a 'long-billed' population thought to be from Canada and / or Greenland (Rae *et al.* 1986, Nicoll *et al.* 1988, Summers *et al.* 1992). The small number of Purple Sandpipers that breed in the Highlands of Scotland (Dennis 1983) probably form part of the Norwegian population. In Britain, birds of these two populations winter primarily on northern and eastern coasts: long-billed birds predominate in north and west Scotland and short-billed birds on the eastern coasts of Scotland and England (Nicoll *et al.* 1988). On southern and south-eastern coasts of England a small long-billed population occurs, possibly, as with some continental birds, of Siberian origin (Boere *et al.* 1984, Summers 1987, Nicoll *et al.* 1988, Summers and Rogers 1991, Dierschke 1995). The Purple Sandpiper winters further north than any other species of wader and in comparison to an estimated winter population of 19,000 in Britain (Nicoll *et al.* 1988), tens of thousands of Purple Sandpipers are thought to winter in Norway (Folkestad 1975, Alerstam 1982, Cramp and Simmons 1983) and Iceland (Cramp and Simmons 1983, Summers *et al.* 1988a).

Turnstones and Purple Sandpipers are the only species of shorebird that winter in Britain whose preferred feeding habitats are found on rocky shores (Cramp and Simmons 1983, Summers *et al.* 1988b). Purple Sandpipers are the more specialised, feeding by sight or using touch sensitive bills on molluscs including mussels *Mytilus edulis*, periwinkles *Littorina* spp. and dog-whelks *Nucella lapillus*, barnacles *Balanus* spp., amphipods, algae and less frequently on the adults, pupae and larvae of the kelp fly *Coelopa frigida* (Feare 1966, Smith and Bleakney 1969, McKee 1982, Strann and Summers 1990, Summers *et al.* 1990a, Dierschke 1993, Summers 1994). They are better adapted to the cold winters of northern latitudes than other waders, having heavy insulative plumage and possibly generating additional heat with their large breast muscles (Summers *et al.* 1992, Davidson 1990). Turnstones find prey visually and in addition to taking mussels, periwinkles and barnacles are commonly found feeding at wrack beds and scavenging along tide-line deposits or even at carrion or scraps thrown away by man (Selway and Kendall 1965, Groves 1978, Harris 1979, McKee 1982, Cramp and

Simmons 1983, Whitfield 1990). They are perhaps less well adapted to cold weather than Purple Sandpipers, putting on proportionally more mass in winter, though less than most other shorebird species in Britain (Johnson 1985, Summers *et al.* 1989, 1992). The differences in diet and energetic needs and the difference in size between the species, (Turnstones are on average 23cm in length to the Purple Sandpiper's 21cm; Cramp and Simmons 1983), are of importance in comparisons of aspects of both the species' feeding and roosting behaviour. Comparisons were also made throughout the study with other species of wader that winter in the northern hemisphere, most of which prefer shores of soft substrata.

1.3. The study area.

1.3.1. Low water sites.

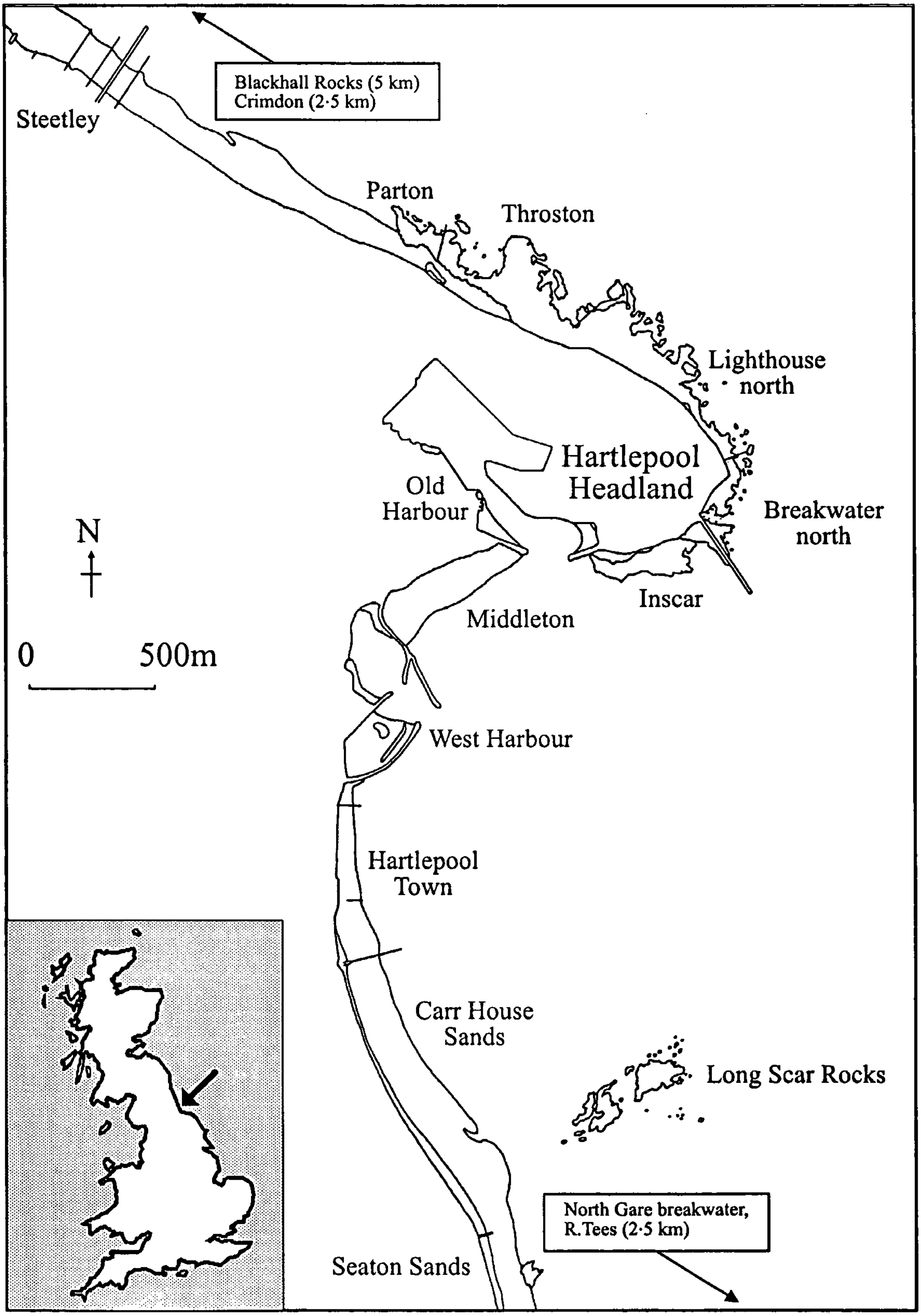
The study was based at Hartlepool in Cleveland and covered 13 km of coast from Blackhall Rocks in the north to North Gare breakwater, at the mouth of the River Tees, in the south (Fig. 1.1). The coast here is composed of long stretches of sandy shore which are interspersed with varying lengths of rocky outcrop. At low water, Hartlepool Headland forms the largest stretch of intertidal rocky shore and covers the area from Parton to Inscar. To the north, rocky shore occurs from Crimdon to Blackhall Rocks and in the south includes the offshore Long Scar rocks, (which are covered by water on extreme neap low tides), an area on Seaton Sands and North Gare breakwater. In the centre of the study site, at the entrance to Hartlepool Docks, is West Harbour, whose piers form another area of 'rocky shore'. Pipes and groynes at Steetley, Hartlepool Town and on Seaton Sands also form further small areas of such 'rocky shore'.

Six habitats were defined for low water feeding areas:

1). Exposed rock, *i.e.* bedrock and areas of loose rock and boulders, that are bare of surface material. Such areas are often partially covered by barnacles.

2). Musselbeds: areas where mussels cover at least one third of the ground surface (see Metcalfe 1984a).

Fig.1.1. Location of the study area at Hartlepool, Cleveland, showing defined low water feeding areas



3). Live wrack (*Fucus* spp.): areas where living wrack covers at least one third of the ground surface.

4). Dead wrack: washed up deposits of wrack, typically found at the high tide line.

5). Algae: areas where algae - particularly *Enteromorpha* spp., (but excluding *Fucus* spp.) - cover at least one third of the ground surface.

6). Strand: areas of soft substrate, *i.e.* sandy or muddy shores, which may include non-wrack tide line deposits.

On the areas of rocky or man-made outcrop described above, musselbeds predominate on Hartlepool Headland, (from Parton to Breakwater north), at West Harbour, Hartlepool Town and on Seaton Sands. Large areas of live wrack are found at Inscar and between Crimdon and Blackhall Rocks. Exposed rock predominates at North Gare breakwater and above the tidal limit of musselbeds, where the surface is often covered by barnacles. Algae (excluding *Fucus* spp.) are also typically found above the musselbeds amongst areas of exposed rock.

1.3.2. High water sites.

Fieldwork at high water was concentrated at two sites: West Harbour and Hartlepool Headland. West Harbour contains the main high water roost in the area for shorebirds and prior to the study, three species occurred at the site in nationally important numbers: Purple Sandpiper regularly and Knot *Calidris canutus* occasionally in winter and Turnstone during autumn passage. The site also regularly held over two hundred Oystercatchers *Haematopus ostralegus*, whilst Redshank *Tringa totanus* and Dunlin *Calidris alpina* were present occasionally. During the first two years of the study, this site underwent a number of changes during a large scale redevelopment of the docks and their vicinity. The background to the redevelopment and the changes to the harbour itself are described below.

A number of sites on Hartlepool Headland are used by Turnstones and Purple Sandpipers over high water. Rocky outcrops below the promenade between Throston and Breakwater north and a shingle beach at Inscar are used by both species for roosting and for feeding. The grass area of Town Moor above Lighthouse north is also used occasionally as a high water site by a few Turnstones. On spring high tides many sites along the promenade become flooded and birds are restricted to the beach at Inscar and to Town Moor.

A third site, above Seaton and Carr House Sands, was also surveyed during the first year of study. This site consists of a shingle beach, backed by a promenade and grass and was used for both roosting and feeding by Turnstones. Purple Sandpipers were only rarely seen there over high water.

West Harbour first became important as a shorebird roost site in the 1960s when the old 'inner pier' became detached from the south pier, thus forming a safe haven at high water. Subsequently, during the early 1980s, the south pier itself collapsed to leave a series of structures, which during high tides became islands. These attracted even more birds to the roost (R.T. McAndrew pers. comm.; Fig. 1.2).

During the late 1980s proposals by the Teesside Development Corporation (TDC) for a redevelopment of Hartlepool Docks and for a marina with an entrance through West Harbour led to a planning application for new sea defences to replace the nineteenth century stone piers. Because of the national importance of the site for Purple Sandpipers during winter, this application led the TDC into consultations with the National Rivers Authority, the Royal Society for the Protection of Birds and Cleveland Wildlife Trust. As a result, agreement was reached to build a replacement roost site, in the form of an island, for the birds and a programme of work, which gave rise to the present study, was commissioned from Durham University to monitor its use. The redevelopment of the site began in the summer of 1991; the island was completed in November 1991 and the new south pier in February 1992. The island was built to a kidney-shaped design, with its longest face on the north side towards the harbour

Fig.1.2. Detail of the shorebird roost sites at West Harbour, Hartlepool, before summer 1991

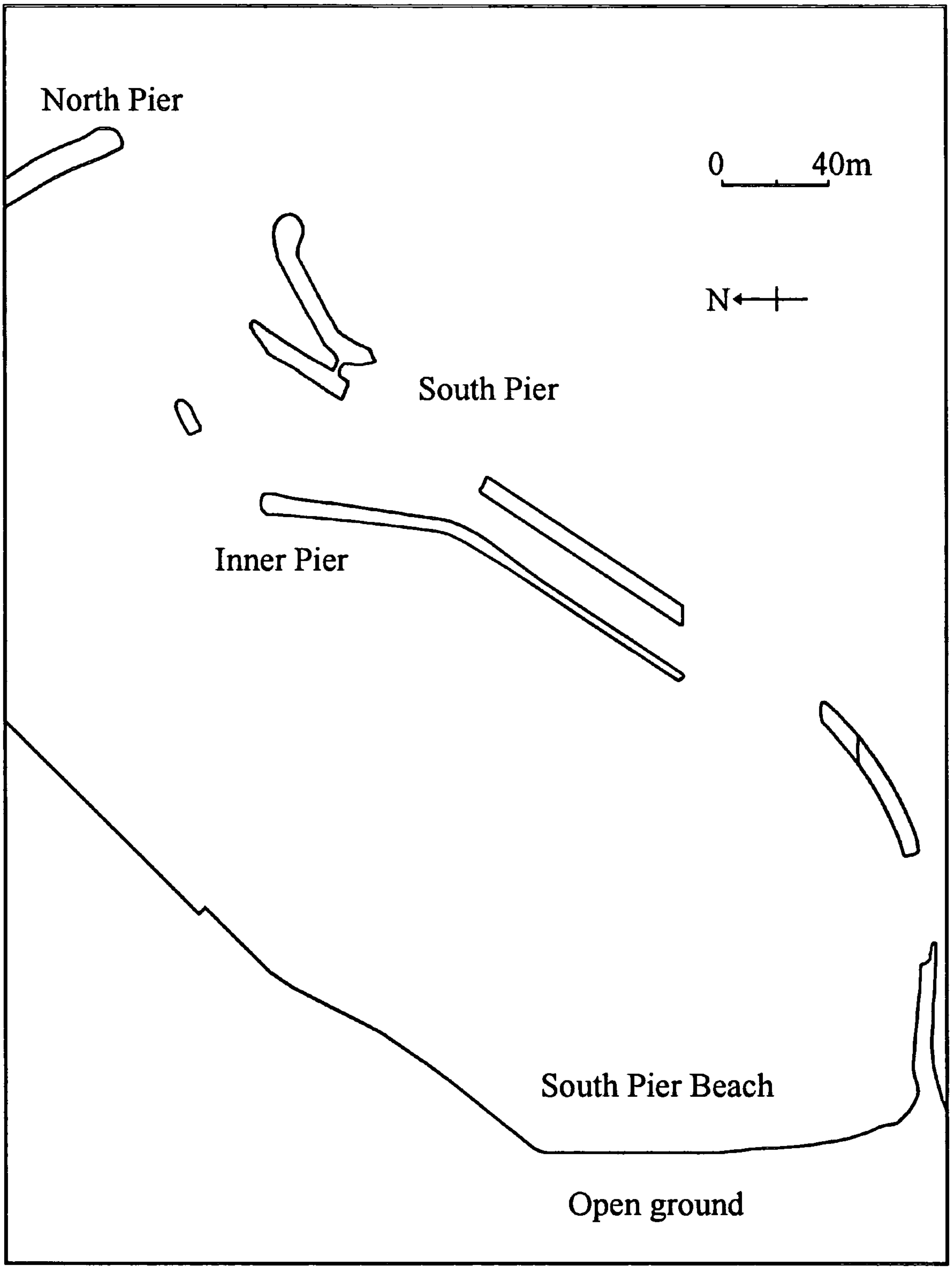
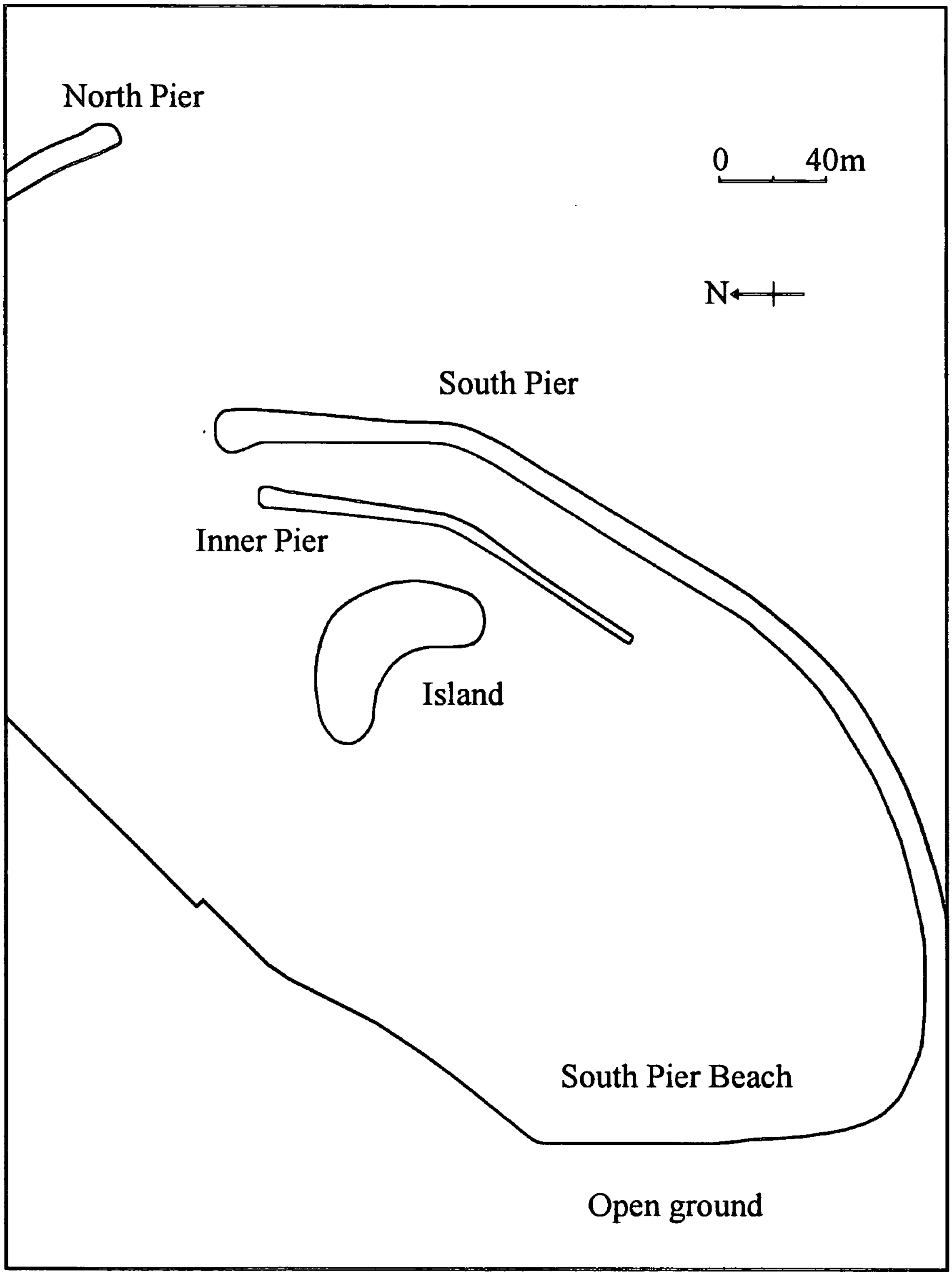


Fig.1.3. Detail of the shorebird roost sites at West Harbour, Hartlepool, post spring 1992

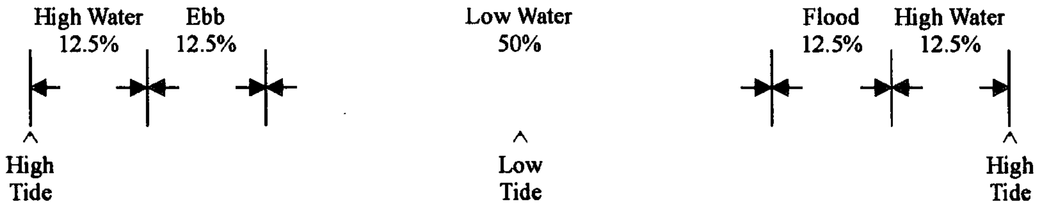


entrance, from which the most severe sea-swell would enter. The steep sides of the island were faced with stone blocks, to provide shelter for roosting shorebirds and its top (which was over 3m above the highest spring tides) was castellated. In addition to the new island and south pier, the old inner pier was left standing between the two as an alternative roost site and beams were attached to its west side for use, specifically, by Purple Sandpipers. A present plan of West Harbour is shown in Fig. 1.3.

1.4. General methods.

Fieldwork was undertaken between July 1991 and May 1994 and included detailed observations of individuals as well as low and high water surveys. Low water, flood, high water and ebb periods are defined in the diagram below. The high water period was considered as the part of the cycle when most of the intertidal habitats used for feeding by shorebirds were covered by water. Low and high water surveys took place only within the respective defined periods, their primary aim being to obtain counts of the two species. Observations, whenever possible, took place from a car, though at Blackhall Rocks, Crimdon, Steetley, Lighthouse north and Breakwater north on Hartlepool Headland, parts of West Harbour, south Seaton pipe and North Gare breakwater, surveys were made on foot. All observations were made with either a 20-45x Nikon Fieldscope telescope or 8.5x Swift Audubon binoculars. Most observations were made during daylight hours, though a few surveys were also occasionally undertaken at night in order to establish the species' behaviour at this time.

Fig. 1.4. Definition of low water, flood, high water and ebb periods.



In order that the individual behaviour of birds of both species could be studied, birds were caught during the study period and individuals given an unique combination of colour-rings, together with a metal ring inscribed with a unique number. Birds of both species were caught mainly by cannon-netting, either on beaches within West Harbour or on Carr House Sands. Additional attempts to catch Purple Sandpipers were made by mist-netting at night at West Harbour or on Hartlepool Headland. A total of 39 Purple Sandpipers, (including 12 first-winter individuals) and 52 Turnstones, (including 30 first-winter individuals), were individually colour-ringed during the study, the latter supplemented by a number of birds colour-ringed within or near the study area in previous years. In addition, many Turnstones were fitted with numbered metal rings.

Data were analysed primarily with the SPSS for Windows package (Norušis / SPSS Inc. 1993). In non-parametric tests, corrections were used for all tied data. Additional references used included Siegel (1956) for the use of Sign Tests, Zar (1984) for the use of Kruskal-Wallis tests with small samples, and Fowler and Cohen (1986).

Chapter 2.

Site-fidelity and Survival.

2.1. Introduction.

Waders wintering on the coasts of Britain and north-western Europe show considerable variation in their site-faithfulness, both between and within winters. Many species regularly return to the same stretch of coast each year, for example Dunlin (Clark 1983) and Curlew *Numenius arquata* (Bainbridge and Minton 1978, Townshend 1981). Within winters, some species may be faithful to one particular area, *e.g.* Redshank and Oystercatcher (Goss-Custard *et al.* 1982b, Symonds *et al.* 1984), whilst others, such as Knot, frequently move between estuaries (Dugan 1981). The degree of site-fidelity exhibited by different wader species may be determined largely by the temporal stability of their food resources (Evans 1981). Dunlin on the Tees estuary are known, for example, to feed on invertebrates associated with stable sediments and are thus typically site-faithful there during winter (Evans 1981). Sanderling *Calidris alba*, in contrast, may switch between residency and itinerancy within winters due to the less predictable nature of their food supplies (Myers and McCaffrey 1980, Evans 1981, Myers 1984, Roberts 1991). A knowledge of the site-fidelity of a species is important when considering threats to its environment (Goss-Custard 1985, Goss-Custard and Durell 1990). More mobile species may, for example, be better equipped to cope with a reduction or loss of habitat (Prater 1981).

In contrast to most other waders, Turnstones and Purple Sandpipers winter chiefly on rocky shores (McKee 1982, Cramp and Simmons 1983). Here the predictability of food resources may differ considerably from that in estuaries. The degree of site-fidelity exhibited by Turnstones and Purple Sandpipers may, accordingly, differ from that seen in other waders.

The stability and predictability of food resources are important determinants not only upon the site-fidelity of species, but also upon their survival. Species which have reliable sources of prey will, in addition to showing fidelity to an area, be less at risk to starvation or the problems of severe weather (Davidson 1981).

The redevelopment of the wader roost site at Hartlepool West Harbour forms an important backdrop to the present study. The implications of this redevelopment to the local Turnstone and Purple Sandpiper populations are, in part, dependent upon the species' fidelity to the area, which is considered in this chapter, together with their year-to-year survival. In relation to this, consideration is given to the relative seasonal mass changes of each species and also to differences between the masses of adult and first-winter birds. Many wader species put on weight in winter (*e.g.* Johnson 1985), as protection against food shortages and cold weather, and mortality is likely to be greatest amongst those individuals that are low in mass. If individuals are unable to meet their energy requirements feeding in one area, due to their inexperience or subordination for example, they may be forced to search elsewhere for food. First-winter birds are thus predicted to be more itinerant than adults.

Finally, as a basis for later studies of individual behaviour, this chapter also examines correlations between different measures of body size (see Piersma and Davidson 1991) and the origins of the populations of Turnstones and Purple Sandpipers wintering at Hartlepool. Purple Sandpipers vary in size according to sex and geographical origin (Tatarinkova 1977, Cramp and Simmons 1983) and this may have implications for their individual behaviour.

2.2. Methods.

2.2.1. The classification of residents, visitants and passage birds.

Individuals of both Turnstones and Purple Sandpipers varied in the frequency that they were seen on the study site. Individuals were classed as resident within the study area if they were seen ten times or more on *c*.20 low and *c*.20 high water surveys from the start of winter until their spring migration; (winter was defined as 25 October to 31 March for Turnstones and 15 November to 31 March for Purple Sandpipers; see Chapter 3). Individuals seen only between one and ten times on the study site during winter and spring were classed as visitants. Individuals seen only in autumn (*i.e.* prior to 25 October for Turnstones and prior to 15 November for Purple Sandpipers), and / or spring (*i.e.* after 31 March) were classed as passage birds.

A number of individuals of both species were also first caught and colour-ringed during February and March. Such individuals were classed as residents if they were seen five times or more within the study site, prior to migration. Individuals that were caught during winter and seen less than five times within the study site were not classified.

Resident individuals were classified according to their low water feeding areas. An individual was classified as a 'Headland' (North) resident if 70% or more of low water sightings of that individual were on Hartlepool Headland. Similarly an individual was classified as a 'West Harbour to North Gare' (South) individual if 70% or more of low water sightings of that individual were to the south of the Headland, *i.e.* between West Harbour and North Gare breakwater. An individual was classified as a 'North and South' resident if less than 70% of low water observations of that individual were on Hartlepool Headland and less than 70% between West Harbour and North Gare.

2.2.2. Survival.

Minimum annual survival rates of colour-ringed individuals were calculated from 1 April each year and were subdivided into an over-summer 'return' rate (1 April to 30 October for Turnstones; 1 April to 30 November for Purple Sandpipers, covering both migrations and the breeding season) and a winter survival rate. The survival or return rate was calculated as the proportion of individuals alive at the start of a period that were recorded again in the study area at the end of that period. Only individuals classified as residents prior to the start of the period were included in the calculation of survival rates. A minimum annual survival rate was calculated as the product of over-summer return rate and winter survival.

2.2.3. Age structure of the population.

In order to further understand how the local populations of both species might be changing, estimates were made of the percentages of first-year birds present in each population in each year. Individuals were aged in the field and in the hand as first-year birds or adults according to plumage characteristics (Prater *et al.* 1977). The number and proportion of first-winter birds present in roosting flocks, (of a minimum size of ten birds), were recorded in early winter for each species and from the flocks sampled, an average calculated of the proportion of first-winter birds present in the wintering population. Individuals were not aged in the field after mid-winter, as wear of feathers made first-winter birds of both species difficult to separate from adults in the field (Prater *et al.* 1977, Cramp and Simmons 1983). The proportion of first-winter birds in catches of both species was also calculated when sample sizes exceeded ten.

2.2.4. Biometrics.

Measurements were taken of both Turnstones and Purple Sandpipers caught during the study period. Mass was recorded to the nearest 1g and wing-length (maximum chord) to the nearest 1mm with a stopped rule (Evans 1976b). The bill-length of Purple Sandpipers was also measured (to the base of the feathers on the bill) to the nearest 0.1mm with dial callipers. Additional biometric data on Purple Sandpipers caught at Hartlepool or nearby were available from the Tees Ringing Group (bill-length was sometimes measured only to the nearest 1mm in these data).

Purple Sandpipers are sexually dimorphic in size, females being larger than males (Tatarinkova 1977, Cramp and Simmons 1983), and also vary in size according to geographical origin. Two populations have been identified as wintering in Britain by analysis of bill-lengths: one a 'short-billed' population from Norway (Atkinson *et al.* 1981, Rae *et al.* 1986, Summers *et al.* 1992) and the other a 'long-billed' population which may originate from Canada and Greenland (Nicoll *et al.* 1988, Summers *et al.* 1992). Males from Norway have bill-lengths of less than 27.6mm and females from the long-billed population have bill-lengths greater than 32.2mm (Nicoll *et al.* 1988, Summers *et al.* 1992). Long-billed males and short-billed females overlap in bill-length between 27.6mm and 32.2mm. Colour-ringed individuals are classified to one of these three bill-length size classes (small, medium or large) following Summers *et al.* (1992). The proportion of Purple Sandpipers belonging to the short-billed and long-billed populations are estimated following the methods of Nicoll *et al.* (1988).

Purple Sandpipers from the Norwegian population arrive in their British wintering quarters from July each year and those from the long-billed population only from mid-October onwards. Any colour-ringed individuals from the medium bill-length size class that arrived back at Hartlepool prior to October therefore were classified as females of the Norwegian population.

2.3. Results.

2.3.1. Turnstone.

2.3.1.1. The classification of residents, visitants and passage birds.

Table 2.1 shows the number of Turnstones that were classed as residents, visitants or as passage birds at Hartlepool during each of the three years of study. All passage birds were recorded in autumn only. The figures in parentheses give the most reliable estimates of the proportion of residents within the adult population; these range from 63.0% ($n = 46$) in 1992/93 to 50.0% in 1991/92 ($n = 20$). There was no significant difference in the proportion of such residents in each of the three years ($\chi^2 = 0.981$, d.f. = 2, n.s.).

Six Turnstones classed as resident in 1991/92 became visitants in 1992/93, whilst one 1991/92 visitant became resident the following year. Seven Turnstones resident in 1992/93 became visitants in 1993/94, whilst one 1992/93 visitant became a resident. As there was no difference in the number of observation days each winter, it was therefore apparent that there was a tendency for Turnstones resident at Hartlepool to become visitants in following years, rather than *vice versa* (Sign Test for the two years combined: $P < 0.01$, $n = 15$).

The classification of residents according to their low water feeding areas is shown in Table 2.2 for each of the three winters. Eight resident Turnstones changed their 'home area' between years (17.8%, $n = 45$). Three birds classed as 'West Harbour to North Gare' residents one year became 'North and South' residents the next and one became a 'Headland' resident. Three Turnstones classed as 'North and South' residents one year became Headland residents the next and one became a West Harbour to North Gare resident. No individuals resident on the Headland changed to other areas in subsequent years.

Individual resident Turnstones were seen on a median of 39.7% of low water surveys ($n = 59$, range = 15.8 - 83.3%). First-winter resident Turnstones were seen as

Table 2.1. The numbers of individually-marked resident, visitant and passage Turnstones at Hartlepool in each of the three winters of study.

	1991/92	1992/93	1993/94
Residents	43 (10)	37 (29)	26 (23)
Visitants	37 (10)	36 (17)	25 (16)
Passage Birds	12	5	3

Figures in parentheses refer to those individuals caught within the study site prior to the start of the winter in question; (passage birds are not included in these figures).

Table 2.2. The numbers of individually-marked Turnstones resident in defined low water areas at Hartlepool.

	1991/92	1992/93	1993/94
Headland	20	17	17
West Harbour - North Gare	17	14	4
North and South	4	6	4
Unclassified	2	0	1

frequently as adults (Mann-Whitney $z = 0.291$, n.s.). Individual Turnstones tended, though not significantly, to be seen less regularly in autumn than in winter (Wilcoxon $z = 1.649$, $P < 0.10$), but as regularly in winter as in spring ($z = 0.490$, n.s.). Those individuals classed as Headland residents were however significantly more likely to be seen than those classed as West Harbour to North Gare residents ($z = 2.780$, $P < 0.01$).

2.3.1.2. Survival.

Minimum survival rates of Turnstones are shown in Table 2.3. Survival rates were similar over summer and winter. The proportion of first winter birds that returned after summer 1992 for a second winter was similar to that of adults (Table 2.4). It should be noted that actual annual survival may be higher than the figures shown, as some individuals may not return to the same wintering area each year.

2.3.1.3. The age structure of the Turnstone population.

The mean proportion of first winter birds present in roosting flocks of Turnstones at Hartlepool in each of the three winters is shown in Table 2.5. (N.B. A test using colour-ringed birds of known age showed that ageing by observation was not inaccurate - see Appendix 1). The proportion of first winter birds in winter roosting flocks was significantly higher in 1991/92 than in 1992/93 and 1993/94 (Kruskal-Wallis $\chi^2 = 8.143$, d.f. = 2, $P < 0.05$). First-winter birds comprised 8.1% ($n = 321$) of a catch at Seaton Carew on 26 February 1992 and 23.5% ($n = 17$) of a catch at West Harbour on 3 March 1992. A catch on 23 September 1993 at West Harbour contained 8 first-winter birds (28.6%, $n = 28$). Small catches thus tended to contain a higher proportion of first-winter birds and it should therefore be noted that the roosting flocks surveyed in 1991/92 were smaller than in subsequent years.

Table 2.3. Over-summer return rates and winter and annual survival rates of Turnstones classed as resident at Hartlepool.

	Proportion that survived	
	1992/93	1993/94
Over-summer return rate	0.881 (42)	0.828 (29)
Over-winter survival rate	0.811 (37)	0.875 (24)
Minimum annual survival rate	0.714	0.724

Over-summer return rates refer to the summer prior to the winter in question. Numbers of birds present at the start of each period, from which return rates have been estimated, are given in parentheses.

Table 2.4. Turnstone return rates over summer 1992 and age.

	Number that survived (%)	*n*
Adult	23 (85.2%)	27
First-winter	12 (92.3%)	13

Table 2.5. The mean proportion of first-winter birds in winter roosting flocks of Turnstones at Hartlepool.

	1991/92	1992/93	1993/94
Mean	0.253	0.061	0.097
Range	0.049-0.450	0-0.167	0.056-0.188
Number of roosting flocks counted	12	5	5
Range of flock sizes	12-70	12-193	16-206

2.3.1.4. Biometrics.

Differences in the masses and wing-lengths of adult and first-winter Turnstones were investigated using data from catches on 26 February 1992 and 23 September 1993, (data are shown in Appendix 2). On the former date, the masses of adults (mean = 104.4g, $n = 26$) and first-winter birds (mean = 102.3g, $n = 19$) were found to be similar ($t = 1.384$, d.f. = 43, n.s.). The wing-lengths of adults (mean = 153.8mm, $n = 16$) were however greater than those of first-winter birds (mean = 148.6mm, $n = 17$), ($t = 4.033$, d.f. = 31, $P < 0.01$). Mass and wing-length were not correlated amongst either adults ($r = -0.235$, d.f. = 14, n.s.), or amongst first-winter birds ($r = 0.142$, d.f. = 15, n.s.). On 23 September 1993, adults (mean = 111.1g, $n = 19$) were found to be significantly heavier than first-winter birds (mean = 99.9g, $n = 7$), (Mann-Whitney $z = 2.668$, $P < 0.01$), but had similar wing-lengths (adult mean = 156.1mm, $n = 8$; first winter mean = 153.3, $n = 7$; $t = 1.722$, d.f. = 13, n.s.). Mass and wing-length were again not correlated either amongst adults ($r = 0.492$, d.f. = 6, n.s.) or amongst first-winter birds ($r = 0.107$, d.f. = 5, n.s.).

Data from 1991/92 showed that mass changed seasonally. The masses of adult Turnstones were compared from catches on 24 October 1991 on North Gare Sands, 26 February 1992 at Seaton Carew and on 3 March 1992 at West Harbour. Mass was found to be significantly greater on 24 October 1991 (mean = 109.6g, $n = 5$) than on 26 February 1992 (mean = 104.4g, $n = 26$) and 3 March 1992 (mean = 102.2g, $n = 14$); ($F_{2,42} = 3.331$, $P < 0.05$).

2.3.2. Purple Sandpiper.

2.3.2.1. The classification of residents, visitants and passage birds.

Four of five purple Sandpipers caught and individually colour-ringed during winter 1991/92 were classed as resident, having been seen a minimum of five times before spring migration during weekly low and high water surveys (Table 2.6). A fifth bird was not seen after capture. In addition one individual, originally colour-ringed in Finland on 13 December 1972, was seen between 14 April and 11 May 1992 and was classed as a passage bird.

Five colour-ringed Purple Sandpipers were present at the start of winter 1992/93 and were subsequently seen more than ten times during winter and thus classed as resident. A further 30 birds caught and individually colour-ringed on 4 March 1993 were also classed as resident, having been seen a minimum of five times subsequent to that date. The passage bird from the previous year was again present during spring (from 15 to 28 April 1993).

Twenty colour-ringed Purple Sandpipers were known to be alive at Hartlepool at the start of winter 1993/94 and again all were classed as resident. Two other individuals, caught on 22 February 1994, were also classed as resident, having been seen a minimum of five times subsequently.

Purple Sandpipers caught within the study area had a higher probability of subsequently being classed as resident than those Turnstone also caught within the study area (N.B. This analysis only includes those individuals faithful to the study area or its vicinity during winter and thus excludes passage birds; Table 2.7; $\chi^2 = 9.406$, d.f. = 1, $P < 0.01$).

Resident Purple Sandpipers were classified according to their low water feeding areas in 1992/93 and 1993/94 (Table 2.8). In 1992/93, most Purple Sandpipers were caught in late winter and as each was seen only a few times before spring migration, they were classified as either 'Headland' or 'West Harbour to North Gare' residents. One Purple Sandpiper classified as a West Harbour to North Gare resident in 1992/93 was classified as a Headland resident in 1993/94 ($n = 18$). Two other 1992/93 West Harbour to North Gare residents were classified as 'N and S' residents in 1993/94.

Table 2.6. The numbers of individually-marked resident, visitant and passage Purple Sandpipers at Hartlepool in each of the three winters of study.

	1991/92	1992/93	1993/94
Residents	4	35	22
Visitants	0	0	0
Passage Birds	1	1	0

Table 2.7. The number of birds classified as resident or visitant in the first complete winter after their original capture.

	Resident	Visitant
Purple Sandpiper	23	0
Turnstone	33	19

Table 2.8. The numbers of individually-marked Purple Sandpipers resident in defined low water feeding areas at Hartlepool.

	1992/93	1993/94
Headland (N)	17	12
West Harbour - North Gare (S)	16	8
N and S	-	2
Unclassified	2	0

Individual Purple Sandpipers were seen on a median of 49.3% of low water surveys (n = 38, range = 18.2 - 87.5%). First-winter Purple Sandpipers tended to be seen less often than adults, though this trend was not significant (Mann-Whitney $z = 1.194$, $P = 0.116$ one-tailed). Those individuals classified as Headland residents were significantly more likely to be seen than those classed as West Harbour to North Gare residents ($z = 3.510$, $P < 0.001$). Individual Purple Sandpipers were seen as regularly in the autumn as in the winter (Wilcoxon $z = 0.700$, n.s.) and as regularly in the winter as in the spring ($z = 0.627$, n.s.).

Purple Sandpipers resident on the Headland were significantly more likely to be seen than those Turnstones resident in the same area ($z = 2.758$, $P < 0.01$). There was no significant difference in the probability of seeing individual Purple Sandpipers and Turnstones resident between West Harbour and North Gare ($z = 0.994$, n.s.).

2.3.2.2. Survival.

Minimum survival rates of Purple Sandpipers are shown for three summers and two winters in Table 2.9. There was 100% survival over winter in each year, though a lower return rate after the summer, notably in 1993, when only 20 of 35 individuals returned to the study area. Return rates did not differ significantly however over the summers of 1993 and 1994 ($\chi^2 = 1.601$, d.f. = 1, n.s.). 'Survival' rates over the winter and summer periods differed significantly ($\chi^2 = 8.801$, d.f. = 1, $P < 0.01$). (N.B. It should be noted that one individual, caught as a first-year in winter 1991/92 and resident in the winters of 1991/92 and 1992/93, was absent the following winter but returned to the study area in 1994/95; this bird was classified as one of those that did not 'return' after summer 1993 and was not included in subsequent survival rate calculations).

The proportion of first-winter birds that returned after summer 1993 for a second winter was similar to that of adults (Table 2.10). The proportion of birds from the small and medium bill-length size classes that returned to the study site was however higher than that of the large bill-length size class (Table 2.11).

Table 2.9. Over-summer return rates and winter and annual survival rates of Purple Sandpipers classed as resident at Hartlepool.

	Proportion that survived		
	1992/93	1993/94	1994/95
Over-summer return rate	0.750 (4)	0.571 (35)	0.773 (22)
Over-winter survival rate	1.000 (3)	1.000 (20)	-
Minimum annual survival rate	0.750	0.571	-

Over-summer return rates refer to the summer prior to the winter in question. Numbers of birds present at the start of each period, from which return rates have been estimated, are given in parentheses.

Table 2.10. Purple Sandpiper return rates over summer 1993 and age.

	Number that returned (%)	*n*
Adult	14 (58.3%)	24
First-winter	6 (54.5%)	11

Table 2.11. Purple Sandpiper return rates over summer 1993 and bill-length size class.

Bill-length size class	Number that returned (%)	*n*
Small	6 (75.0%)	8
Medium	13 (65.0%)	20
Large	1 (14.3%)	7

From 1 April 1993 to 30 March 1994, the minimum survival rate of Purple Sandpipers was similar to that of Turnstones ($\chi^2 = 1.012$, d.f. =1, n.s.). The return rate of Purple Sandpipers was slightly, though insignificantly, lower over summer 1993 than that of Turnstones ($\chi^2 = 3.725$, d.f. = 1, $P < 0.10$); it should be noted however that Purple Sandpiper summer survival is calculated over eight rather than seven months.

2.3.2.3. The age structure of the Purple Sandpiper population.

Juvenile Purple Sandpipers began to arrive at Hartlepool in August each year, though the proportion present at roosts remained low until October. Table 2.12 shows the mean proportion of first-winter birds found in roosting flocks in each of the three winters.

There was no significant difference in the proportion of first-winter birds found in roosting flocks between years (Kruskal-Wallis $H_{5,4,1} = 4.860$). A catch on 4 March 1993 contained a higher proportion of first-winter birds (29.0%, n =31) than seen previously in roosting flocks that winter. (It was not possible to test the accuracy of ageing Purple Sandpipers in the field prior to mid-winter when these observations were taken, as no first-year Purple Sandpipers were ringed prior to February).

2.3.2.4. Biometrics.

Histograms of the bill-lengths of Purple Sandpipers are shown for all the birds caught at Hartlepool during the defined winter period (15 November to 31 March) (Fig. 2.1) and for a single catch on 4 March 1993, that forms a subset to these (Fig. 2.2). Table 2.13 shows the frequency and proportion of birds in each bill-length size class for each of these two cases. In each case the proportion of adults and first-winter birds in each size class was similar.

An estimated 64.0% of Purple Sandpipers caught at Hartlepool were from the 'long-billed' population and 36.0% from the 'short-billed' population (see Nicoll *et al.* 1988 for

Table 2.12. The mean proportion of first-winter birds in roosting flocks of Purple Sandpipers at Hartlepool.

	1991/92	1992/93	1993/94
Mean	0.227	0.153	0.107
Range	0.144-0.333	0.114-0.250	0.107
Number of roosting flocks counted	4	5	1
Range of flock sizes	13-174	16-223	131

Table 2.13. Frequencies of Purple Sandpipers in bill-length size classes.

Bill-length Size Class	All birds caught during winter		4 March 1993	
	Adult	First-Winter	Adult	First-Winter
Small	8 (16.3%)	2 (12.5%)	6 (27.3%)	2 (22.2%)
Medium	32 (65.3%)	13 (81.3%)	10 (45.5%)	7 (77.8%)
Large	9 (18.4%)	1 (6.3%)	6 (27.3%)	0 (0%)

Fig.2.1. Purple Sandpiper bill-length distribution; data from all birds caught at Hartlepool during winter.

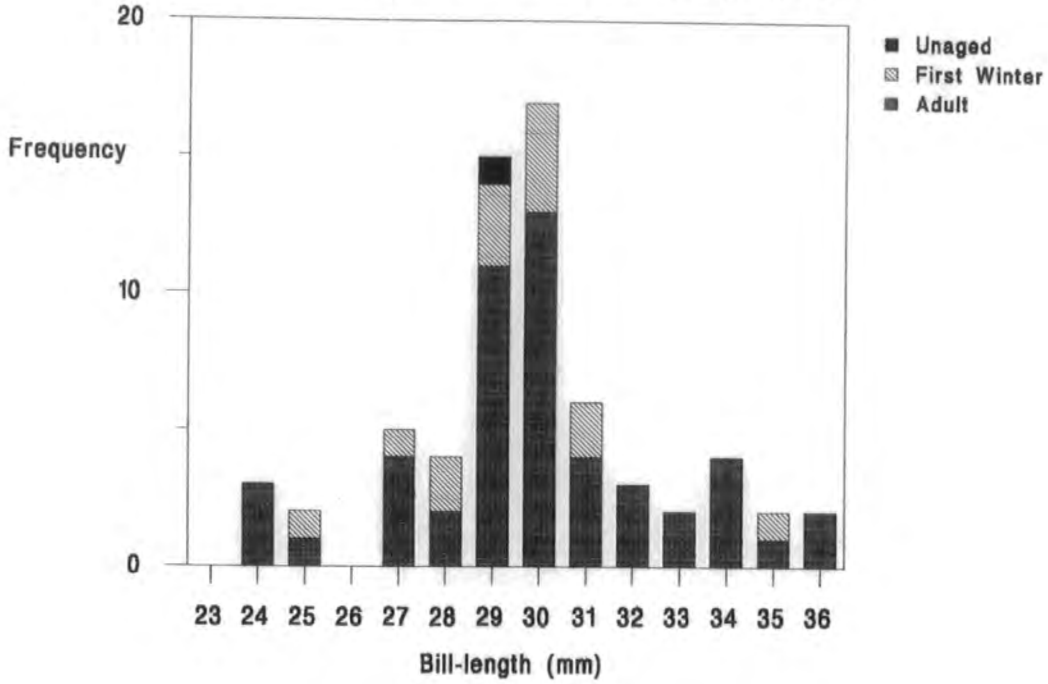
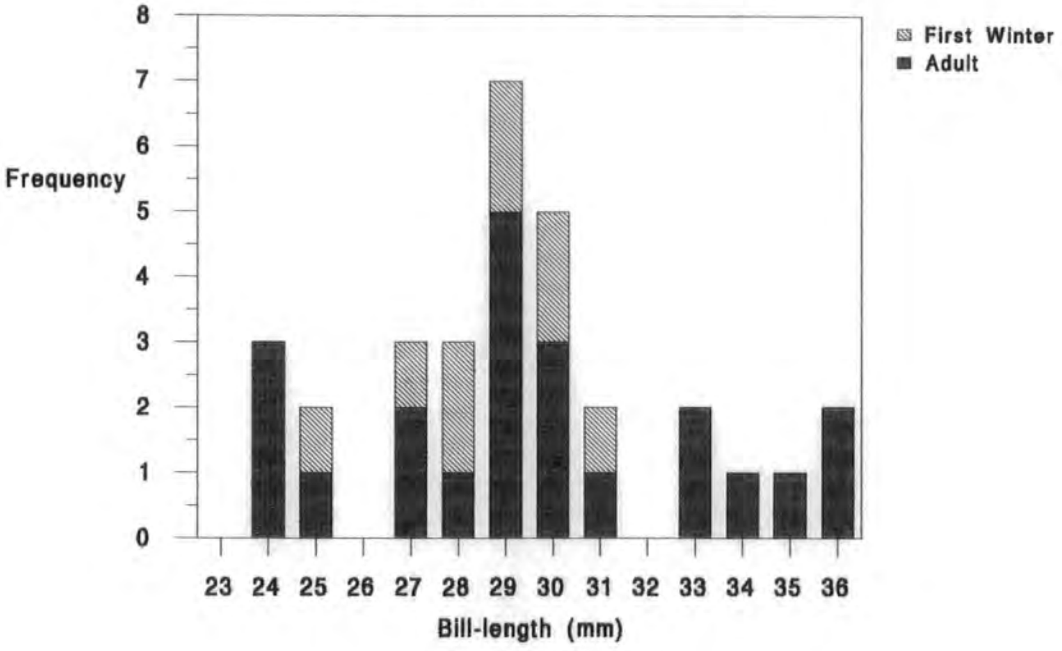


Fig.2.2. Purple Sandpiper bill-length distribution; from a catch at Hartlepool on 4 March 1993.



methods). Data from the single catch of 4 March 1993 suggested that 57.1% of Purple Sandpipers were long-billed and that 42.9% were short-billed.

The relationships between biometric measurements were investigated using data from a catch on 4 March 1993 (see Appendix 2), when data was available from both adult and first-winter birds. There was no significant difference in mass (t = 0.852, d.f. = 29), wing-length (t = 0.943, d.f. = 29) or bill-length (t = 0.789, d.f. = 29) between birds from the two age classes. Using data from adults only, it was found that there were correlations between bill-length size class and mass (one-way ANOVA $F_{2,19} = 22.124$, $P < 0.001$) and between bill-length size class and wing-length ($F_{2,19} = 9.126$, $P < 0.01$): birds of the large size class were heaviest and had the longest wings, birds of the small size class were lightest and had the shortest wings. Mass and wing-length were also positively correlated ($r = 0.856$, d.f. = 20, $P < 0.001$ one-tailed). When data from all individuals were considered, bill-length was similarly related to mass (one-way ANOVA $F_{2,28} = 28.569$, $P < 0.001$) and wing-length ($F_{2,28} = 11.579$, $P < 0.001$), whilst mass and wing-length were also positively correlated ($r = 0.841$, d.f. = 29, $P < 0.001$).

2.4. Discussion.

2.4.1. Site fidelity within winter.

Once autumn passage had finished, Turnstones and Purple Sandpipers were both largely resident within the study site during winter; individuals were seen, on average, on every other low water count. Individuals of both species were seen more often if resident on the Headland rather than between West Harbour and North Gare. This is undoubtedly largely because West Harbour to North Gare residents used the offshore Long Scar rocks, (which are only exposed over low water), and thus were frequently absent from the mainland shore. West Harbour to North Gare residents may also have been seen less often than those on the Headland due to the smaller area of feeding habitat available to them, which may have caused them to be more itinerant.

Previous studies have also shown high within-winter site-fidelity for both Turnstones (Brearey 1982, Symonds *et al.* 1984, Metcalfe and Furness 1985, Whitfield 1985a) and Purple Sandpipers (Atkinson *et al.* 1978, 1981, Metcalfe 1984a, Summers *et al.* 1990b). The high degree of residency shown by both species is probably a consequence of the reliability of their usual rocky shore food resources (Evans 1981). Prey species on rocky shores are readily available (Becuwe 1973, Dierschke 1993) and unlike those in soft substrates are not usually affected by wave action or sediment erosion (Ratcliffe *et al.* 1981, Myers 1984, though see Paine and Levin 1981) or made less accessible by cold weather (Evans 1976a, Ratcliffe *et al.* 1981).

Metcalfe (1984a) suggested that Purple Sandpipers were more mobile within winter than Turnstones and Feare (1966) similarly found that Purple Sandpipers frequented different localities after mid-January. In the present study, in contrast, individual Purple Sandpipers were completely resident over the winter period and were more frequently seen than Turnstones. No Purple Sandpipers caught and colour-ringed within the study site were subsequently seen outside it during winter. The sighting of one Purple Sandpiper on the Farne Islands, Northumberland on 4 July 1993, over two months before returning to Hartlepool (Appendix 3), does however suggest that some individuals may use other areas for lengthy periods in autumn, perhaps during wing moult. The proportion of Turnstones originally caught within the study site and classed as visitants was relatively high and was greater than that recorded by Metcalfe and Furness (1985) in their study in south-west Scotland (though methods of classification differed between the studies). The suggestion of some vagrancy amongst Turnstones is supported by observations of two colour-ringed birds. One bird was resident in the study site during winter 1991/92 and was present again in early winter 1992/93 before leaving and subsequently being seen at Seaham, 19km to the north. A second individual, resident in the winters of 1991/92 and 1992/93, was present at Hartlepool early in winter 1993/94 and again in March and April 1994, but in midwinter was seen at Salterfen Rocks 23km to the north. Turnstones are less dependent than Purple

Sandpipers upon rocky shores for their food supplies (McKee 1982, Summers *et al.* 1988b) and are great opportunists (Fleischer 1983, Botton *et al.* 1994), frequently feeding upon invertebrates in tideline deposits of wrack or other algae (Groves 1978). To search for such profitable prey they may leave their 'home' areas relatively often.

The relatively high proportion of visitants amongst the Turnstone population may partly be a result of surveying and sampling methods. As Turnstones are less restricted than Purple Sandpipers to a single habitat during winter, they are firstly perhaps more easily overlooked. Additionally, many colour-ringed Turnstones were initially caught towards the southern edge of the study site and were thus more liable to be visitants from neighbouring areas.

Metcalfe (1986) found that Turnstones were more mobile before and after winter and suggested that they may have sampled other areas outside of their home range in autumn in order to reduce the need for exploration later in times of stress. In the present study no such seasonal differences in mobility were seen in either species. It is perhaps interesting to note however, that an individual Turnstone classified as an autumn passage bird by Brearey (1982) in his study south of the Tees estuary, was classified as a resident at Hartlepool in the first year of the present study.

2.4.2. Site fidelity between winters and survival.

Site fidelity between winters has been recorded in a number of studies of both Turnstones (Branson *et al.* 1978, Brearey 1982, Symonds *et al.* 1984, Metcalfe and Furness 1985, Whitfield 1985a) and Purple Sandpipers (Atkinson *et al.* 1978, Summers *et al.* 1990b, K-B. Strann pers. comm., V. Dierschke pers. comm.). In the present study, Turnstones were particularly site-faithful, with 88.1% of colour-ringed individuals present at Hartlepool in spring returning after summer 1992 and 82.8% after summer 1993. These rates are however lower than those of 95.0% recorded for adults by Metcalfe and Furness (1985) and 96.0 - 98.4% recorded for adults by Whitfield (1985a), suggesting either that there was slightly poorer summer survival, or that a few individuals had moved to different wintering areas. Both the present study and that of Metcalfe and Furness (1985) found that a few individuals changed status between years from residency to visitancy, or *vice versa*, as a result of a shift of a few kilometres in their wintering areas. Some individuals may move to completely new areas: an individual ringed as a first-winter bird in Lothian, Scotland in November 1986 was recovered three winters later in North Carolina in the United States (Mead and Clark 1990). In the present study, more residents became visitants in later years than *vice versa* and there may therefore have been a tendency for individuals to move away from the study area.

Baker (1978) proposed that first-winter birds may be more mobile during a single winter than adults in order to sample possible alternative future wintering sites. Although Metcalfe and Furness (1985) found this in Turnstones, neither their nor the present study found differences in the return rates of first-winter and adult Turnstone to their wintering areas.

The return rate of Purple Sandpipers in 1993 was notably lower than that of Turnstones and suggests that either Purple Sandpiper survival was low over summer or that some birds changed their wintering sites. Previous studies have suggested that site fidelity is high: in northern Norway for example, 87% of colour-ringed birds returned to the same wintering area after the breeding season (K-B. Strann pers. comm.). In the present study however, the sighting of one colour-ringed individual, a first-winter bird resident at Hartlepool in winter 1992/93, in Lothian, Scotland in December 1993 (Appendix 3) and the return of an individual to the study area after being 'missing' for a winter, suggest that a proportion of Purple Sandpipers do move to different wintering areas. A few other records exist of Purple Sandpipers changing their wintering grounds between winters: one bird ringed in Lincolnshire as an adult in October 1983 was subsequently seen in Halland, Sweden in March 1987 (Mead and Clark 1988), whilst an individual ringed as a first-winter bird on Helgoland, Germany in November 1991 was seen in December 1993 on an island

45km to the south (V. Dierschke pers. comm.). Purple Sandpipers attempting to winter in Finland are frequently forced to migrate further south because of the development of sea ice and thus regularly change their wintering areas (V. Vänskä pers. comm.); this though is clearly a different situation. It is possible that a number of factors affect the degree of site-fidelity exhibited by Purple Sandpipers and it is interesting to note that, in the present study, Purple Sandpipers of the small bill-length size class, (males from the Norwegian population), had higher over-summer return rates than those of the large bill-length size class (females from what is thought to be the Greenland / Canada population). It is thus possible that either male Purple Sandpipers or birds from the Norwegian population may tend to be more site-faithful between winters.

Studies in Helgoland have found that the return rates of adult Purple Sandpipers after summer are greater than those of first-year birds (84 - 88% compared to 50 - 70% respectively; V. Dierschke pers. comm.), indicating either that there is a greater mortality in first summer birds or that there is some movement to different sites between the first and second winter. The only record of such a change of wintering site in that study involved a first-year bird. The tendency for first-winter Purple Sandpipers to be seen less often than adults at Hartlepool indicates a greater mobility amongst first-year birds, which may, as Baker (1978) hypothesised, be prospecting for alternative future wintering quarters.

The return rates of Turnstones over summer were similar to the survival rates over winter, suggesting that migration to and from the Arctic breeding grounds and breeding itself were not great causes of mortality. Indeed Evans and Pienkowski (1984), Metcalfe and Furness (1985) and Whitfield (1985a) all suggest that winter mortality is marginally greater than that over summer. In comparison to most other wader species however, Turnstone seem to be less at risk to severe winter weather (Pilcher *et al.* 1974, Norman and Coffey 1994; though see Davidson and Clark 1985). The increase in mass in midwinter shown by Turnstones, (there was, in the present study, a difference of 7.2% between the mean mass recorded in late October and that in March), is notably less proportionally than that seen in other, estuarine waders (Johnson 1985, Summers *et al.* 1975, 1989, 1992). The relative lack of impact of severe weather upon the invertebrates found on rocky shores ensures that Turnstones, in contrast to most other waders, have a relatively stable food supply throughout winter and hence they may not need to lay down large fat stores as a reserve (Evans and Smith 1975). In contrast to adults, first-winter Turnstones are less efficient at feeding, at least in the autumn (Groves 1978), and may have lower masses as a result (the present study; Summers *et al.* 1989). Little evidence however exists to suggest that, in consequence, first-winter Turnstones have lower winter survival rates (Metcalfe and Furness 1985, Whitfield 1985a).

Overall Turnstone minimum annual survival rates at Hartlepool were relatively high, though slightly lower than the rate of 86% recorded by Metcalfe and Furness (1985) and that of 78% recorded by Bergman (1946) in a study of breeding birds in Finland. Evans and Pienkowski (1984) recorded a return rate, from autumn to autumn, of 85% for colour-ringed Turnstones on the coast south of Teesmouth. The slightly lower rate in the present study may be due to movement away from Hartlepool both within and between winters. It is possible that the numbers of Turnstone at Hartlepool may be declining: the proportion of first-winter birds in flocks in 1992/93 and 1993/94 seemed insufficient to balance losses over each year and was lower than that seen in other previous studies (Branson *et al.* 1979, Whitfield 1985a). Both Brearey (1982) and the present study however suggest that first-winter birds may be underrepresented at large roosts, perhaps due to their need for additional feeding over the high water period (see Chapter 5). The proportion of first-winter birds present in the wintering Turnstone population may thus be underestimated.

The annual survival rates do suggest however that Turnstones may be long-lived and Cramp and Simmons (1983) have reported an instance of an individual living 19 years. Several individual Turnstones colour-ringed at Teesmouth during the 1970's were seen during the present study. Of these, the oldest was an individual ringed as an adult in May

1977 and last seen in November 1993, and therefore known to be a minimum of 18 years old.

In contrast to Turnstones, no Purple Sandpipers were recorded to have died at Hartlepool during the winter. Purple Sandpipers increase their mass only marginally during winter (Atkinson *et al.* 1981, Davidson 1990, Summers *et al.* 1992, Dierschke 1993) and are well adapted to cold winters through having heavy plumage and large breast muscles (Davidson 1990), which may act as heat generators (Summers *et al.* 1992). As a result, they may be at considerably less risk than other waders to severe weather conditions and the problems of food availability. The prey found on rocky shores are less susceptible to cold than are the invertebrates found in estuaries (Goss-Custard 1969, Ratcliffe *et al.* 1981) and are easily accessible (Becuwe 1973). Dierschke (1993) found that Purple Sandpipers spent considerably less time feeding during winter than other waders and suggested that they had no difficulty in fulfilling their energy requirements (at least during calm weather conditions). Mortality during winter may as a consequence be much lower than that seen in other waders. No difference was found in the masses of first-winter and adult Purple Sandpipers in the present study, though adults were found to be marginally heavier through winter by Summers *et al.* (1992). It is likely that there is little difference in the mortality rates of adult and first-winter Purple Sandpipers in Britain in winter.

Minimum annual survival rates of Purple Sandpipers at Hartlepool were largely affected by low over-summer return rates. Although there were proportionally more first-winter Purple Sandpipers than Turnstones in winter flocks at Hartlepool, the numbers of first-year birds may still have been insufficient to maintain the population. There was no evidence that the proportion of first-winter Purple Sandpipers present in the population was underestimated by surveying only roosting flocks.

Assuming that some birds do change wintering areas, Purple Sandpipers may also be long-lived. One individual, originally ringed as an adult on 29 December 1988 at

Steetley, was seen on Seaton Sands on 27 January 1994 and was thus a minimum of six years old (Appendix 3). The passage bird recorded at Hartlepool in the springs of 1992 and 1993 was originally ringed in December 1972 in Finland and was thus a minimum of 20 years old when last seen.

2.4.3. Population structure of the wintering population.

It is now well established that the Turnstones that winter in northern Europe belong to the Greenland / Canada breeding population (Branson *et al.* 1978, Mead and Clark 1988). One recovery from the present study supports this: an adult caught on Seaton Sands on 26 February 1992 was recovered in north-east Greenland on 2 June 1993 (Appendix 3).

Bill-length analysis suggested that the majority of Purple Sandpipers wintering at Hartlepool were also from the probable Greenland / Canada population. Wintering populations elsewhere in north-east England and in eastern Scotland have previously, in contrast, been shown to be dominated by the Norwegian population (Nicoll *et al.* 1988). Two winter controls at Steetley of Purple Sandpipers ringed in north Wales in a previous autumn (Appendix 3) support a link with north-westerly breeding grounds.

The Purple Sandpipers that winter in southern Britain and continental Europe probably include birds from arctic Russia (Boere *et al.* 1984, Nicoll *et al.* 1988, Summers and Rogers 1991, Dierschke 1995, V. Vänskä pers. comm.). The sighting in spring 1992 and spring 1993 of a colour-ringed Purple Sandpiper, originally ringed in Finland in late autumn 1972, suggests that part of this population migrates through north-eastern England, at least in spring.

Summary.

1). All colour-ringed Purple Sandpipers and a high proportion of colour-ringed Turnstones present at the start of winter were resident in the study area throughout the winter. For both species, three resident groups were defined: 'Headland' residents, 'West Harbour to North Gare' residents and ' North and South' residents.

2). Survival of Purple Sandpipers over the winter period was very high and slightly greater than that of Turnstones. In comparison to other shorebird species, Turnstones increased in mass only marginally by midwinter as a survival aid.

3). Most adult Turnstones that survived between spring departure and autumn return, came back to Hartlepool, usually to the same feeding area.

4). A lower proportion of Purple Sandpipers that survived through the summer returned to Hartlepool, particularly in 1993; some returned to winter elsewhere.

Chapter 3

Species Use of Roost Sites.

3.1. Introduction.

Roosting forms an important component of the daily time budgets of wintering shorebirds, occupying (on account of tidal cycles) sometimes fifty percent or more of their time. Despite this, few attempts have been made to show how the use of roosts and other high tide areas varies between or within species. The use of sites may be limited by the tide, but also may vary, less predictably, according to weather conditions, disturbance and the birds' own feeding requirements. Usually a number of high water sites are available (Furness and Galbraith 1980b), though typically waders roost as close as possible to their low water feeding grounds (Furness 1973a, Robertson and Dennison 1979, Brearey 1982, Swennen 1984). The availability of alternate roosts is important though, for example when disturbance forces birds to leave a particular site. Tubbs *et al.* (1992) found that Dunlin flocks on the Solent spent a large proportion of the high tide period on the wing due to disturbance at roost sites and suggested that the lack of safe high tide roosts had, in part, led to the species' decline in the area.

At Hartlepool a number of roost sites, in addition to West Harbour, were available to waders over high water. Waders which foraged over the low water period on Hartlepool Headland, had the choice, over high water, of staying on the Headland or flying to West Harbour one to two kilometres to the south-west. Preliminary studies investigated the control of the tide and weather on the numbers of Turnstones and Purple Sandpipers found in these two areas at high tide.

Disturbance to wintering waders may have considerable impact, typically forcing birds into temporary flight, though sometimes even causing their departure from an area (Furness 1973b, Kirby *et al.* 1993). Previous studies of disturbance have focused on the loss of feeding time to foraging waders (Goss-Custard and Verboven 1993) and on the variety and scale of disturbance at roosting sites (Furness 1973b, Handel and Gill 1992, Kirby *et al.* 1993). Smit and Visser (1993) have usefully summarised existing knowledge from Dutch studies, whilst Davidson and Rothwell (1993) have assessed some of the conservation implications of human disturbance. The present study aimed to underline the importance of disturbance in influencing the choice of roost site. The importance of different disturbance factors was assessed at West Harbour and on Hartlepool Headland and the varying susceptibility of species to them was gauged. Furness (1973b) found that the tolerance of different species to different factors varied considerably and that their choice of roost site reflected this. Only a few studies have looked at the possible effects on local shorebird populations of the disturbance, change or loss of roosting sites. Studies in Britain on the Dee estuary (Mitchell *et al.* 1988), on the Solent (Tubbs *et al.* 1992), in the Netherlands (Zwarts 1972) and in the United States (Pfister *et al.* 1992) have all linked declines in shorebird populations to the disturbance or loss of roosting sites, though on the Dee numbers of shorebirds have recently begun to increase, perhaps due to control of disturbance factors (Kirby *et al.* 1993). The present study examined whether changes in the numbers of shorebirds at West Harbour, through and after its redevelopment (see Chapter 1), were associated with changes in the local numbers of birds, changes in national numbers or with disturbance. The development of the marina at West Harbour was predicted to lead to increased levels of disturbance to roosting shorebirds particularly from boats; likewise, beaches and piers would be increasingly frequented by the public after the redevelopment and birds roosting there were predicted to suffer increased human disturbance. The increase in disturbance from these two factors was thus likely to increase the overall levels of disturbance at the site, unless special measures were taken to control it. Full discussion of the effects of the development is provided later in the general discussion (Chapter 7), after analysis of the changes in the numbers of locally feeding birds (Chapter 4) and with reference to survival rates (Chapter 2).

The exact location of roosting birds within a site is frequently determined by energetic considerations (Siegfried 1971, Francis 1976, Jenni 1991) or again by disturbance. At West Harbour the new island was expected to provide shelter from winds from all directions and its use by roosting Turnstones and Purple Sandpipers was investigated in this study in relation to wind speed. Data from sunny and windy days are analysed separately to determine whether sunshine allowed birds to be more tolerant of high wind speeds. Turnstones and Purple Sandpipers were expected to use the sloping sides of the island (and the latter the beams on the inner pier), but it was anticipated that other species that tended to roost on flatter open sites, such as Oystercatcher and Knot, would not find the crenellated top of the island as attractive as the old stone piers. The success of the island as a roost site was assessed in relation to the use of other sites within the harbour.

The foraging and energetic requirements of waders vary widely seasonally. Many species put on weight during winter (Johnson 1985), when daylight hours are short, and before spring migration considerable fat deposits are built up (Clapham 1979, Prys-Jones *et al.* 1992, Summers *et al.* 1992). These requirements may be reflected in species' roosting behaviour: in winter for example, foraging may occur at high water, whilst energy saving behaviour, such as sleeping with a tucked in bill (Midtgård 1978) may increase. The behaviour of Turnstones and Purple Sandpipers was recorded at the West Harbour roost in relation to the tidal cycle and season. In addition, comparison was made between West Harbour and Hartlepool Headland of the proportion of birds of both species seen feeding at high water. (Observations on the night-time roosting and feeding behaviour of Turnstones and Purple Sandpipers is summarised in Appendix 4).

3.2. Methods.

3.2.1. Roosting Numbers.

The West Harbour roost was surveyed typically once weekly at high water between July 1991 and June 1994. In June and July each year, when few shorebirds were present at

Hartlepool, the West Harbour roost was only surveyed once a month. The number of birds of each species present at high water, their locations at the roost and factors which affected the pattern of usage of the roost, *viz.* the predicted height of high water and the wind speed (estimated on the Beaufort scale) and direction, were recorded. Counts from between February and July 1991 were available from Robinson (1992) and from the University of Durham, and in addition to these data, monthly counts from winters before 1991/92, recorded at high water as part of the British Trust for Ornithology's Birds of Estuaries Enquiry (BoEE) - nowadays the Wetland Bird Survey (WeBS) - are used in this chapter.

Turnstones and Purple Sandpipers were also counted at high water on Hartlepool Headland as frequently as possible: usually once fortnightly.

3.2.2. Disturbance.

During observation periods at West Harbour, the number and source of any disturbances to roosting waders were also recorded. Observations centred around high water (typically covering two hours either side) when the numbers of birds at the roost were at their maximum. Disturbance was recorded only when part or all of the roosting flock was put to flight (see Bélanger and Bédard 1989, Kirby *et al.* 1993). Flights caused by unknown sources of disturbance were distinguished from natural flights by the simultaneous take-off of the individuals involved. Typically birds returned to the roost after a short period, though on occasion disturbance led to birds departing from the roost. For each category of disturbance, the proportion of disturbances that caused one or more birds to leave the roost was calculated. Rates of disturbance, (numbers of disturbances / time spent observing), were calculated for each three month period from 1 July 1991.

The effect of disturbance on the numbers of Purple Sandpipers using the West Harbour roost was investigated in more detail during March 1993. The number of disturbances in a two hour period and the total number of 'bird-minutes' of disturbance (the product of the number of birds put to flight and the time spent in flight) were compared with the difference between the observed and expected number of roosting birds the following day. The expected number of Purple Sandpipers at the roost was calculated in relation to predicted tide height and wind speed, by applying the formula described later (see section 3.3.2.4).

The rates of disturbance and the susceptibility of Turnstones and Purple Sandpipers to different disturbance factors were also studied at Inscar beach on Hartlepool Headland (see Fig. 1.1) for comparison.

3.2.3. Choice of position at the roost site.

The position and species' composition of all flocks of shorebirds present at the West Harbour roost were recorded at high water. The positions of the flocks that contained the majority of the Turnstones and Purple Sandpipers on the island were additionally noted. A shelter index for roosting birds was calculated by relating the orientation of the island's face at these positions to the wind direction: + 4 (facing directly away from the wind), through 0 (perpendicular to the wind), to - 4 (facing directly into the wind).

Wind speed measurements were made on 9 March 1992 to investigate how much shelter the island actually gave. In this study, measurements were taken at ten points around the island and at the bottom, middle and top of the slope at each position. Wind readings were taken with an anemometer held at a height of 15cm, in a direction that was perpendicular to the face of the island.

3.2.4. Behaviour at the West Harbour roost.

The behaviour of Turnstones and Purple Sandpipers at the West Harbour roost was recorded using the scan sampling method (Altmann 1973). Flocks were scanned at high water and at one hour intervals before and after, and the number of birds engaged in the following activities recorded: standing, sleeping (head turned with bill resting on back), preening, bathing, feeding, running (including walking, flying and swimming) and involved in agonistic behaviour. Bathing was only rarely recorded and was combined with preening for analyses. The behaviour of all visible birds in a flock was recorded, with a minimum sample size of twenty. (Small samples give less reliable estimates of true time budgets, particularly when activities are of a short duration, *e.g.* agonistic behaviour, Pöysä 1991).

In addition to recording behaviour at the West Harbour roost, comparison was made between the proportion of birds in flocks that were feeding at high water at West Harbour and on Hartlepool Headland: the number of birds in the flock and the number feeding were recorded.

3.3. Results.

3.3.1. Roosting numbers.

3.3.1.1. Seasonal patterns.

3.3.1.1.1. Turnstone.

The monthly maximum numbers of Turnstones at the West Harbour roost are shown for each year from July 1990 in Fig. 3.1. Numbers of Turnstone rose quickly each summer, as birds returned from their breeding grounds, numbers peaking during the autumn passage season, notably in 1991 and 1992. Typically numbers became stable from mid-October, after passage birds had departed, though during the winters of 1992/93 and 1993/94, roosting numbers fluctuated markedly. Turnstones migrated from the area in April and May, only a few one-year old birds being recorded in June.

Winter was defined for Turnstones as the period between 25 October and 31 March each year, *i.e.* the period after autumn and before spring passage when numbers at Hartlepool were stable. Summer was defined for Turnstones as the period when only first-year over-summering birds were present at Hartlepool.

Fig. 3.1. Monthly maximum counts of Turnstones roosting at West Harbour, Hartlepool, between July 1991 and June 1994.

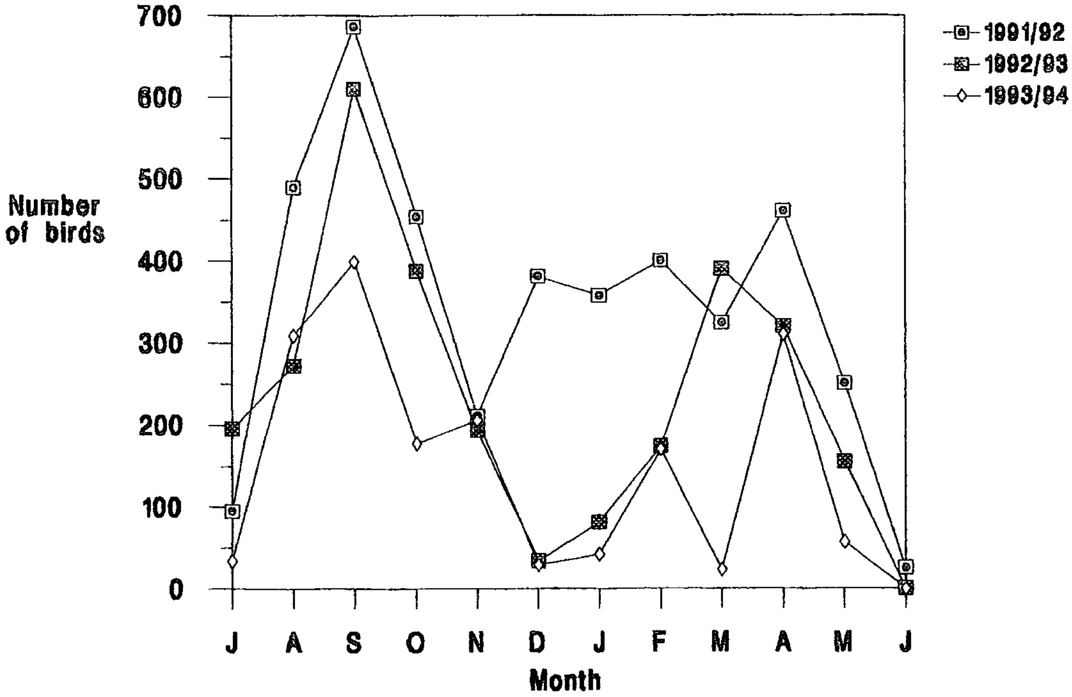
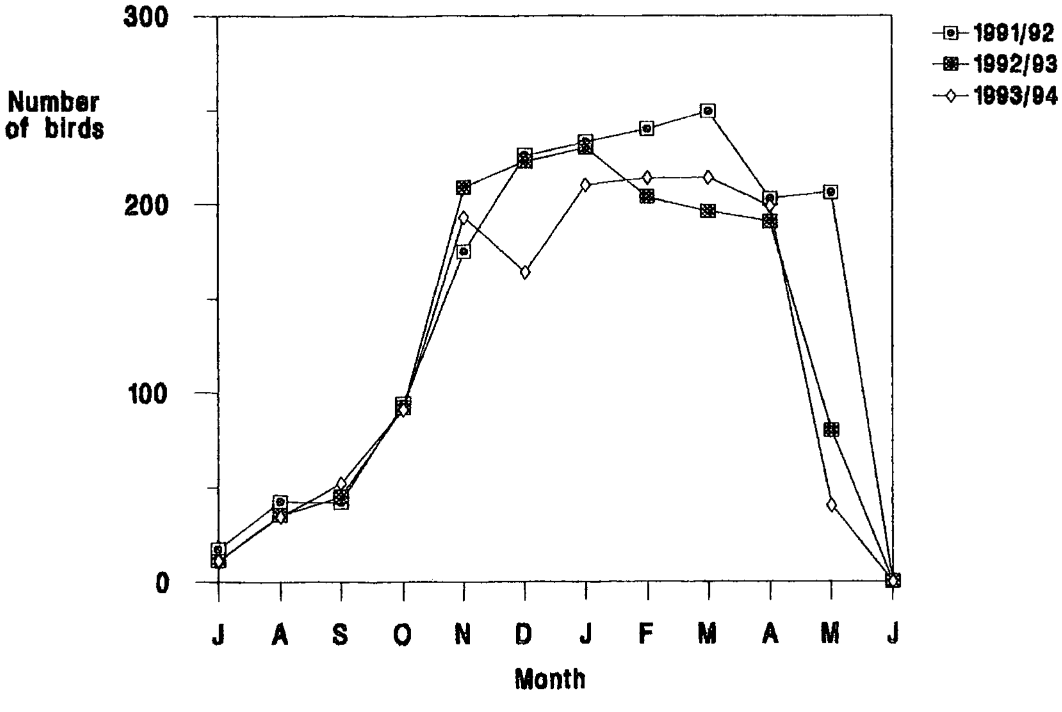


Fig. 3.2. Monthly maximum counts of Purple Sandpipers at West Harbour, Hartlepool, between July 1991 and June 1994.



3.3.1.1.2. Purple Sandpiper.

Monthly maximum numbers of Purple Sandpipers at the West Harbour roost are shown for each of the three years of study in Fig. 3.2. Purple Sandpipers first returned to the Hartlepool area in July each year, though numbers at the roost remained low throughout summer. Numbers rose sharply in late September and October, before becoming stable for the winter from mid-November. Purple Sandpipers migrated from the area in April and May, no birds being recorded at the roost in June.

Neither species appeared to be affected by building work that took place within West Harbour during 1991/92. Numbers of each followed similar monthly patterns to those seen the previous year.

Winter was defined for Purple Sandpipers as the period between 15 November and 31 March each year, when numbers at Hartlepool were stable after autumn and before spring passage. Summer was defined as the period between the departure of all Purple Sandpipers from Hartlepool in spring and their return in autumn.

3.3.1.2. The effects of tide and wind.

3.3.1.2.1. Turnstone.

During the defined period of winter stability, Turnstone numbers at the West Harbour roost were positively correlated with the height of high water (HW) in each of the three years of study (Figs. 3.3 - 3.5) and were negatively correlated with the wind speed (W) in two of the winters. (The height of high water and wind speed were not correlated in any of the three winters: 1991/92 $r = 0.297$, d.f. = 23, n.s.; 1992/93 $r = 0.236$, d.f. = 24, n.s.; 1993/94 $r = -0.039$, d.f. = 19, n.s.).

1991/92: No. of Turnstone = -768.3 + 205.1 HW (m) - 47.5 W (Beaufort)
$r^2 = 0.580$; t (tide) = 5.293, d.f. = 22, $P < 0.001$; t (wind) = -3.056, $P < 0.01$.

Fig. 3.3. Turnstone numbers at the West Harbour roost and their relationship with tide: 1991/92.

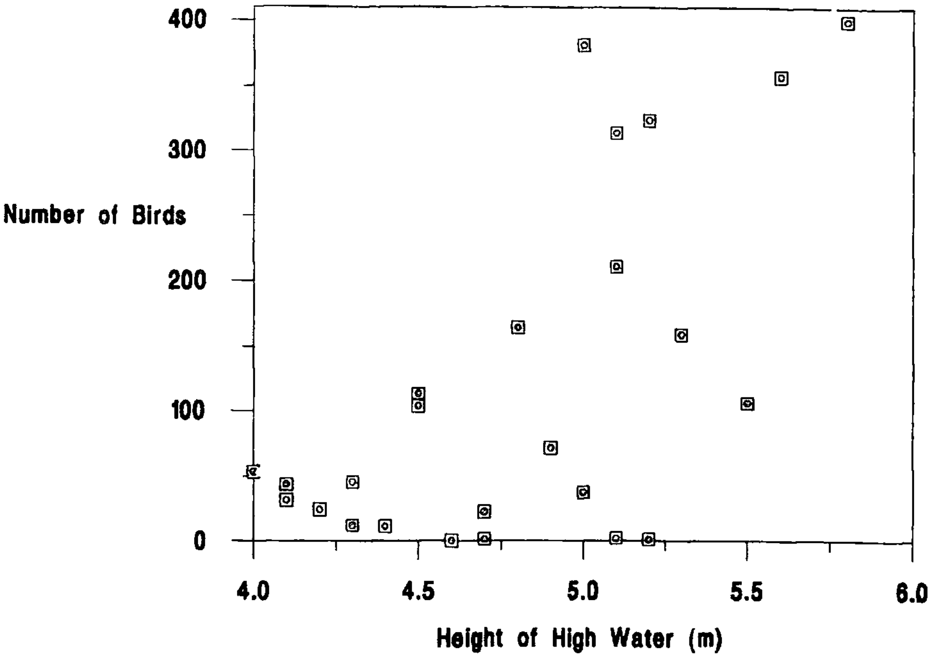


Fig. 3.4. Turnstone numbers at the West Harbour roost and their relationship with tide: 1992/93.

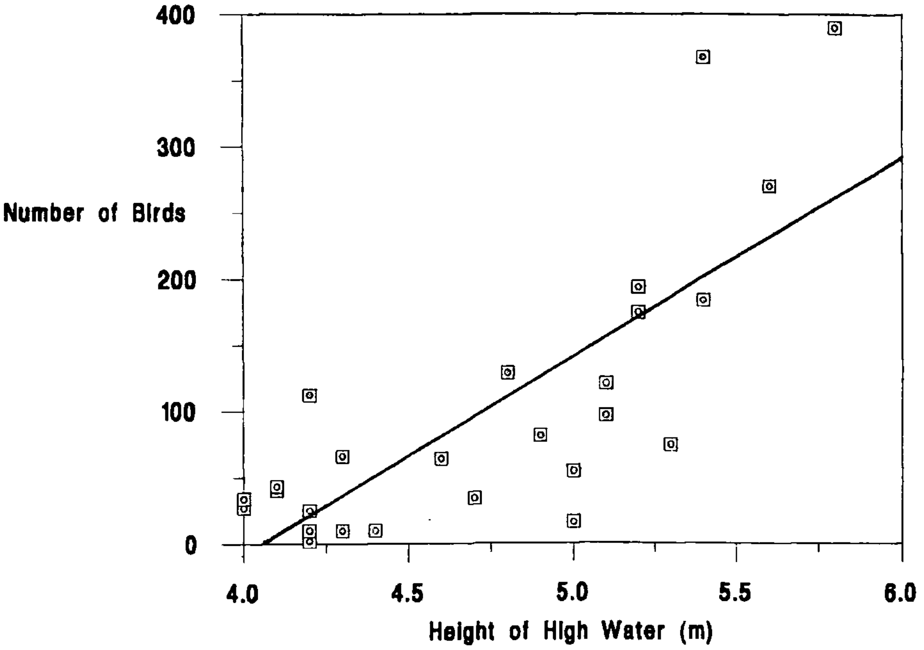


Fig. 3.5. Turnstone numbers at the West Harbour roost and their relationship with tide: 1993/94.

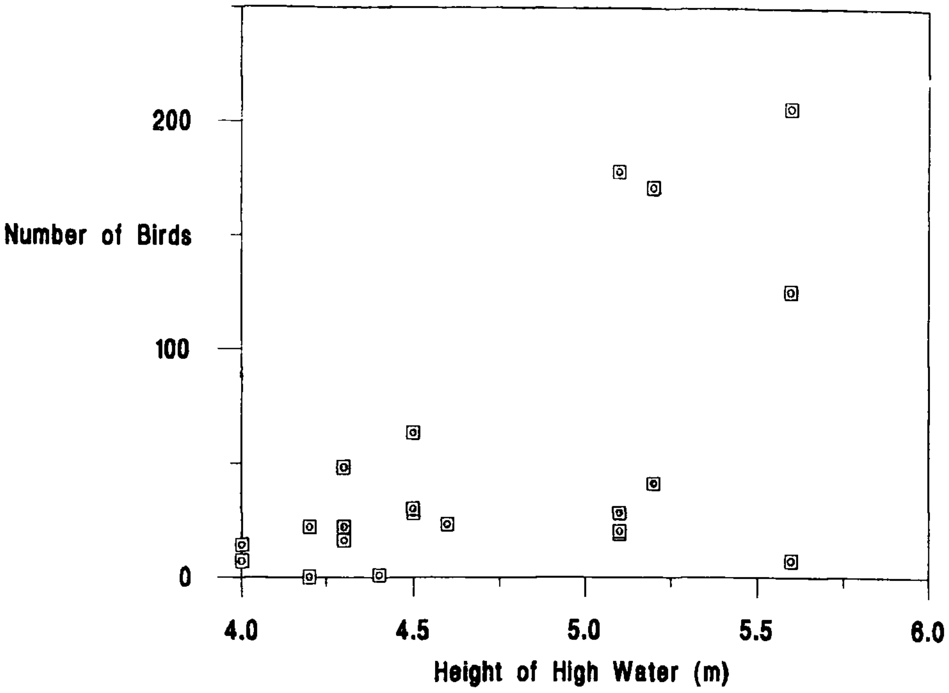


Fig. 3.6. Turnstone numbers over high water on Hartlepool Headland and their relationship with tide: 1991/92.

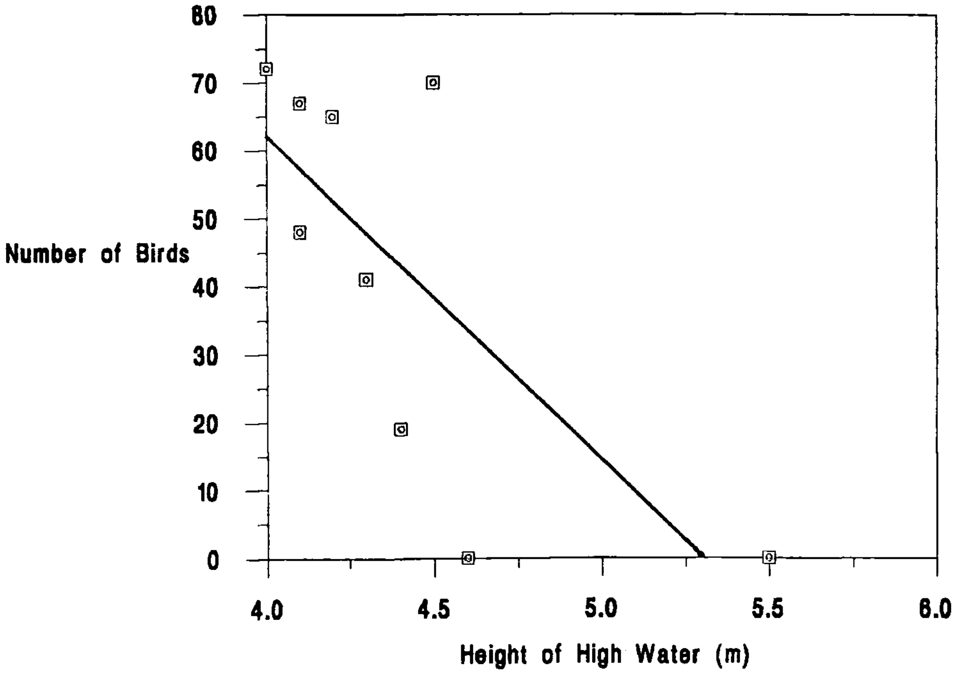


Fig. 3.7. Turnstone numbers over high water on Hartlepool Headland and their relationship with tide: 1992/93.

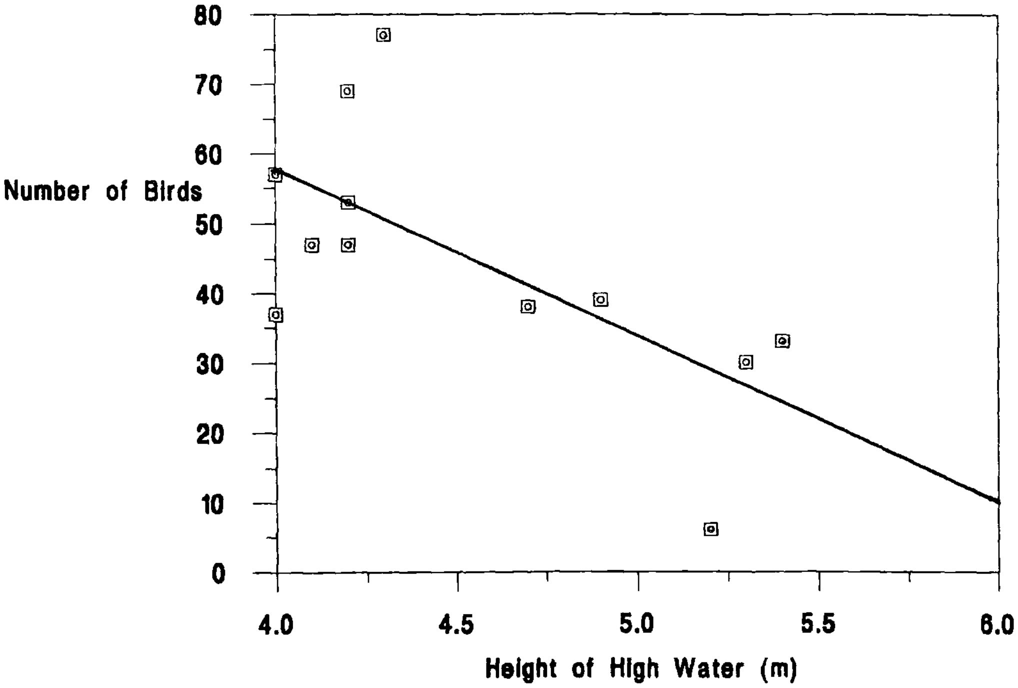
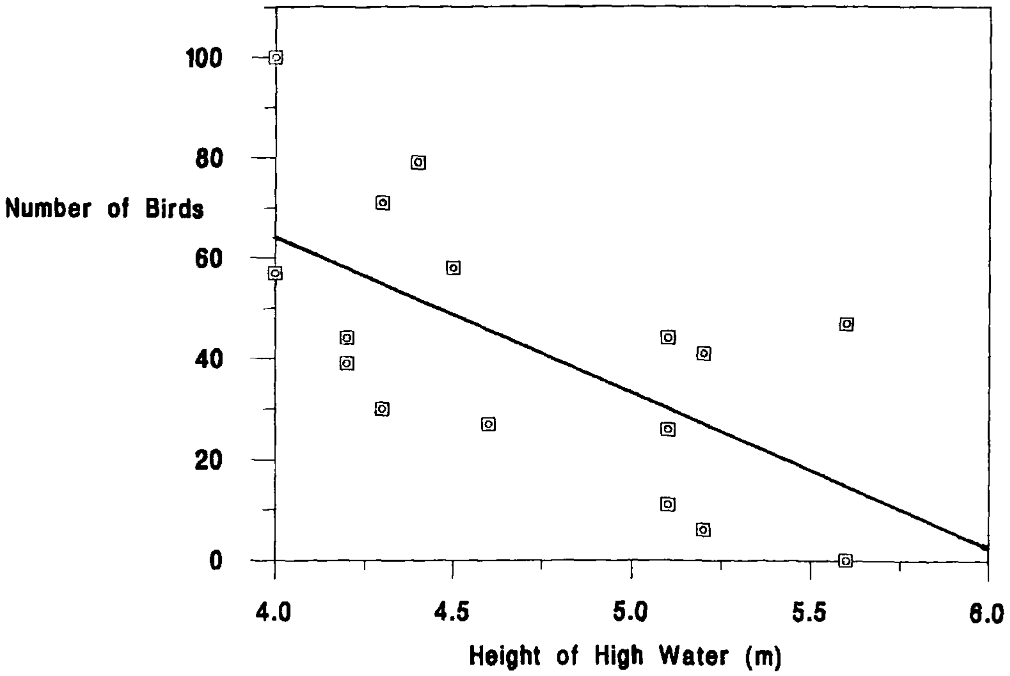


Fig. 3.8. Turnstone numbers over high water on Hartlepool Headland and their relationship with tide: 1993/94.



1992/93: No. of Turnstone = -608.5 + 149.8 HW (m)

$r^2 = 0.601$; t (tide) = 6.017, d.f. = 24, $P < 0.001$; t (wind) = -1.536, n.s.

1993/94: No. of Turnstone = -168.9 + 64.8 HW (m) - 21.0 W (Beaufort)

$r^2 = 0.653$; t (tide) = 4.001, d.f. = 18, $P < 0.001$; t (wind) = -4.071, $P < 0.001$.

Conversely the numbers of Turnstones recorded at high water on Hartlepool Headland were negatively correlated with the height of high water (Figs. 3.6 - 3.8). The only stretch of shore left exposed for waders on spring high tides was Inscar beach; Turnstones were also found feeding on Town Moor. On neap high tides, a number of rock outcrops between Throston and the Headland Breakwater were also exposed and wader numbers on the Headland were consequently higher. (The height of high water and wind speed were not correlated in either 1992/93: $r = 0.325$, d.f. = 10, n.s or 1993/94 $r = 0.050$, d.f. = 14, n.s. In 1991/92 however, there was a correlation between the height of high water and wind speed: $r = 0.811$, d.f. = 7, $P < 0.01$ and because of this no analysis was made on the effects of wind speed on high water Turnstone numbers on the Headland in this winter).

1991/92: No. of Turnstone = 250.2 - 47.1 HW (m)

$r^2 = 0.528$; t (tide) = -2.796, d.f. = 7, $P < 0.05$ (one-tailed).

1992/93: No. of Turnstone = 151.8 - 23.6 HW (m)

$r^2 = 0.448$; t (tide) = -2.849, d.f. = 10, $P < 0.01$ (one-tailed); t (wind) = 0.185, n.s.

1993/94: No. of Turnstone = 188.0 - 30.9 HW (m)

$r^2 = 0.403$; t (tide) = -3.073, d.f. = 14, $P < 0.01$ (one-tailed); t (wind) = -0.120, n.s.

3.3.1.2.2. Purple Sandpiper.

Purple Sandpiper numbers at West Harbour were also positively correlated with the tide height in each of the three winters, whilst negatively correlated with wind speed in two (Fig. 3.9 -3.11). (The height of high water and wind speed were not correlated in any of the three winters: 1991/92 $r = 0.228$, d.f. = 20, n.s.; 1992/93 $r = 0.195$, d.f. = 22, n.s.; 1993/94 $r = -0.084$, d.f. = 16, n.s.).

1991/92: No. of Purple Sandpiper = -416.1 + 115.7 HW (m)
$r^2 = 0.451$; t (tide) = 4.051, d.f. = 20, $P < 0.001$; t (wind) = -0.684, n.s.

1992/93: No. of Purple Sandpiper = -380.0 + 112.8 HW (m) - 18.7 W (Beaufort)
$r^2 = 0.608$; t (tide) = 5.432, d.f. = 21, $P < 0.001$; t (wind) = -2.794, $P < 0.05$.

1993/94: No. of Purple Sandpiper = -354.7 + 109.3 HW (m) - 16.9 W (Beaufort)
$r^2 = 0.705$; t (tide) = 5.246, d.f. = 15, $P < 0.001$; t (wind) = -2.435, $P < 0.05$.

Similarly, Purple Sandpiper numbers recorded at high water on Hartlepool Headland were negatively correlated with the height of high water (Figs. 3.12 - 3.14). Wind speed was negatively correlated with the numbers of Purple Sandpipers recorded over high water on the Headland in the winter of 1992/93. (The height of high water and wind speed were not correlated in either 1992/93: $r = 0.331$, d.f. = 8, n.s or 1993/94 $r = 0.007$, d.f. = 13, n.s. In 1991/92 however, there was a correlation between the height of high water and wind speed: $r = 0.762$, d.f. = 8, $P = 0.01$ and because of this no analysis was made on the effects of wind speed on high water Purple Sandpiper numbers on the Headland in this winter).

1991/92: No. of Purple Sandpiper = 270.7 - 49.8 HW (m)
$r^2 = 0.401$; t (tide) = -2.316, d.f. = 8, $P < 0.05$ (one-tailed).

1992/93: No. of Purple Sandpiper = 568.7 - 97.0 HW (m) - 10.7 W (Beaufort)
$r^2 = 0.902$; t (tide) = -6.365, d.f. = 7, $P < 0.001$ (one-tailed); t (wind) = -2.537, $P < 0.05$.

1993/94: No. of Purple Sandpiper = 266.9 - 50.4 HW (m)
$r^2 = 0.516$; t (tide) = -3.725, d.f. = 13, $P < 0.01$ (one-tailed); t (wind) = 0.455, n.s.

Fig. 3.9. Purple Sandpiper numbers at the West Harbour roost and their relationship with tide: 1991/92.

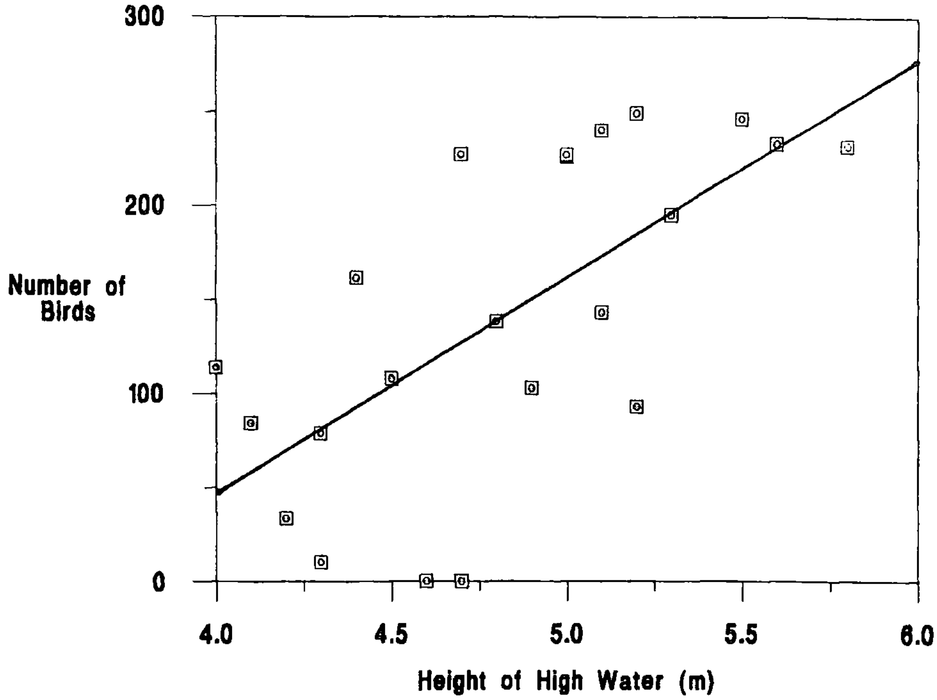


Fig 3.10. Purple Sandpiper numbers at the West Harbour roost and their relationship with tide: 1992/93.

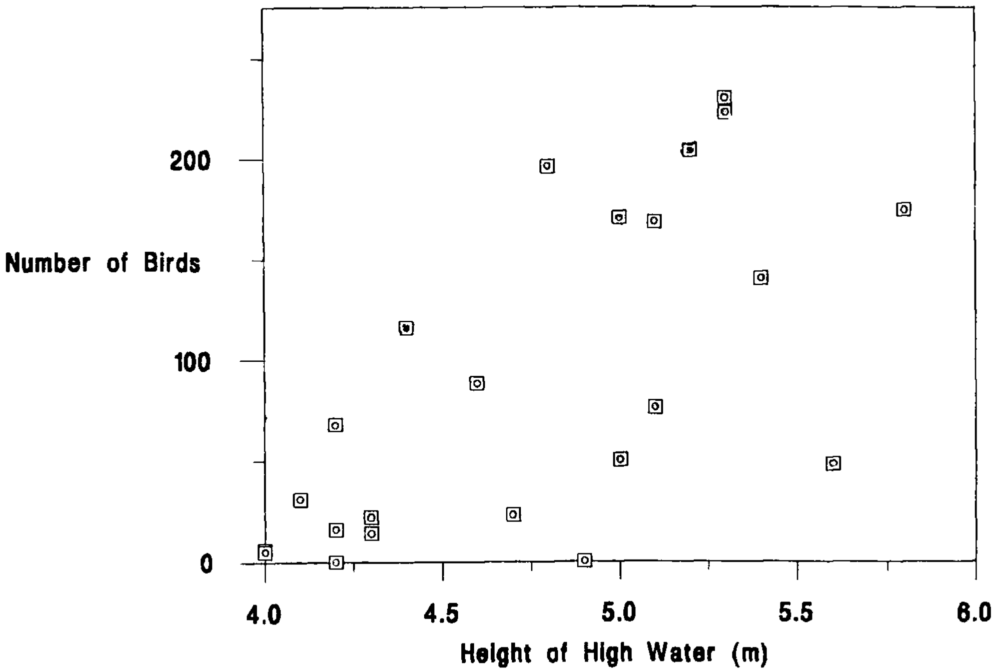


Fig. 3.11. Purple Sandpiper numbers at the West Harbour roost and their relationship with tide: 1993/94.

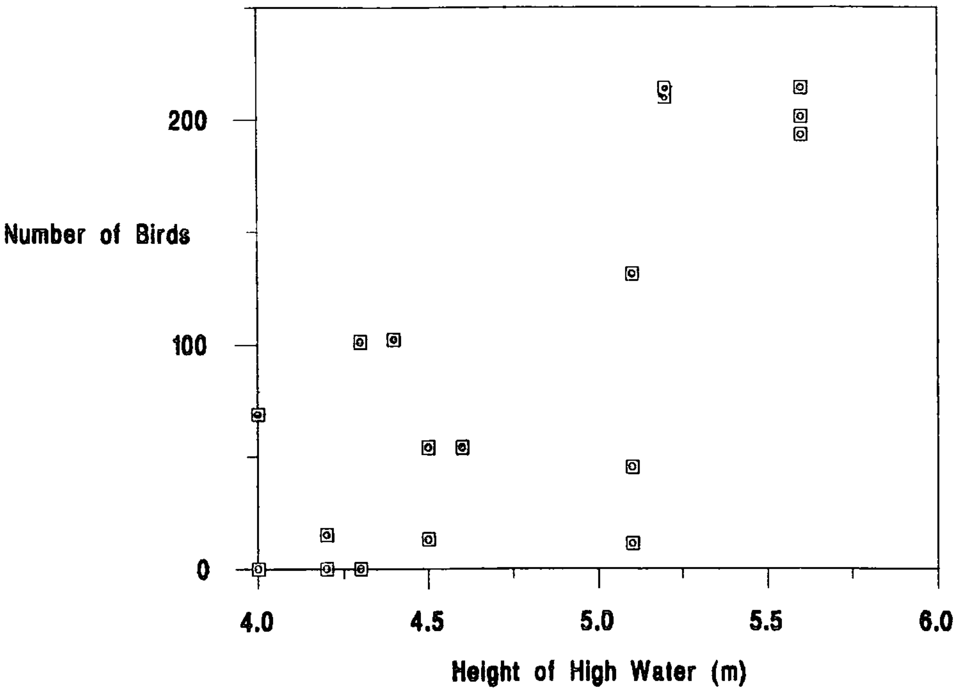


Fig. 3.12. Purple Sandpiper numbers over high water on Hartlepool Headland and their relationship with tide: 1991/92.

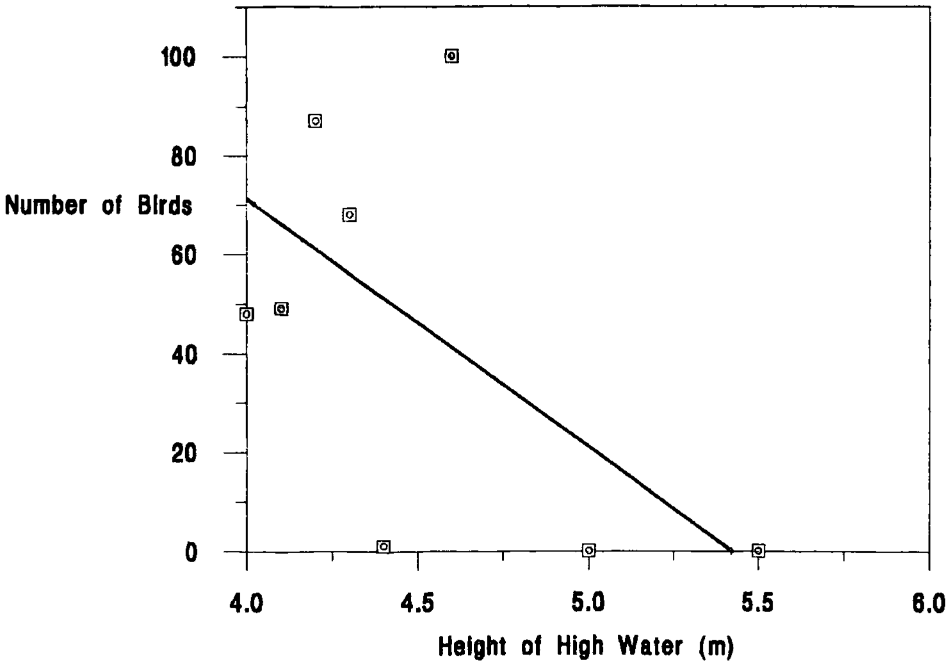


Fig. 3.13. Purple Sandpiper numbers over high water on Hartlepool Headland and their relationship with tide: 1992/93.

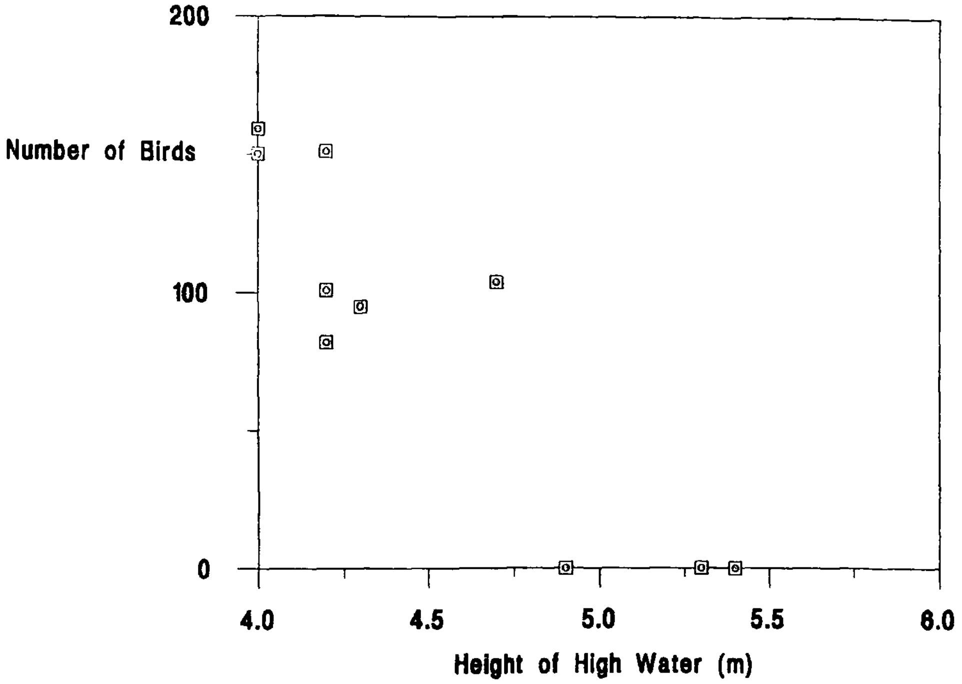
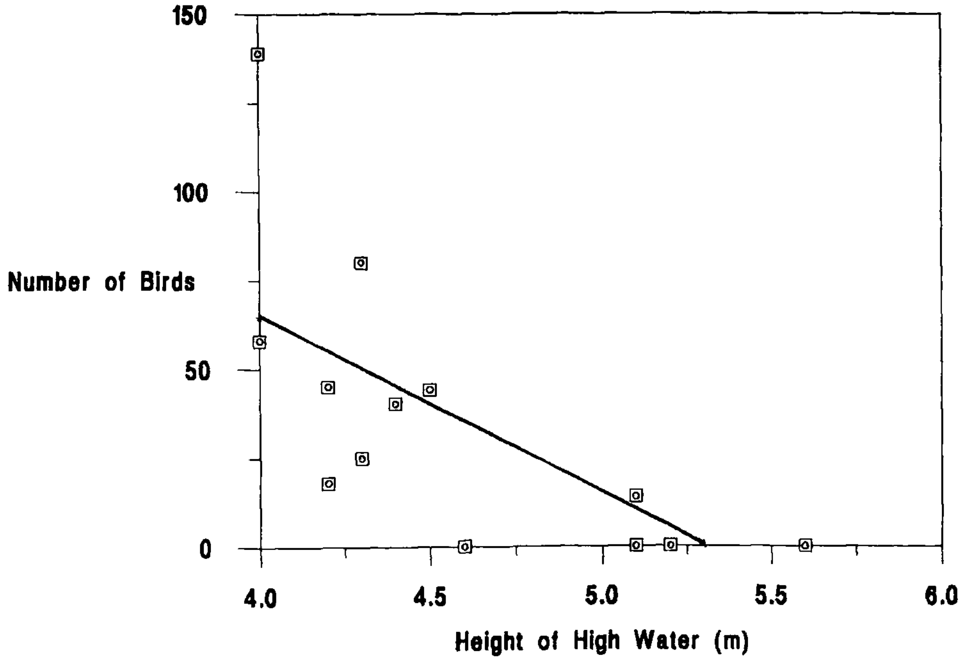


Fig. 3.14. Purple Sandpiper numbers over high water on Hartlepool Headland and their relationship with tide: 1993/94.



3.3.1.3. Long-term trends in roosting numbers.

Long-term trends in roosting numbers were investigated using yearly winter maxima counts for each species . BoEE data were used for winters prior to 1990/91. Averages of numbers counted were not used as, firstly, there was a high daily variation in the number of birds using the roost due to the tide and weather conditions (see section 3.3.1.2) and secondly, data were sparse prior to 1991.

The maximum numbers of each species observed at the West Harbour roost each winter are shown in Table 3.1. The maximum numbers of Purple Sandpipers recorded at the roost have declined fairly steadily over the eight years ($r_s = -0.857$, d.f. = 8, $P < 0.05$), the decline commencing before but continuing after the start of the harbour's redevelopment in 1991. The maximum numbers of Turnstone recorded at high water declined sharply in 1993/94, numbers showing no marked trends in earlier years.

In addition to analysing trends in winter numbers, trends in each species' relative frequency of use of the West Harbour roost were investigated. The proportion of counts at the roost when 50% or more of the peak winter number of birds was present was calculated for each species during each winter (December to March inclusive). Table 3.2 shows that not only have the maximum numbers of Turnstones and Purple Sandpipers (and Oystercatchers) using the roost declined, but also that the frequencies with which the numbers of roosting birds exceeded 50% of these maxima were lower in 1993/94 than in 1991/92, the winter of most intense building work.

The maximum winter numbers of Purple Sandpipers recorded over high water on Hartlepool Headland (Table 3.3) have declined over the study period much more steeply than in the decline noted at West Harbour (Table 3.2); yet these birds would normally fly to West Harbour on spring tides and represent a high proportion (70% or more) of the Purple Sandpipers present in the whole area. A smaller proportion (*c*.50%) of Turnstones present

Table 3.1. Yearly winter maxima of Turnstones and Purple Sandpipers roosting at high water at West Harbour.

	1986/87	1987/88	1988/89	1989/90	1990/91	1991/92	1992/93	1993/94
Turnstone	410	440	420	410	544	400	390	206
Purple Sandpiper	296	360	330	245	277	249	230	214
Oystercatcher	225	246	230	240	396	319	116	106
Knot	3200	3400	2500	1300	4100	2174	550	862
Redshank	50	31	64	1	67	31	41	277

Table 3.2. The frequency of use of the West Harbour roost during winter.

	1991/92	1992/93	1993/94
Turnstone	0.217 (23)	0.083 (24)	0.125 (16)
Purple Sandpiper	0.522 (23)	0.360 (25)	0.375 (16)
Oystercatcher	0.522 (23)	0.333 (24)	0.188 (16)
Knot	0.043 (23)	0.080 (25)	0.063 (16)
Redshank	0.043 (23)	0.120 (25)	0.063 (16)

The index shown is the proportion of counts when 50% or more of the peak winter number of birds were present at the roost. Data are taken from December to March inclusive each winter. Figures in parentheses are numbers of counts.

Table 3.3. Yearly winter maxima of Turnstones and Purple Sandpipers present over high water on Hartlepool Headland.

	1991/92	1992/93	1993/94
Turnstone	127 (9)	77 (15)	100 (16)
Purple Sandpiper	201 (13)	159 (11)	139 (15)

Figures in parentheses are numbers of counts.

in the study area use Hartlepool Headland over high water on neap tides. Maximum numbers in winter have not shown a clear trend over the three winters.

To determine whether these local changes reflect national trends, comparison is made with national wintering shorebird indices (Underhill and Prys-Jones 1994). These indices are based largely on counts from estuaries and are therefore not available for Purple Sandpiper, a species almost entirely restricted to rocky coasts during winter. Data were available until winter 1992/93. No correlations were found between the winter maxima of birds at West Harbour and yearly national winter indices for Turnstone ($r_s = 0.126$, $n = 7$, n.s.) or for other shorebird species (Oystercatcher: $r_s = 0.214$, $n = 7$, n.s.; Knot: $r_s = -0.429$, $n = 7$, n.s.; Redshank: $r_s = -0.631$, $n = 7$, n.s.).

3.3.2. Disturbance.

3.3.2.1. Disturbance factors.

256 disturbances were recorded at the West Harbour roost in a total of 245 hours of observation. Including disturbance from unknown sources, 15 different factors were involved. The number of times these were observed in each year of study is summarised in Table 3.4.

The proportion of disturbances attributable to different factors varied between the years (combining boats and helicopters; rats, raptors, skuas and crows as 'predators'; Oystercatchers, pigeons, partridges, eiders and cormorants as 'other birds': $\chi^2 = 82.807$, d.f. $= 12$, $P < 0.001$). Disturbance from building work ceased after 1992 as the south pier and island and repairs on old piers were completed. Disturbance from boats and from unknown factors increased in proportion over the three years. A number of different types of boats caused disturbance: small and medium sized fishing boats, small yachts, canoes, outboards, speedboats and water-skiers and jet skis. Yachts, outboards, speedboats and jet skis were noted to cause disturbance only in the latter two years.

Table 3.4. Frequencies of disturbance factors at the West Harbour roost.

Factor	July 1991 to June 1992	July 1992 to June 1993	July 1993 to June 1994	Total (%)
Building Work	34	9	0	43 (16.8)
Man	6	10	8	24 (9.4)
Boats	4	15	14	33 (12.9)
Helicopters	1	0	1	2 (0.8)
Gulls	32	54	10	96 (37.5)
Rats [a]	0	2	3	5 (2.0)
Raptors	2	3	0	5 (2.0)
Arctic Skuas [b]	0	0	1	1 (0.4)
Crows [c]	0	1	0	1 (0.4)
Oystercatchers	8	5	1	14 (5.5)
Pigeons [d]	1	0	0	1 (0.4)
Partridges [e]	0	1	0	1 (0.4)
Eiders [f]	0	0	1	1 (0.4)
Cormorants [g]	0	0	1	1 (0.4)
Unknown	0	17	11	28 (10.9)
Total	88	117	51	256

[a] - Common Rat *Rattus norvegicus;* [b] - *Stercorarius parasiticus;* [c] - Carrion Crow *Corvus corone;* [d] - Feral Pigeon *Columba livia;* [e] - Common Partridge *Perdix perdix;* [f] - *Somateria mollissima;* [g] - *Phalacrocorax carbo.*

Gulls were the most important disturbance factor in 1992/93 (causing 46.2% of disturbances), but were much less important the following year (causing only 19.6% of disturbances). Typically disturbance was caused when gulls walked too close to roosting waders, flew close by or when they landed at the roost, rather than by actual attacks. Similarly disturbance from Oystercatchers and other large non-predatory bird species was normally caused when they landed at the roost site. The disturbance from pigeons and partridges however occurred as the birds flew low over the roost island, surprising the roosting waders in a similar manner to an attacking raptor.

Of the five disturbances caused by raptors, two were caused by Merlins *Falco columbarius*, one by a Kestrel *Falco tinnunculus*, one by a Sparrowhawk *Accipiter nisus* and one by an unidentified species. The disturbances from the Merlins and the unidentified species were associated with attacks on the waders at the roost, (at least one of which was unsuccessful). The disturbances from the Sparrowhawk and the Kestrel were merely due to their presence as they flew past the roost. Disturbance from the Arctic Skua occurred as the skua chased an individual Turnstone past roosting birds, whilst that from the Carrion Crow was again due merely to the bird's presence at the roost. Rats caused disturbance when present on the roost island, but were not seen to attack the roosting waders.

There was no significant difference in the factors that were seen to disturb Turnstones and Purple Sandpipers at the West Harbour roost (Table 3.5; combining boats and helicopters; rats, raptors, skuas and crows; Oystercatchers, pigeons, partridges, eiders and cormorants: $\chi^2 = 7.045$, d.f. = 6, n.s.).

Of the 256 disturbances recorded at West Harbour, 16 (6.25%) resulted in one or more waders departing from the roost. Table 3.6 shows the number and percentage of these disturbances attributable to each disturbance factor and the proportion of all disturbances attributable to each factor that resulted in departures from the roost. There was a high probability that disturbance from avian predators (*i.e.* raptors, skuas and crows), rats,

Table 3.5. Factors causing disturbance to Turnstones and Purple Sandpipers at the West Harbour roost.

Factor	Turnstone	Purple Sandpiper
Building Work	25 (14.2%)	14 (9.0%)
Man	21 (11.9%)	13 (8.4%)
Boats	25 (14.2%)	24 (15.5%)
Helicopters	1 (0.6%)	1 (0.6%)
Gulls	63 (35.8%)	55 (35.5%)
Rats	4 (2.3%)	3 (1.9%)
Raptors	4 (2.3%)	4 (2.6%)
Arctic Skuas	1 (0.6%)	0
Crows	1 (0.6%)	0
Oystercatchers	11 (6.3%)	10 (6.5%)
Pigeons	1 (0.6%)	1 (0.6%)
Partridges	1 (0.6%)	1 (0.6%)
Eiders	1 (0.6%)	1 (0.6%)
Cormorants	0	1 (0.6%)
Unknown	17 (9.7%)	27 (17.4%)
Total	176	155

Figures represent numbers of disturbances recorded; figures in parentheses are percentages of the total number of disturbances recorded for that species.

Table 3.6. Disturbance factors causing departures form the West Harbour roost.

Factor	Number of disturbances causing roost departures (%)	Proportion of disturbances resulting in roost departures (*n*)
Building Work	2 (12.5)	0.047 (43)
Man	0	0 (24)
Boats	5 (31.3)	0.152 (33)
Helicopters	1 (6.3)	0.500 (2)
Gulls	1 (6.3)	0.010 (96)
Rats	2 (12.5)	0.400 (5)
Avian Predators	2 (12.5)	0.286 (7)
Other Birds	1 (6.3)	0.056 (18)
Unknown	2 (12.5)	0.071 (28)

Table 3.7. Species variation in the proportion of disturbances that caused roost departures.

	% of disturbances resulting in roost departures (*n*)
Turnstone	4.0 (176)
Purple Sandpiper	2.6 (155)
Oystercatcher	13.7 (51)
Knot	7.7 (13)
Redshank	23.8 (21)
Dunlin	0 (16)

helicopters and boats would result in birds departing from the roost. The probability that disturbance from man or gulls would result in departures, however, was low.

Of 176 disturbances recorded to roosting Turnstones at West Harbour, 7 (4.0%) resulted in one or more Turnstone leaving the roost. Four (2.6%) of 155 disturbances to roosting Purple Sandpipers resulted in one or more birds departing. Oystercatchers and Redshanks left the roost relatively more often on account of disturbance (Table 3.7). The number of disturbances causing roost departures was too low to allow for analysis of these figures.

3.3.2.2. Disturbance rates.

An overall rate of 1.05 disturbances per hour was recorded at the West Harbour roost (256 disturbances in 245 hours). During individual periods of observation (minimum period one hour) the rate varied between 0 and 8.40 disturbances per hour (14 disturbances in 1 hour 40 minutes). Over three month periods the rate varied between 0.43 and 2.15 disturbances per hour (see Appendix 5).

Excluding disturbance from building work and thus including only that from factors occurring both before and after the harbour's redevelopment, the rate of disturbance has increased over the period of study (Fig. 3.15; $r_s = 0.517$, $n = 12$, $P < 0.05$ one-tailed). Increased rates of disturbance have been observed from man ($r_s = 0.606$, $n = 12$, $P < 0.05$), boats ($r_s = 0.599$, $n = 12$, $P < 0.05$ one-tailed) and from unknown factors ($r_s = 0.795$, $n = 12$, $P < 0.01$). Disturbance rates from gulls ($r_s = -0.189$, $n = 12$), predators, *i.e.* raptors, rats, skuas and crows ($r_s = 0.004$, $n = 12$) and Oystercatchers and other birds ($r_s = 0.036$, $n = 12$) have not changed significantly. The disturbance rate from raptors (including skuas) was however significantly seasonal (Kruskal-Wallis $H_{c3,3,3,3} = 8.768$, $P < 0.01$); all disturbances occurring between January and March or between July and September. The rate of disturbance from gulls was positively related to the mean number of gulls present at the roost (Fig. 3.16; $r = 0.682$, $t = 2.952$, d.f. $= 10$, $P < 0.01$ one-tailed). No relationship

Fig. 3.15. Frequency of disturbance of roosting shorebirds caused by building work (x) and other factors (+) at West Harbour, Hartlepool, between July 1991 and June 1994.

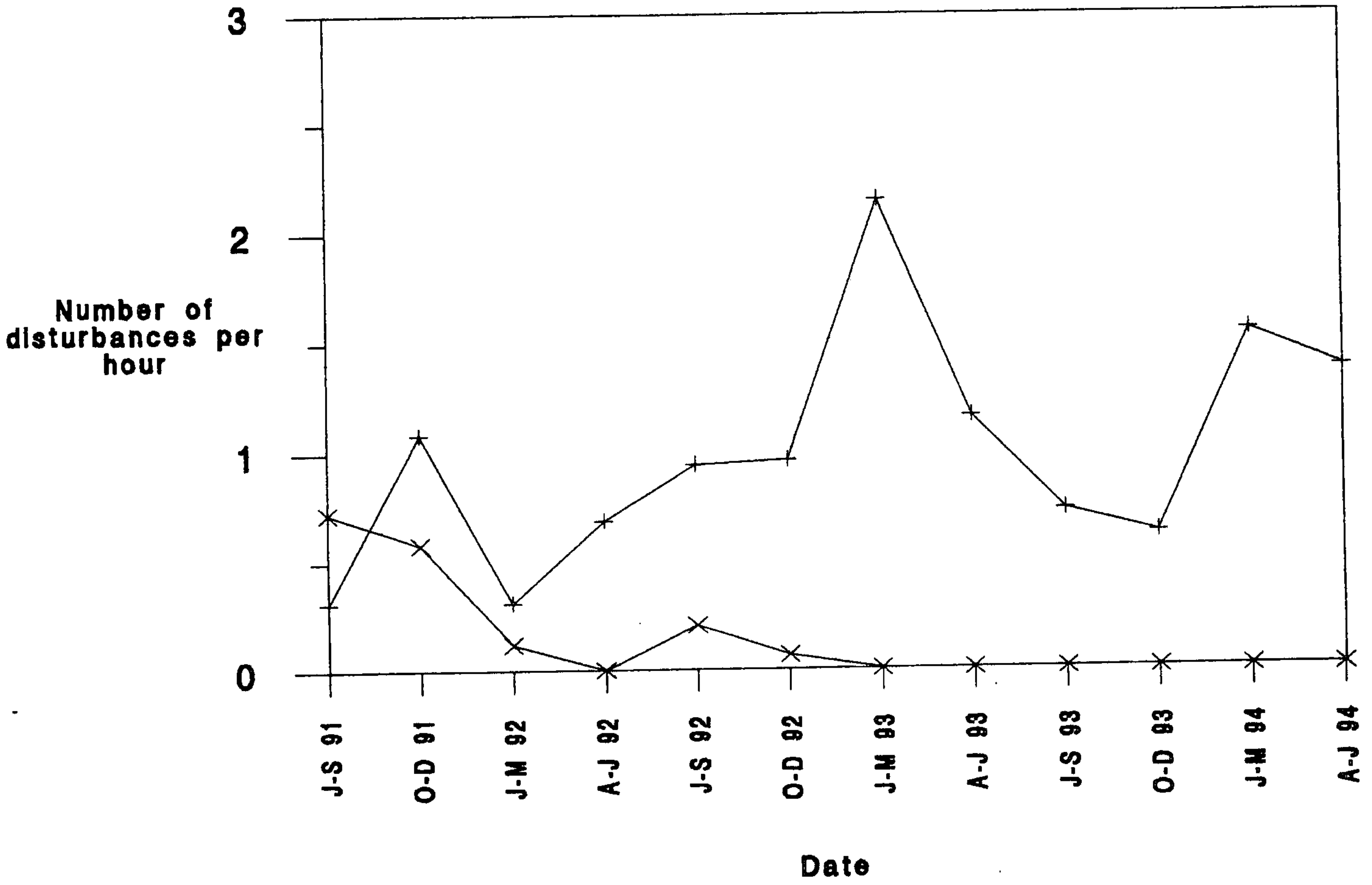


Fig. 3.16. Rates of disturbance to roosting shorebirds by gulls at West Harbour, Hartlepool; (data are three month averages from July 1991 to June 1994).

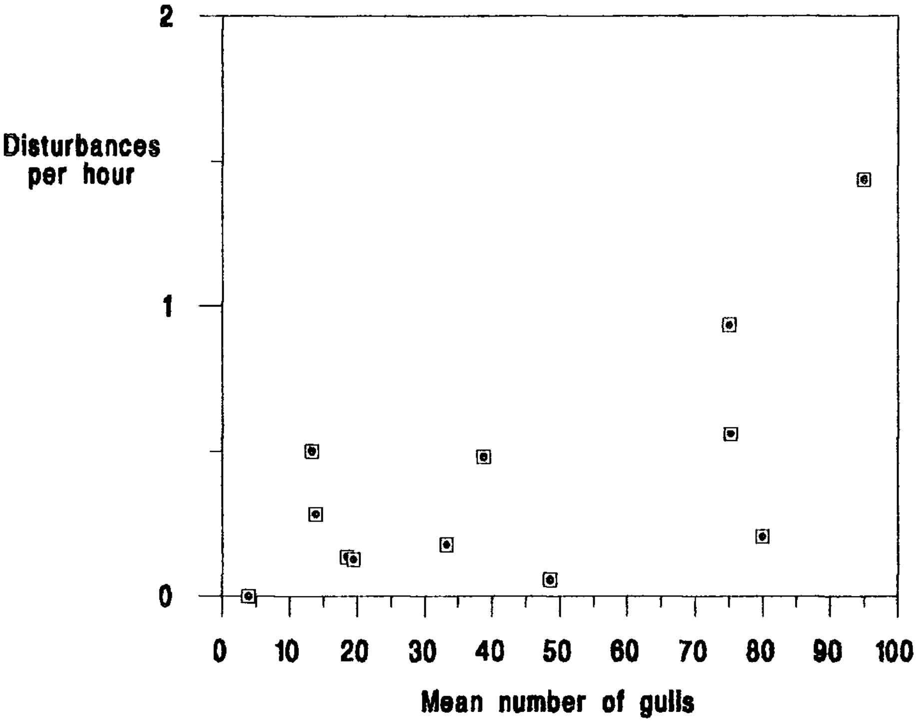
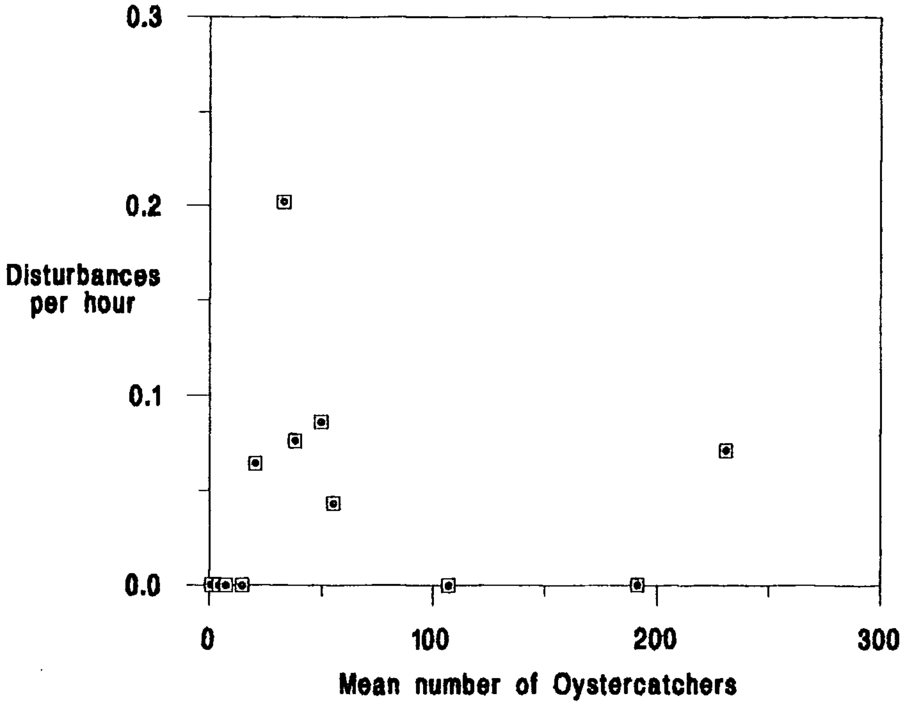


Fig. 3.17. Rates of disturbance by Oystercatchers to other roosting shorebirds at West Harbour, Hartlepool; (data are three month averages from July 1991 to June 1994).



was however found between the rate of disturbance from Oystercatchers and the mean number of Oystercatchers present at the roost (Fig. 3.17; $r = -0.001$, $t = -0.004$, d.f. = 10, n.s.). Only the disturbance rate from building work has significantly decreased ($r_S = -0.811$, $n = 12$, $P < 0.001$, one-tailed) during the three years of observation.

Disturbance to Turnstones was recorded at a rate of 0.76 disturbances per hour (176 disturbances in 232 hours 25 minutes) and to Purple Sandpipers at a rate of 0.68 disturbances per hour (155 disturbances in 229 hours 5 minutes). The rate of disturbance from factors other than building work for these species alone also increased significantly over the three year period; (for Turnstones: $r_S = 0.531$, $n = 12$, $P < 0.05$ one-tailed; for Purple Sandpipers: $r_S = 0.699$, $n = 12$, $P < 0.01$ one-tailed).

(Disturbance rates are shown in full in Appendix 5).

3.3.2.3. Susceptibility to disturbance.

The susceptibility to disturbance of each species to each factor was calculated as the sum of the percentages of a species put to flight per hour by that factor. This is an adaptation of a technique employed by Furness (1973b), taking into account the different time periods spent observing different species. Data are taken from July 1991 to June 1992. The index reflects both species' variation in response to a factor and the relative frequency of a factor's disturbance of each species. Factors that disturb more frequently thus tend to give higher susceptibility values.

Table 3.8 shows that smaller species, such as Turnstone, Purple Sandpiper and Dunlin, were more susceptible to disturbance from most factors than were larger species such as Oystercatcher and Knot. Little difference existed however between Turnstones and Oystercatchers in their susceptibility to disturbance from raptors.

Boats often passed the roost repeatedly and for Turnstones and Purple Sandpipers their effects diminished with each pass (Table 3.9).

Table 3.8. Susceptibility to disturbance factors at the West Harbour roost.

	Work	Man	Boats	Gulls	Raptors	Oystercatchers
Oystercatcher	1.60	0	0.23	0.54	0.48	-
Knot	2.99	0	-	1.52	-	0
Turnstone	4.00	2.01	1.09	5.46	0.39	0.71
Purple Sandpiper	3.94	2.31	1.34	7.54	0.98	3.07
Dunlin	3.37	2.94	-	4.97	-	0

The index shown is the sum of the percentages of a species put to flight per hour by that factor (data from July 1991 to June 1992). (Species are placed in order of decreasing body mass; Cramp and Simmons 1983).

Table 3.9. The effects of repeated passes of boats on roosting birds.

Pass No.	Number of birds put to flight						
	27 February 1994				11 April 1994		
	Turnstone	Purple Sandpiper	Other Species		Turnstone	Purple Sandpiper	Other Species
1	50	190			75	195	5 Oy[a], 7 Rk[a]
2	50	190			80	190	
3		50			4	8	
4		50	21 Rk[a]				
5	25						
6			20 Oy[a]				

Oy = Oystercatcher; Rk = Redshank; [a] = birds departed from the roost.

3.3.2.4. The effects of disturbance on numbers.

The effects of disturbance on a particular day on the numbers of Purple Sandpipers coming to the West Harbour roost on the following day were investigated during March 1993. Data collected between 15 November 1992 and 31 March 1993, (excluding the data used in this investigation), were used to derive the following equation relating bird numbers at the roost to predicted tide height and wind speed in 1992/93 and hence to calculate the numbers expected on a particular day.

Number of Purple Sandpipers = -379.5 + 109.3 Height of High Tide (m) - 16.0 Wind Speed (Beaufort).

(This equation differs from the one quoted earlier because of the exclusion of data from the period that this investigation took place).

Disturbance to Purple Sandpipers at the West Harbour roost was not found to affect their numbers there on subsequent days (Table 3.10). The difference between observed and expected numbers was correlated neither with the number of disturbances seen (in a two hour period) the previous day ($r_s = 0.088$, $n = 6$, n.s.) nor with the number of 'bird-minutes' of disturbance ($r_s = 0.486$, $n = 6$, n.s.). The only day when the observed number fell below the expected however was following a day when a Merlin attacked the roosting birds, causing 110 Purple Sandpipers present to leave, probably to Hartlepool Headland.

3.3.2.5. Disturbance on Hartlepool Headland.

Disturbance rates to waders were also recorded over high water at Inscar beach on Hartlepool Headland. 26 disturbances were observed in 12 hours and 45 minutes of observation, a rate of 2.04 disturbances per hour. 18 disturbances were attributable to man (1.41 disturbances / hour) and 8 to dogs (0.63 disturbances / hour). The susceptibility of Turnstones and Purple Sandpipers to disturbance factors at Inscar are shown in Table 3.11. Susceptibility to disturbance was much higher for both species than at West Harbour. As at

Table 3.10. The effect of disturbance to Purple Sandpipers on subsequent numbers.

Date	Height of High Water	Wind Speed (Beaufort)	Number of Purple Sandpipers			No. of Disturbances the Previous Day	Bird-minutes of Disturbance the Previous Day
			Observed (O)	Expected (E)	O - E		
20/3/93	4.6m	4	88	59.3	28.7	3	290
21/3/93	4.8m	2	196	113.1	82.9	1	26
22/3/93	5.0m	4	170	103.0	67.0	6	522
23/393	5.1m	5	142	97.9	44.1	6	552.5
24/3/93	5.1m	4	76	113.9	-37.9	4	[a]
25/3/93	5.1m	2	168	145.9	22.1	3	68

[a] - 110 of the 142 Purple Sandpipers present on the previous day departed from the roost following disturbance from a Merlin; the number of bird-minutes of disturbance is assumed to be greater than on all other days.

Table 3.11. Susceptibility to disturbance factors at Inscar.

	Man	Dogs
Turnstone	54.63	24.54
Purple Sandpiper	85.18	23.77

West Harbour however, Purple Sandpipers had a higher susceptibility to disturbance from man than Turnstones; both species showed a similar susceptibility to disturbance from dogs.

3.3.3. Choice of position at the roost site.

Both Turnstones and Purple Sandpipers increasingly sought sheltered positions on the roost island as wind speed increased (Figs. 3.18 - 3.21). For Turnstones, there was a significant correlation between the shelter index and wind speed on cloudy days ($r_s = 0.339$, $n = 42$, $P < 0.05$ one-tailed), though not on sunny days ($r_s = 0.198$, $n = 48$, n.s.). For Purple Sandpipers, the correlation was more significant on cloudy days ($r_s = 0.411$, $n = 53$, $P < 0.01$ one-tailed), than on sunny days ($r_s = 0.245$, $n = 53$, $P < 0.05$ one-tailed).

Wind speeds were recorded around the island on 9 March 1992, with a force 4 'moderate breeze' blowing from the SSW; (readings are shown in Appendix 6). The highest speeds occurred on the SSW face of the island, the lowest on the NNE face. Wind speeds at the bottom of faces were on average 53.6% ($n = 10$) of those at the top.

An 'environmental shelter' index was calculated by the following formula:

$$\text{Environmental Shelter (ES)} = 100 - (100 \ W_i / W_{ref})$$

where W_i = wind speed at point i and W_{ref} = wind speed at a reference point (Whitlock 1979). The reference point used was the middle point of the side facing directly into the wind.

Roosting at the bottom of the NNE face on the day that measurements were taken would have given a maximum environmental shelter value of 94.8%. At a force 4 wind speed, on days with cloud, the median shelter index of both Turnstones and Purple Sandpipers was +3, whilst on sunny days it was +2 for both species (see Figs. 3.18 - 3.21). A shelter index of +3 in a force 4 wind from the SSW would give an mean environmental shelter value of 83.1% ($n = 6$), and an index of +2, a mean value of 54.4% ($n = 3$). Roosting

Fig. 3.18. Shelter indices of Turnstones on cloudy days and their relationship to wind speed.

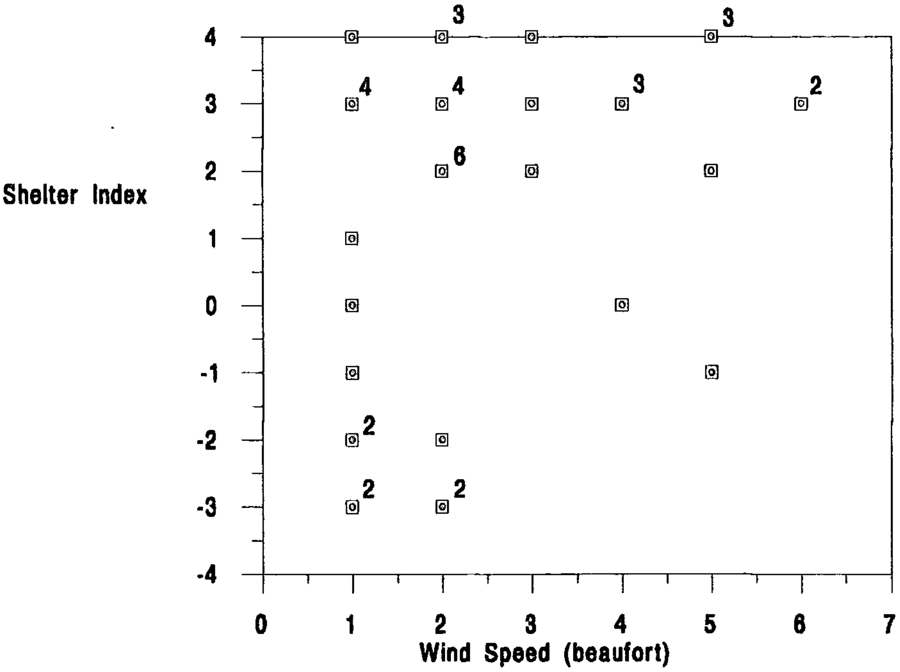


Fig. 3.19. Shelter indices of Turnstones on sunny days and their relationship to wind speed.

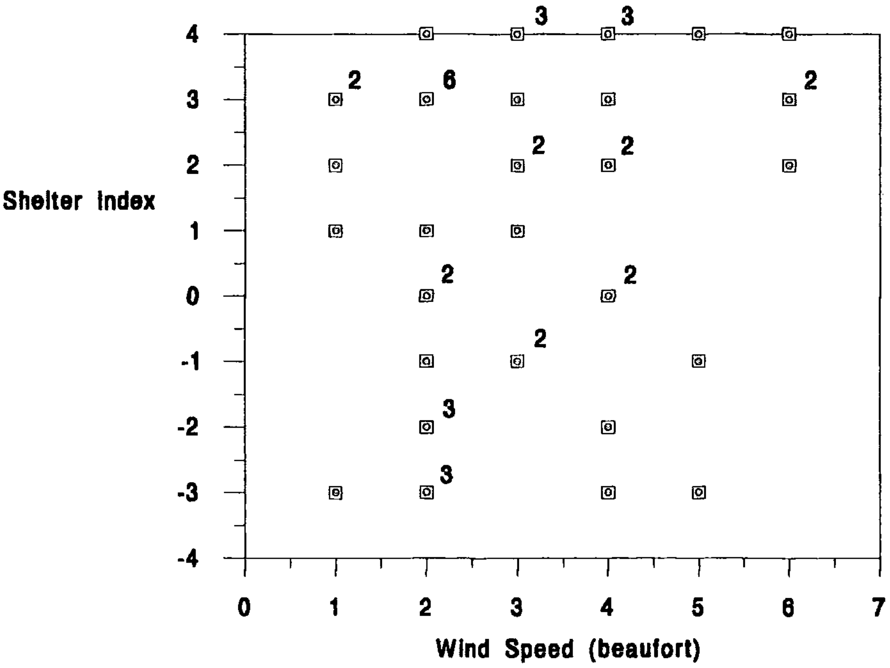


Fig. 3.20. Shelter indices of Purple Sandpipers on cloudy days and their relationship to wind speed.

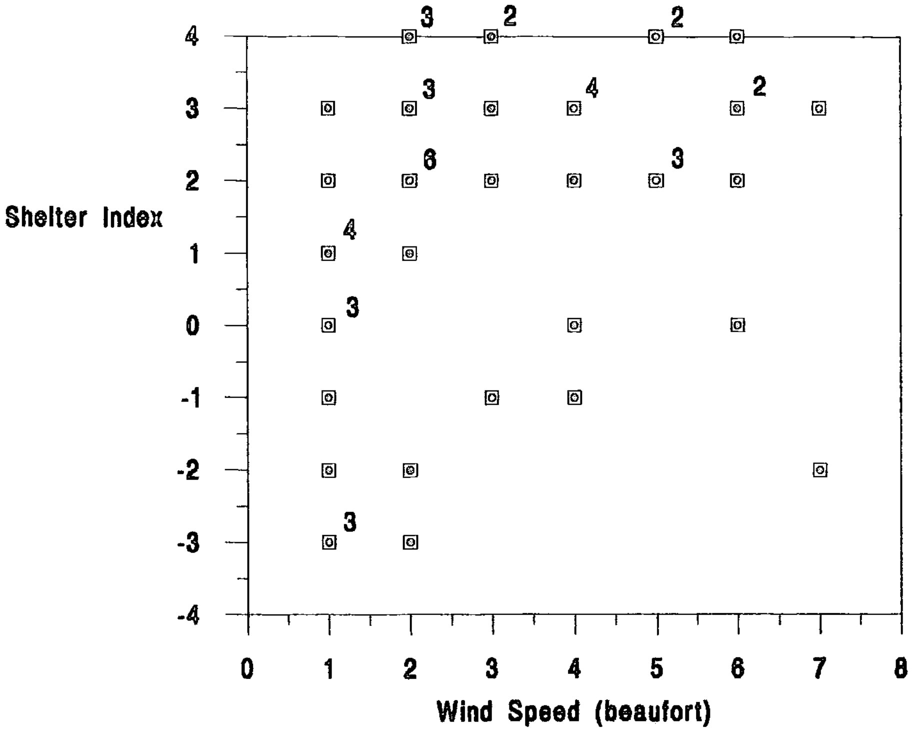
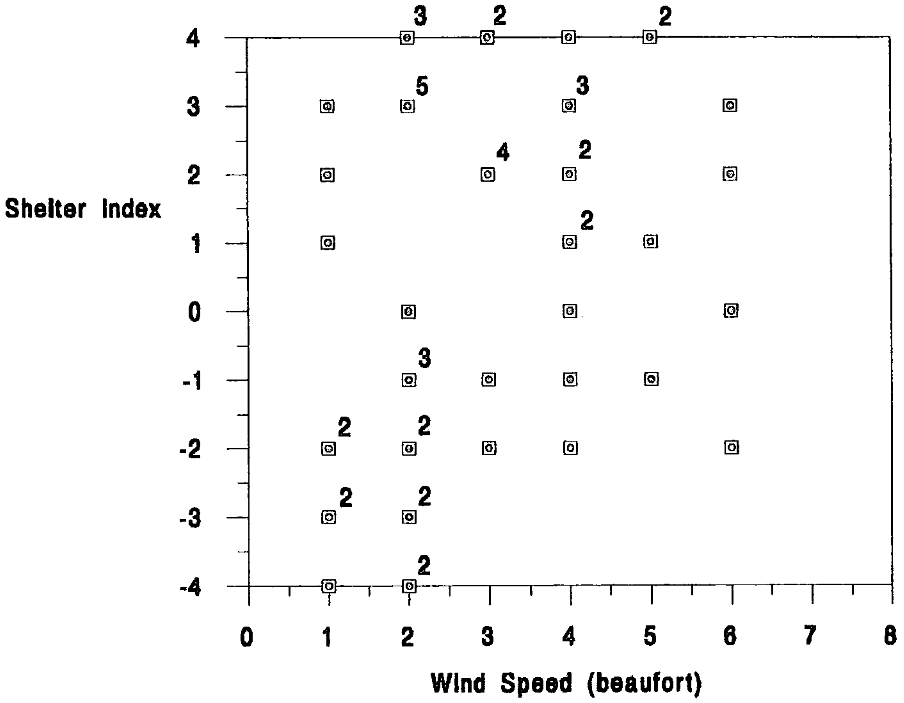


Fig. 3.21. Shelter indices of Purple Sandpipers on sunny days and their relationship to wind speed.



on the top of the island gave a mean environmental shelter value of 63.4% ($n = 2$). The use of the island for shelter, as displayed by Turnstones and Purple Sandpipers, may thus reduce the rate of heat loss considerably.

The relative importance of the island as a roosting site within West Harbour was gauged by comparing the mean proportion of birds that used each of the roosting sites within the harbour, *i.e.* the island, piers, beaches and the open ground adjacent to the harbour (see Fig. 1.3). Data are taken from the island's completion in November 1991 until May 1994.

The roost island was the preferred site for all species, though Turnstones (and Knots) often used other sites (Table 3.12). Piers were used most often by Turnstones and Purple Sandpipers, beaches by Turnstones and Redshanks and open ground by Turnstones and Knots. The mean proportion of Turnstones that used the island has declined since its completion ($r_s = -0.392$, $n = 127$, $P < 0.001$). Purple Sandpipers showed no such changes in behaviour ($r_s = -0.052$, $n = 122$, n.s.).

The way in which each species used the island was determined by the mean proportions of birds of that species that roosted on its top or sides. All species used the sides of the island much more than the top (Table 3.13), (though Knot relatively infrequently).

A distinction was also made as to whether the majority of each species was roosting on the exposed top of the piers or island or on their sides, where visibility was more limited. Data were not included from days when the majority of birds used the beaches or open ground, areas which offered particularly varied shelter. Turnstones roosting at West Harbour used the top surfaces of structures significantly less in winter, when temperatures were low, than at other times of year ($\chi^2 = 14.387$, d.f. = 2, $P < 0.001$; Table 3.14). Purple Sandpipers only used the tops of structures in spring, when temperatures were higher. In addition to this, the mean proportion of Purple Sandpipers roosting at the harbour that used the beams on the side of the inner pier was calculated. These beams were attached, specifically

Table 3.12. Relative use of the island and other sites by waders roosting at West Harbour, Hartlepool.

Species	Island	Piers	Beaches	Open ground	*n*
Turnstone	0.565	0.180	0.142	0.112	127
Purple Sandpiper	0.792	0.115	0.092	0.001	122
Oystercatcher	0.943	0.057	0	0	67
Knot	0.646	0.044	0.083	0.227	22
Redshank	0.755	0	0.237	0.008	27

Figures represent the mean proportion of the total number of birds of each species roosting at high water at each site within West Harbour. A minimum of 10 birds of a species was required for data to be included; *n* = the number of days of observation.

Table 3.13. Relative use by roosting waders of the top and sides of the West Harbour roost island.

Species	Top	Sides	*n*
Turnstone	0.092	0.908	83
Purple Sandpiper	0.005	0.995	100
Oystercatcher	0.062	0.938	64
Knot	0.231	0.769	16
Redshank	0	1.0	18

Figures represent the mean proportion of birds of each species roosting at high water on the island in each position. Data are taken from the island's completion in November 1991 until May 1994; *n* = the number of days of observation. A minimum of 10 birds of a species were required to be on the island for data to be included.

Table 3.14. The position of Turnstones and Purple Sandpipers on structures at the West Harbour roost.

'Season'	Turnstone			Purple Sandpiper	
	Top	Side		Top	Side
21/6 - 22/9	15	10		0	21
23/9 - 19/3	4	27		0	47
20/3 - 20/6	7	7		5	13

Figures represent the number of days that the majority of birds of that species present in the harbour roosted in each position. Data are taken from July 1992 until May 1994. The year is divided into 'seasons' according to daylength.

for use by Purple Sandpipers in August 1992. A mean of only 1.1% of Purple Sandpipers roosted there, however (data from September 1992 to May 1994, $n = 80$ days).

3.3.4. Behaviour at the West Harbour roost.

3.3.4.1. Turnstone.

The behaviour of Turnstones at the West Harbour roost was recorded over a range of tides, though the proportion of birds engaged in each activity was not related to the height of high water on the day measurements were taken (see Appendix 7).

Sleeping was the main activity of Turnstones at the West Harbour roost, comprising an average of 59.0% of recorded behaviour ($n = 57$ scan samples). Preening (23.7%) was the second most common behaviour, followed by standing (8.2%), feeding (5.6%) and running (2.0%). Bathing (0.8%) and agonistic behaviour (0.7%) were recorded only infrequently. (Data are shown in Appendix 7).

Turnstone behaviour varied over the tidal cycle (Fig. 3.22), the proportion of birds sleeping increasing significantly towards high water (Kruskal-Wallis $\chi^2 = 19.653$, d.f. = 6, $P < 0.01$) and staying high afterwards. Preening and bathing were most important prior to high water ($\chi^2 = 22.184$, d.f. = 6, $P < 0.01$).

The behaviour of Turnstones also changed seasonally (Fig. 3.23), the proportion of birds standing being lowest in the autumn and early winter ($\chi^2 = 11.005$, d.f. = 4, $P < 0.05$).

Proportionally fewer Turnstones tended to be seen feeding at West Harbour at high water than at Hartlepool Headland (data from 1993/94, see Appendix 8; Wilcoxon $z = 1.732$, $P < 0.10$). The proportion of Turnstones feeding at West Harbour was less on spring tides than on neaps, as more of the intertidal feeding zone was available ($r_s = -0.759$, $n = 18$, $P < 0.001$ one-tailed); no such relationship was observed for Turnstones on the Headland ($r_s = 0.149$, $n = 20$, n.s.).

Fig. 3.22. Turnstone behaviour at the West Harbour roost in relation to time (n = number of samples).

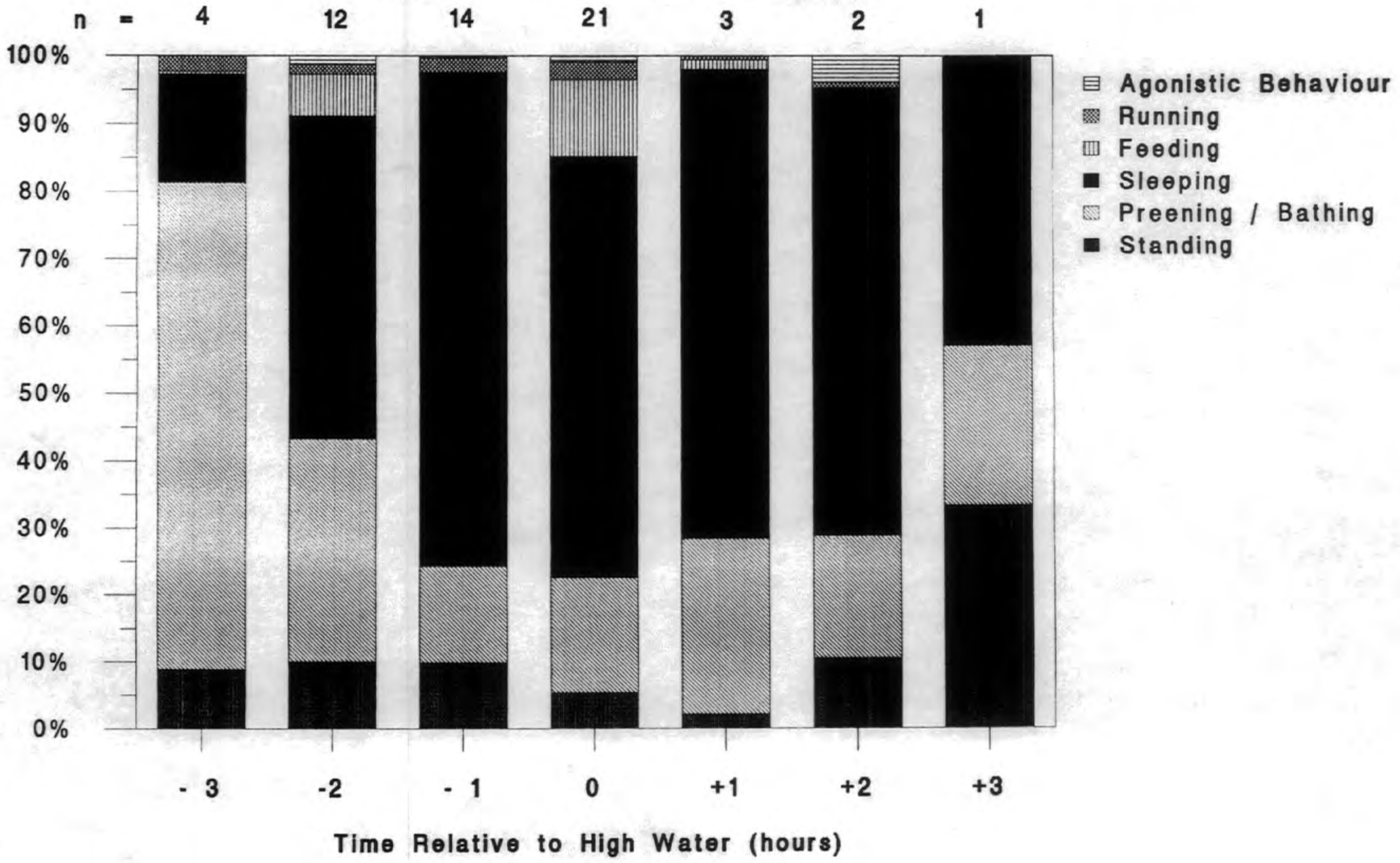
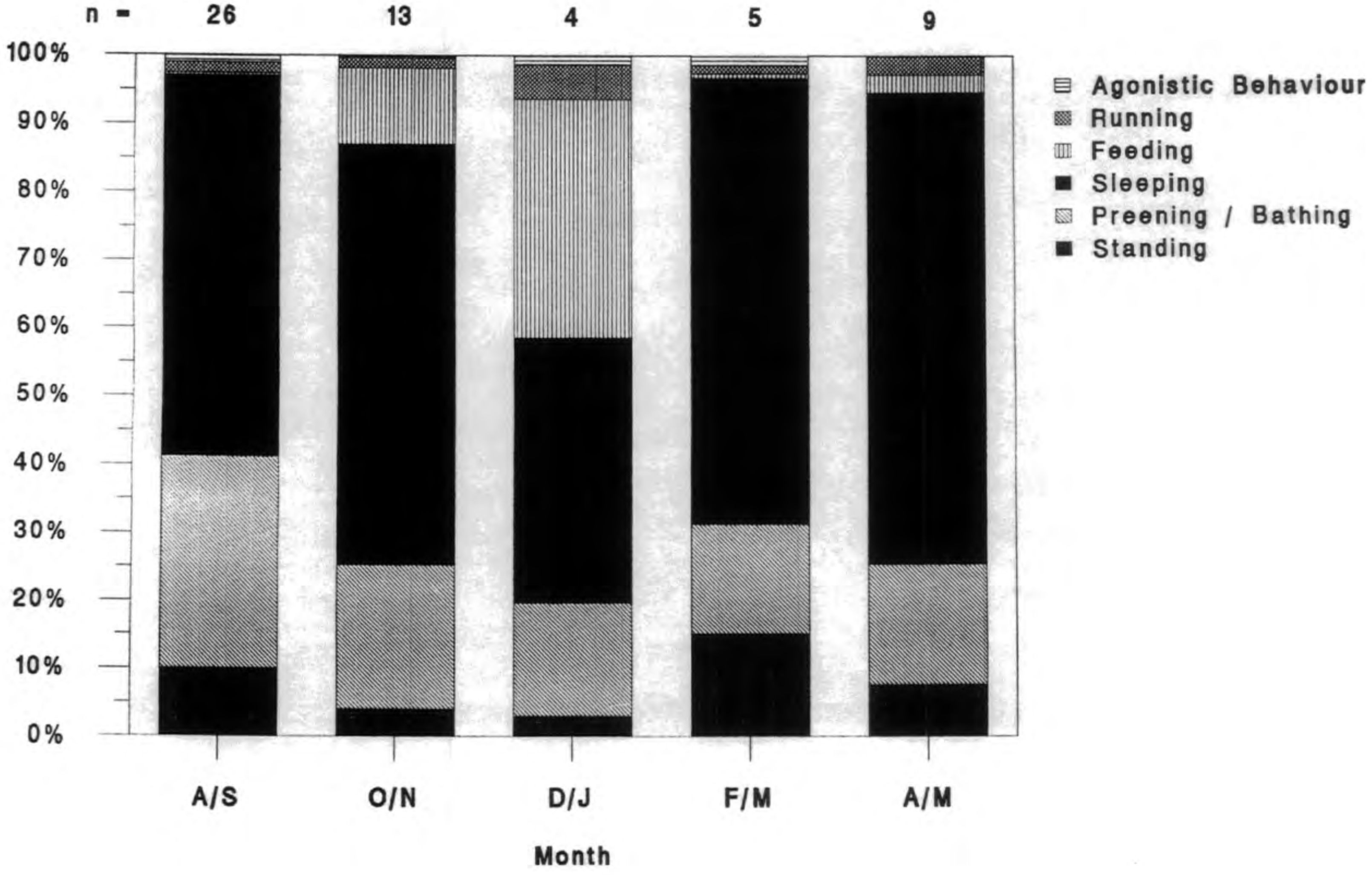


Fig. 3.23. Turnstone behaviour at the West Harbour roost in relation to season (n = number of samples).



3.3.4.2. Purple Sandpiper.

As for Turnstones, the behaviour of Purple Sandpipers at the West Harbour roost was recorded over a variety of tides. Only the proportion of birds recorded running was however found to be correlated to the height of high water ($r_s = 0.298$, $n = 46$, $P < 0.05$; see Appendix 7).

Sleeping was also the predominant activity of Purple Sandpipers at the West Harbour roost, comprising an average of 72.4% of all recorded behaviour ($n = 46$ scan samples). Standing (12.9%) was the second most important activity, followed by preening (6.7%), running (1.1%) and agonistic behaviour (1.0%). Purple Sandpipers were only infrequently recorded feeding (0.9%), whilst bathing was insignificant (Data are shown in Appendix 7). Proportionally, Purple Sandpipers slept more than Turnstones (Wilcoxon $z = 4.193$, $n = 35$ scan samples, $P < 0.001$), but preened and bathed less ($z = -4.521$, $n = 35$, $P < 0.001$) and ran less ($z = -1.981$, $n = 35$, $P < 0.05$).

The behaviour of Purple Sandpipers changed over the tidal cycle (Fig. 3.24). As with Turnstones, the proportion of birds sleeping increased towards and after high water (Kruskal-Wallis $\chi^2 = 11.007$, d.f. = 3, $P < 0.05$). Agonistic behaviour ($\chi^2 = 12.941$, d.f. = 3, $P < 0.01$) and running ($\chi^2 = 8.717$, d.f. = 3, $P < 0.05$) were most common early in the tidal cycle, when birds were still arriving at the roost.

There was also seasonal variation in the behaviour of Purple Sandpipers at the roost (Fig. 3.25). Preening was most important in late summer and autumn ($\chi^2 = 12.277$, d.f. = 4, $P < 0.05$), whilst running was significantly more important in winter and spring ($\chi^2 = 18.213$, d.f. = 4, $P < 0.01$). Agonistic behaviour was proportionally more significant in late winter ($\chi^2 = 10.031$, d.f. = 4, $P < 0.05$).

Proportionally fewer Purple Sandpipers were seen feeding at West Harbour at high water than at Hartlepool Headland (data from 1993/94, see Appendix 8; Wilcoxon $T = 0$, n

Fig. 3.24. Purple Sandpiper behaviour at the West Harbour roost in relation to time (n = number of samples).

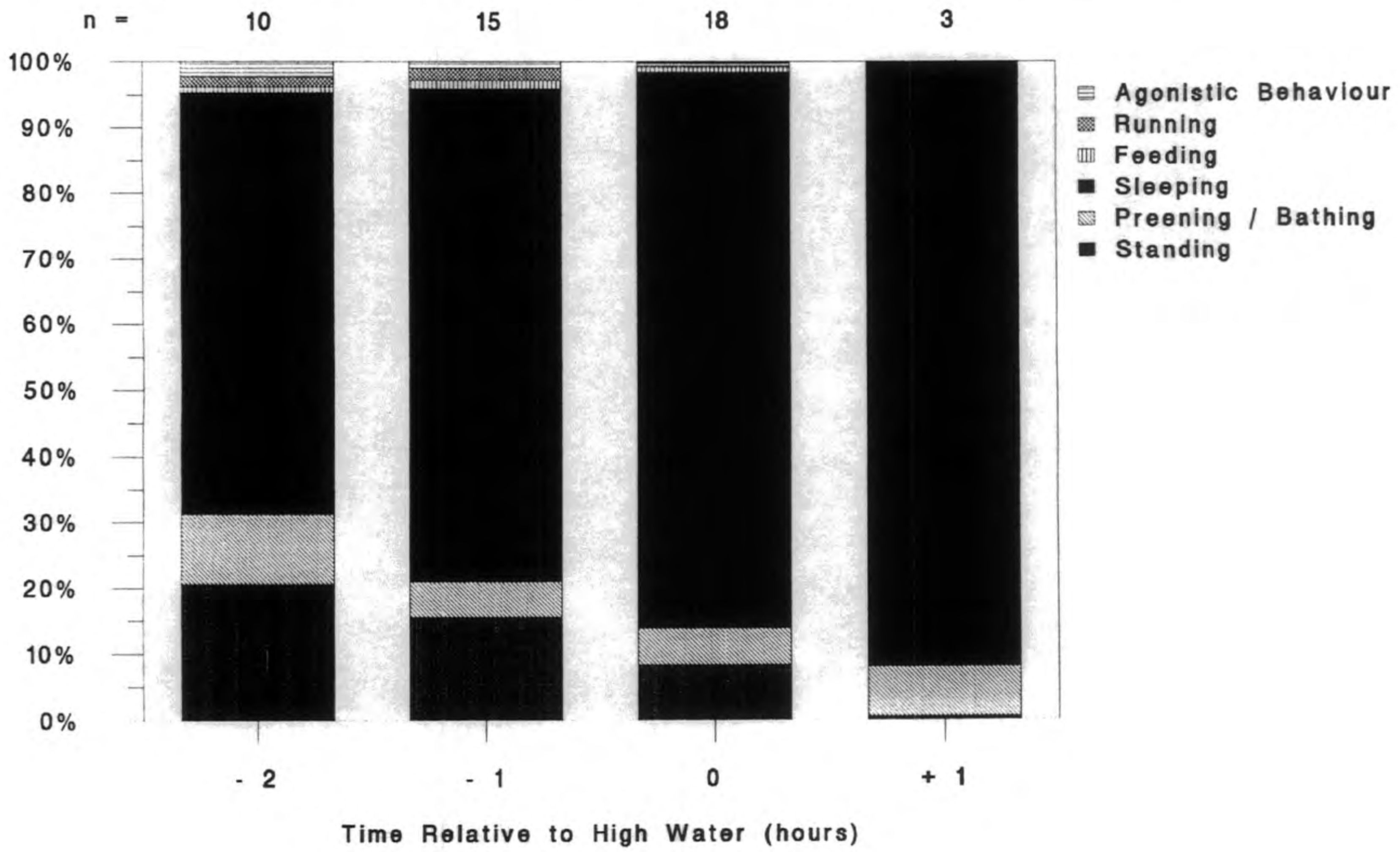
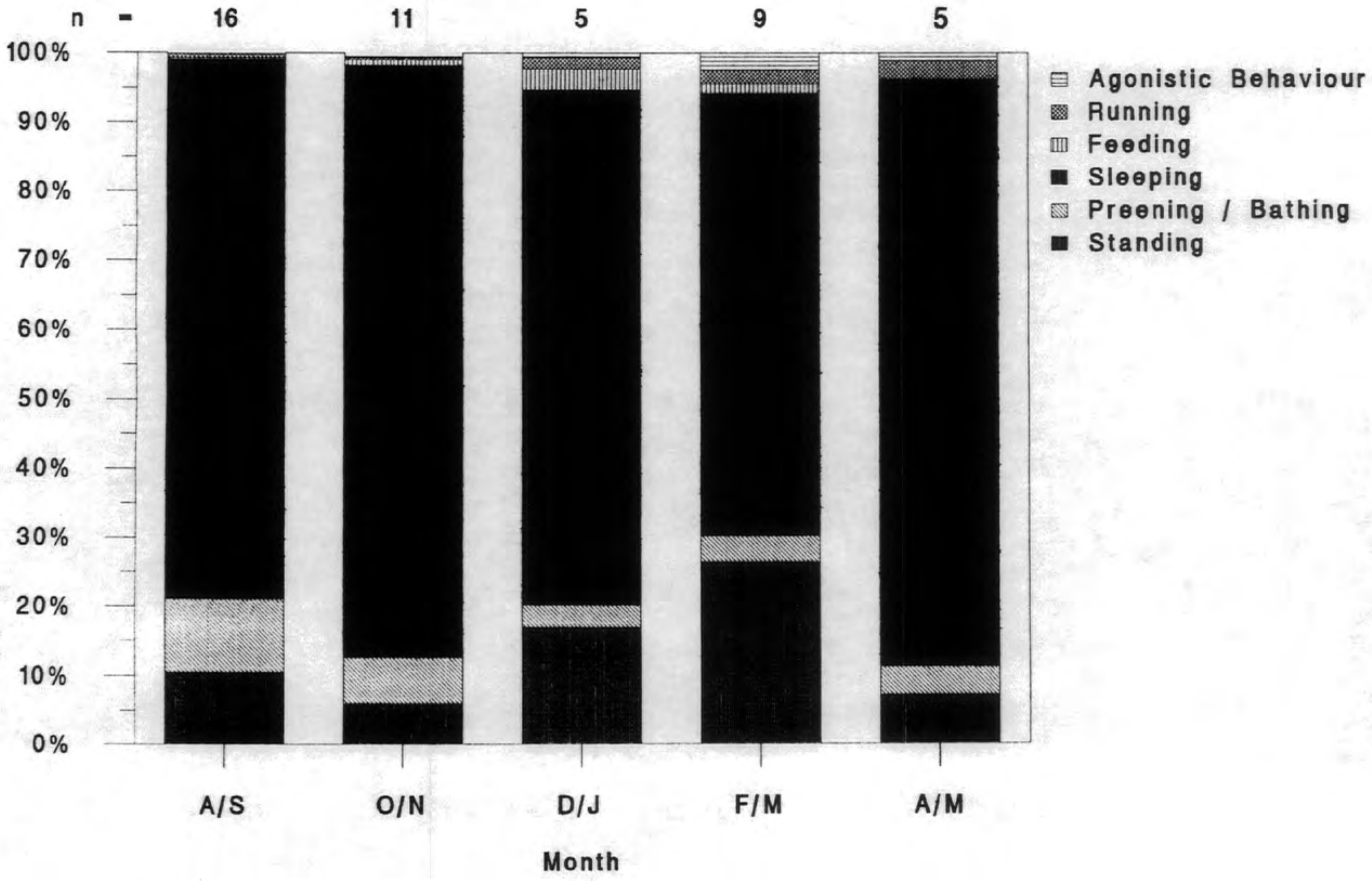


Fig. 3.25. Purple Sandpiper behaviour at the West Harbour roost in relation to season (n = number of samples).



= 8, $P < 0.05$). The proportion of Purple Sandpipers feeding at West Harbour was less on spring tides than on neaps, as more of the intertidal feeding zone was available ($r_s = -0.632$, $n = 10$, $P < 0.05$ one-tailed); no such relationship was observed for Purple Sandpipers on the Headland ($r_s = 0.003$, $n = 14$, n.s.). Proportionally fewer Purple Sandpipers fed on the Headland over high water than Turnstones (Wilcoxon $T = 3$, $n = 13$, $P < 0.01$).

3.4. Discussion.

3.4.1. Seasonal numbers and roost use in relation to tide height and wind speed.

The seasonal changes in the numbers of Turnstones and Purple Sandpipers roosting at West Harbour accurately reflect the arrival and departure of the local populations, whilst showing the importance of the area to other passage birds. The first Turnstones arrive back from their Greenland and Canadian breeding grounds in late July (Branson *et al.* 1978, Cramp and Simmons 1983), quickly adding to the numbers of over-summering one-year old birds. In September the numbers of local Turnstones are supplemented by passage birds which use the Hartlepool and Tees estuary area perhaps to refuel for their onward migration or perhaps whilst moulting. These latter birds may include Turnstones from the north European population, which pass through Britain in autumn to wintering areas on the west coast of Africa (Branson *et al.* 1978). Only local residents remain after late October and the relative stability in the maximum monthly numbers at the roost during winter is a reflection of individual Turnstones' site-fidelity at this time of year (Cramp and Simmons 1983, Metcalfe and Furness 1985, Whitfield 1985a, the present study).

Maximum winter high water counts from West Harbour of both Turnstones and Purple Sandpipers probably reflect the sizes of the local populations particularly accurately, few other high water sites being available or used on spring high tides. The Turnstone winter maxima at West Harbour are, though, perhaps slight overestimates of this population, as they probably include some birds from the south side of the Tees estuary which may use West Harbour on spring high tides. High water counts at Hartlepool were probably more accurate than is usual in surveys of rocky shores, as, (apart from at West Harbour), no offshore islets were available to roosting waders over this period (Summers *et al.* 1975, da Prato and da Prato 1979). The availability of the tidal Long Scar rocks to foraging waders over low water made counts during this period markedly less accurate. A population of approximately 400 Turnstone used the West Harbour roost each winter, colour-ringing sightings suggesting that the majority of these birds were resident between Crimdon and North Gare (Chapter 2). Fluctuations in the numbers during the winters of 1992/93 and 1993/94 may have been due to poor winter weather, high wind speeds significantly reducing numbers at the roost in two of the three years of study. The numbers at the roost in the winter of 1993/94 were however significantly lower than in previous years. No spring passage of Turnstone was evident from the numbers of birds roosting at West Harbour.

The first Purple Sandpipers return to Hartlepool from Norway in mid-July. Numbers remain low however until October, when returning Norwegian birds are supplemented by 'long-billed' birds from the probable Greenland / Canada population (Nicoll *et al.* 1988). The high increase in numbers at this time reflects the relative importance of this long-billed population at Hartlepool (see Chapter 2) - in contrast to the rest of north-east England. Numbers are generally stable from mid-November, though a few residents do not arrive until December (see Chapter 2; Metcalfe 1984a). The maximum size of the local population fell from 249 birds in 1991/92 to 214 in 1993/94, colour-ringing studies suggesting that these birds were resident between Steetley and North Gare (Chapter 2). A passage of birds through the area in spring was suggested by a colour-ring sighting, though numbers were probably small as this was not reflected in the numbers of birds using the roost.

The numbers of Turnstone and Purple Sandpiper roosting at West Harbour were highest on spring tides, when other alternative high water sites had become flooded. In contrast, Hartlepool Headland was primarily used on neap tides when a greater area of shore was available. Although disturbance rates and susceptibility to disturbance on Hartlepool Headland were extremely high, the closeness of these sites to low water feeding grounds made them preferable to Headland residents whenever tide and weather conditions allowed. Brearey (1982) similarly noted that Turnstones, on the south of the Tees estuary, preferred roosting sites which had rapid access to the first areas exposed after high tide. Stock *et al.* (1987) have also noted that Oystercatchers use a number of roosting sites close to feeding grounds on neap tides, but are forced to use more distant, larger roosts on spring tides. In addition to being close to feeding grounds, Headland sites also offered both species a greater number of foraging opportunities over high water.

High wind speeds reduced the numbers of roosting Turnstones and Purple Sandpipers at West Harbour, perhaps as birds had difficulty in flying to the site in these conditions. Handel and Gill (1992) found that numbers of Dunlin were similarly reduced by high wind speeds at a pre-migratory roost in Alaska. Wind speed had less of an effect on the numbers of birds recorded over high water on the Headland, perhaps due to the variety in orientation of the sites there. Purple Sandpipers resident on the Headland may use Steetley pipes to the north-west when conditions are coincidentally unfavourable at both West Harbour and on the Headland.

3.4.2. Disturbance and the choice of roost site.

Furness (1973a) proposed that the quality of a roost site is determined by its proximity to feeding areas and by the extent to which it protects birds from disturbance. The frequency and intensity of disturbance at a site will influence the number of birds that use it, the susceptibility to disturbance of different species varying between different factors (Furness 1973b). The overall rate of 1.05 disturbances per hour recorded at West Harbour was similar to that seen in another British study of roosting waders on the Dee estuary (Kirby *et al.* 1993), but higher than that (0.33 disturbances per hour) recorded in a study of roosting Dunlin in Alaska (Handel and Gill 1992). The rate of 2.04 disturbances per hour recorded on Inscar beach on Hartlepool Headland was notably higher however, and it is reasonable to assume that disturbance at this site has an important controlling influence on the numbers of roosting waders. Disturbance rates are probably high at other sites on Hartlepool Headland and at Seaton Sands to the south and the traditional popularity of West Harbour as a roost site must, to a large degree, stem from the relatively low levels of disturbance found there.

A high variety of disturbance factors were recorded at the West Harbour roost and different factors had a different influence on roosting waders. Gulls were predictably the most important disturbance factor at West Harbour. Large numbers of Herring Gulls *Larus argentatus* roosted there throughout the year, together with occasional Lesser Black-backed Gulls *Larus fuscus* and Great Black-backed Gulls *Larus marinus* and often large numbers of Black-headed Gulls *Larus ridibundus*. Up to 157 Kittiwakes *Rissa tridactyla* also used the roost in late summer. Gulls were never seen to attack roosting waders, (though they were seen to steal food from foraging waders - see Chapter 4), but were clearly regarded as a threat. The time spent vigilant by roosting Turnstones was positively correlated to the number of gulls in this study (Chapter 6), whilst Metcalfe (1984c) found a similar correlation for foraging Purple Sandpipers. Handel and Gill (1992) recorded one instance of the predation of a Dunlin by a Glaucous Gull *Larus hyperboreus*, though this is a large species, and of the above, only the Great Black-backed Gull, a similar sized species, is known to predate fully-grown waders (Cramp and Simmons 1983). (Despite the possible threat from gulls, it should be noted that Turnstones elsewhere have been seen to benefit from their presence, because of the gulls' ability to drive off predators: Brearey and Hildén 1985). Crows were similarly not seen to be predatory at West Harbour, but were probably also regarded as a threat. Crows were an important source of disturbance in Furness's (1973b) study of roosting waders in Lothian, Scotland, whilst Strann and Summers (1990) noted that crows disturbed flocking Purple Sandpipers.

Only birds of prey and an Arctic Skua were seen to attack roosting waders and only four attacks were recorded in total. Kestrels were the only raptors seen regularly in the area and though they were twice recorded to have taken Turnstones on Hartlepool Headland: in February and December 1994 (C. Bantoft pers. comm.), instances of Kestrels taking fully grown waders are generally rare (McCulloch 1960, Whitfield 1985b). Peregrines *Falco peregrinus* and Merlins, common predators of wintering waders (Page and Whitacre 1975, Kus *et al.* 1984, Whitfield 1985b, Cresswell 1993), regularly winter on the Tees estuary to the south (R. Ward pers. comm.), but do not seem to venture to Hartlepool to hunt. The seasonal variation in the disturbance rate from raptors suggests that the Hartlepool area is generally used by raptors whilst on passage to and from wintering areas. Disturbance by Arctic Skuas was frequently recorded by Handel and Gill (1992) in their study of roosting Dunlin and an Arctic Skua was once seen to attempt to capture a Western Sandpiper *Calidris mauri* in flight.

Roosting waders were occasionally disturbed on the island by rats, though they were not attacked. Predation by rats may be a problem at night however (Corbet and Southern 1964) and this may explain the low numbers of roosting waders that were seen at West Harbour after dark. In Fife, Scotland, Turnstones and Purple Sandpipers are both thought to commute to the Isle of May over night as the island is rat-free (Summers *et al.* 1975, Summers 1994). Hockey (1985) also noted the use of islands for night-roosting by African Black Oystercatchers *Haematopus moquini* in an area where nocturnal mammalian predators predominate.

It is notable that disturbance from predators, though low, caused departures from the West Harbour roost relatively frequently. The influence of predators on the choice of roost site is high and acts from day to day and possibly subsequently. Lack (1966) suggested that if individuals are undisturbed by predators at a roost one day, they will tend to return to the same place the following day, their presence there also indicating to others that the site is safe from predators. The lack of potential diurnal predators at West Harbour may thus be a factor in the attractiveness of the site to roosting waders. When a Merlin did attack roosting Purple Sandpipers at West Harbour, their numbers there were greatly reduced the following day.

Although the West Harbour roost did not attract many predators, communal roosts are noted for their conspicuous nature (Wynne-Edwards 1962, Ward and Zahavi 1973). A roost of Black-tailed Godwits *Limosa limosa* in Holland, for example, frequently attracted Marsh Harriers *Circus aeruginosus* (Piersma 1983). If disturbance levels are high, numbers of waders may be affected and raptors were amongst factors thought to be responsible for decreased numbers of waders roosting on the Dee estuary (Kirby *et al.* 1993).

Some of the instances of flights caused by disturbance from unknown sources may also be a result of anti-predatory behaviour. Lack (1966) speculated that synchronised flights performed prior to entering a roost are a form of behaviour evolved to confuse birds of prey. Flights may initially be a result of increased levels of disturbance causing restlessness in the birds. Ward and Zahavi (1973), in their information-centre theory of communal roosting, considered however that such flights were a form of advertisement to roost sites and noted the aerobatics and switching behaviour of Knot and Dunlin as they flew to roosts. Whilst such behaviour would attract predators, the resultant increase in the number of roosting birds would however only help to reduce the impact of predation through increased predator detection (Pulliam 1973, Powell 1974, Siegfried and Underhill 1975), reduced individual risk (Hamilton 1971, Cresswell 1994, Fox *et al.* 1994) and increased confusion of the predator (Cresswell 1994, Fox *et al.* 1994).

The role of flights as a form of social stimulation to synchronise migration has been hypothesised by Piersma (1983). This theory is supported by the observations of roosting waders of Swinebroad (1964) and of Handel and Gill (1992). In the present study however, most flights caused by unknown sources occurred between January and March, rather than just prior to spring migration. Roosting numbers of Turnstone did however increase after winter and this behaviour perhaps helped to co-ordinate migration.

Human disturbance was common at West Harbour and on Hartlepool Headland and came from a variety of factors. Direct disturbance from man caused extreme levels of disturbance on Inscar beach on the Headland and was frequently accompanied by disturbance from dogs. High levels of disturbance there often caused waders to fly directly to West Harbour. Walkers and dogs were similarly seen to be major causes of disturbance to beach roosting waders in studies on the Dee estuary (Mitchell *et al.* 1988, Kirby *et al.* 1993).

In contrast, the proportion of disturbances within West Harbour directly attributable to man was low, whilst disturbance from dogs was totally absent. Most disturbances from man affected waders roosting on beaches, only one (4.2%) of 24 disturbances affecting waders on the island, a further seven (29.2%) affecting waders on the inner pier. The island is now the preferred roost site within West Harbour for Turnstones and Purple Sandpipers, Oystercatchers and Redshank, and this is no doubt partly attributable to its protection from direct human disturbance. Purple Sandpipers were more susceptible than Turnstones to direct disturbance from man both at West Harbour and on the Headland and their greater preference for the island may be a result of this. It is also notable that West Harbour only became predominant as a roost site once parts of the old piers had become cut off from the shore (R. McAndrew pers. comm.).

Other forms of human disturbance at West Harbour included boats and helicopters. Helicopters only twice disturbed roosting waders, but were a major cause of disturbance, along with aeroplanes, in a number of other studies of roosting and feeding waders (Furness 1973b, Heinen 1986, Visser 1986, Koolhaas *et al.* 1993). Boats commonly caused disturbance and this is no doubt due to the large variety and number of craft using the harbour. Disturbance to roosting waders and Shelduck *Tadorna tadorna* was also recorded from motor boats, wind surfers, sailing boats and canoes in a study by Koepff and Dietrich (1986), canoes disturbing most often due to their capability for close approaches to roosts. Wind surfers, (and other boats and jet skis), were also among factors linked to declines in the numbers of roosting waders on the Dee estuary (Kirby *et al.* 1993) and typically caused waders to fly from the study area, before returning a short time later. In this study a high proportion of disturbances from boats and helicopters resulted in birds departing completely from the roost and of the disturbance factors seen, their effects are perhaps among the most important.

Reactions to disturbance varied between species, smaller species typically being more susceptible to most factors. Oystercatchers and Redshanks were however much more likely to leave the West Harbour roost on account of disturbance, and this perhaps relates to the proximity and quality of alternate roosts. Redshank, for example, also roosted elsewhere within the docks and could fly there if disturbance levels at West Harbour were too high. Disturbance from boats was particularly likely to cause Oystercatchers and Redshanks to leave the roost, the former departing four times on their account and the latter twice.

3.4.3. Position at the roost and shelter.

Whitlock (1979), by modelling wader flocks and using field observations, found that four species, the Oystercatcher, Redshank, Knot and Dunlin, increasingly sought shelter as wind speed increased and that two species, the Curlew and the Lapwing *Vanellus vanellus*, did not. Only Redshank sought more 'environmental' or 'habitat' shelter as wind speed increased. Mutual shelter, obtained by roosting in flocks, increased with wind speed for Redshank, Dunlin and Knot. In the present study, Turnstones and Purple Sandpipers both sought more environmental shelter from the island in periods of high winds. Handel and Gill (1992) also noted that Dunlin sought environmental shelter in high winds by roosting in channels or behind low vegetated islands or drift wood. Purple Sandpipers were twice noted to choose exposed roost positions on the island in moderate gales or strong breezes, (on 29 November 1993 and 27 January 1994). Individuals in these cases were facing into the wind, thus reducing energy loss (Whitlock 1979, Wiersma and Piersma 1994), whilst the flocks were tight and thus offered mutual shelter. Such high winds may eddy around the roost island and thus make it more difficult for birds to find sheltered positions.

Both this study and Whitlock (1979) suggest that smaller species, such as Turnstone, Purple Sandpiper and Dunlin, look for increased shelter in high winds, whilst larger species typically do not. Heat loss due to wind may increase more sharply in small birds as wind speed increases and they may gain proportionally more from the increased use of shelter.

For Purple Sandpipers, the correlation between wind speed and the degree of shelter sought was less strong on sunny than cloudy days and for Turnstone, the correlation was not significant on sunny days. Sunshine thus appeared to make both species more tolerant of wind. Turnstones, in particular, used the top surfaces of the island and piers significantly more in spring and summer, presumably as these surfaces provided considerable reflected warmth at these times of year, whilst the need for shelter from cold winds was also less strong. Wiersma and Piersma (1994) have similarly hypothesised on the energetic benefits to Arctic waders of the radiation reflected from snow. Turnstones were additionally seen to actively seek sunny positions, consistently avoiding shadows when atop piers and the island, and often roosting by sunlit walls to gain added reflected warmth. Whitlock (1979) also noted the use of such suntraps by roosting Redshank, whilst King (1981) saw that Turnstones, roosting in a harbour in autumn and winter, perched on wooden boats in preference to metal ones, presumably to reduce heat loss through their feet. Purple Sandpipers were once noted to stand in snow whilst roosting, in preference to snow-clear areas that were also available to them close by: the snow may have given insulation and helped to prevent heat loss from the birds' legs.

Waders thus used a variety of methods whilst roosting to reduce heat loss or even to gain energy. The island at West Harbour offered considerable environmental shelter, whilst some sites offered reflected warmth at particular times of year. The microclimatic advantages of the West Harbour site clearly attracted waders, though they could not be said to promote roosting. Energy gained through the mutual shelter found within flocks however may provide some incentive for such behaviour. It is though notable that the lowest concentrations of Turnstones at West Harbour occurred in winter, when the energy gains through roosting would have been at their most valuable.

Summary.

1). Turnstone numbers at the West Harbour roost peaked during autumn passage and were stable each year over the defined winter period. Purple Sandpiper numbers at the West Harbour roost were highest and also stable each year over winter; no large autumn or spring passage was evident.

2). Numbers of both species at West Harbour were greatest on spring high tides and lowest on neaps; high winds reduced the numbers of both species. In contrast, numbers of both species at high water at Hartlepool Headland were greatest on neap tides; Purple Sandpiper numbers there were reduced by high winds in one winter.

3). The maximum winter number of Turnstones at West Harbour was stable between 1986/87 and 1992/93, but declined by 50% in 1993/94, 18 months after the harbour's completion. The maximum winter number of Purple Sandpipers at West Harbour has declined fairly steadily over the 8 year period (by *c.*8% per annum). Both species used the West Harbour roost relatively less frequently in 1993/94 than in 1991/92.

4). A wide variety of factors caused disturbance to roosting shorebirds at West Harbour: gulls, boats, building work and humans were amongst the most frequent. Overall disturbance rates and those from boats, man and unknown factors increased over the study period. Avian predators, rats, helicopters and boats were most likely to cause birds to depart the roost. Disturbance to Purple Sandpipers was not found to affect their numbers at the roost on subsequent days; numbers were however depressed following a day when a Merlin attacked the roost.

5). The island was the preferred roost site at West Harbour for both Turnstones and, more particularly, Purple Sandpipers. Both species preferred the sides of the island to the top and used the sheltered sides when wind speeds increased; wind speeds were considerably lower at the base of the leeward side of the island. Turnstones used the tops of the island and piers more frequently in summer and spring than in autumn and winter.

6). Turnstones and Purple Sandpipers spent most of their time at the West Harbour roost sleeping, increasingly so towards and after high water. Preening and standing were also important activities, Turnstones preening more when they first arrived at the roost and Purple Sandpipers more in autumn. Feeding was a less prominent activity at high water for both species at West Harbour than at the Headland.

Chapter 4.

Low Water Foraging Behaviour.

4.1. Introduction.

This chapter summarizes observations of the behaviour of Turnstones and Purple Sandpipers on their low water feeding grounds and has four main aims:

1). To document which areas are important as feeding grounds for the two species and how numbers vary seasonally, with the height of low tide and through the tidal cycle.

2). To determine the causes of aggression between individuals in feeding flocks and to determine how the intensity and rate of aggression vary.

3). To assess the stability of the dominance hierarchies on feeding grounds which result from this aggression and to determine which factors are correlated with dominance.

4). To determine the degree to which individual Turnstones and Purple Sandpipers are sedentary in the non-breeding season through the calculation of their home ranges and to investigate which factors are important in the determination of home range size.

The food requirements of waders vary through the non-breeding season, as daylength, temperature and weather conditions change (Goss-Custard 1969, Heppleston 1971). Many species put on mass around midwinter (Johnson 1985, Norman and Coffey 1994) as protection against forthcoming cold weather and perhaps prey depletion (Pienkowski *et al.* 1979, Davidson 1981, Dugan *et al.* 1981, Summers *et al.* 1992) and after a drop in mass around February, again fatten up prior to their spring migration (Prys-Jones *et al.* 1992, Summers *et al.* 1992). In response to these varying requirements, species may use different feeding areas or change the length of time that they feed during a tidal cycle.

Most waders feed in flocks during the non-breeding season and whilst this provides a number of benefits (Pulliam and Caraco 1984), it is costly in that it results in increased aggression, particularly due to competition for food (*e.g.* Recher and Recher 1969). The variation in aggression rate and intensity was investigated in relation to the birds' food requirements, over a tidal cycle and seasonally and in relation to habitat. Aggression rates are predicted to increase with flock size and wind speed, and be high shortly after roosting, when feeding needs are greatest. Rates are also predicted to be greater during neap tides, when less intertidal area is available for feeding.

The consequences of aggression are found in the dominance of some individuals and the subordination of others. Dominance often results in greater access to resources (*e.g.* Ekman and Askenmo 1984) and greater intake rates (*e.g.* Ens and Goss-Custard 1984) and may thus be seen as advantageous. The position of subordinates in this view is one of 'hopeful dominants' (West Eberhard 1975). An alternative view suggests that dominance and subordination are alternate strategies, but ones with equal fitness (Rohwer and Ewald 1981). Dominance hierarchies may form where the composition of a group is stable and have therefore been found to occur amongst site-faithful non-breeding waders, for example Turnstones (Whitfield 1985a) and Oystercatchers (Ens and Goss-Custard 1984). Within such hierarchies, dominance may be related to age, sex or body-size (Ketterson 1979, Piper and Wiley 1989) and the present study aimed to determine if such relationships occur amongst foraging Turnstones and Purple Sandpipers. Ultimately, through competition for food, dominance may even have a consequence on an individual's survival (*e.g.* Kikkawa 1980) and the relationship between dominance and survival was thus also investigated.

The return dates of resident Turnstones to Hartlepool were analysed in order, firstly, to better understand the seasonal fluctuations in the numbers of birds seen in the study site. Return dates were additionally analysed for this species in order to see if winter dominance may be related to summer breeding success. Whitfield (1985a) has suggested that dominant Turnstones, through improved feeding before and during migration, may arrive on their breeding grounds in better condition than subordinates and in consequence of this and their dominance, may breed more successfully. Failed breeders depart from their nesting areas earlier than those that are successful (Nettleship 1973) and if there is a relationship between breeding success and dominance, subordinates should arrive back at their wintering quarters the earliest, (provided that autumn staging posts are not used for lengthy periods of time).

The site fidelity of both Turnstones and Purple Sandpipers within winter has been demonstrated in this (Chapter 2) and other studies (*e.g.* Atkinson *et al.* 1981, Metcalfe 1984a, Whitfield 1985a, K-B. Strann pers. comm.). Individuals may vary in how sedentary they are however and may occupy 'ranges' of greatly varying size. Such variation may occur due to differences in the quality of feeding grounds or be related to dominance: subordinate Oystercatchers may, for example, be forced to use a number of feeding sites in order to avoid competition from dominants (Ens and Goss-Custard 1984). Home range size may also be related to differences in diet, due to variation in the abundance of prey or variation in the amount of competition between individuals. As diet in Purple Sandpipers is related to bill-length (Summers *et al.* 1990a), differences in home range size are therefore investigated between Purple Sandpipers of different bill-length size class.

4.2. Methods.

4.2.1. Low water feeding numbers and habitat use; the arrival and departure of birds to and from low water feeding areas and the West Harbour roost.

Birds of each species were counted once weekly on their feeding grounds, with counts centred around low water. Due to the length of coast included within the study area, the count was divided over two days, one day covering Blackhall to Breakwater north and the other Inscar to North Gare breakwater. Counts typically took three hours to complete. (Seaton Snook, immediately to the south of North Gare breakwater, was also surveyed in the first-winter, but as no colour-ringed individuals resident in the study area were seen there, it was not surveyed in further years). The coast was divided into sections (see Fig. 1.1) and the numbers of each species counted in each of these sections.

Birds of both species were counted over one tidal cycle at Parton (see Fig. 1.1), in order to assess how numbers varied as the tide ebbed and flooded. Birds were counted at 30 minute intervals relative to low water. Similarly birds were counted at 'pre-roost' and 'post-roost' sites on Hartlepool Headland at 30 minute and 20 minute intervals over the flood and ebb tides respectively, in order to assess their use over the tidal cycle.

In order to understand how the time spent feeding and roosting varied seasonally and according to the height of high water, the median times of arrival of both species to the West Harbour roost were calculated. Individuals of both species were counted as they arrived at West Harbour from their feeding grounds, typically with a viewpoint from the south pier or from the open ground opposite the island (see Figs. 1.2 and 1.3). Total counts were almost certainly slightly low, because either small flocks were missed or flock sizes underestimated as they arrived. Incoming birds were most likely to be overlooked during the peak arrival period, rather than when flying in earlier or later and their omission is therefore assumed not to affect the calculation of median arrival times.

The habitat use of each species at low water was determined by recording the habitat that colour-ringed individuals were using when sighted during low water surveys. Habitat data thus refer only to the low water period.

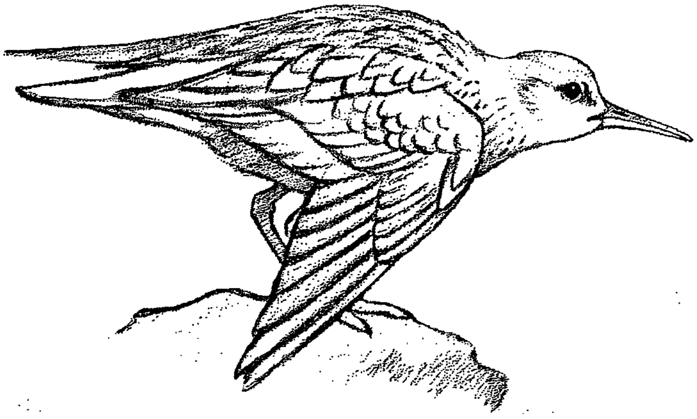
4.2.2. Individual aggression in feeding flocks.

Aggression was recorded in feeding flocks only for focal birds that were colour-ringed. A flock was defined, for both species, as a group of birds where no individual was more than 10m from the closest conspecific. This definition follows that of Metcalfe (1984a). Whenever possible, individuals were watched for five minute periods in order to calculate aggression rates. The following information was recorded: the colour-ring identity of the focal bird and that of the opponent if that bird was also colour-ringed; the species of the opponent; the age of both birds, if possible (adult or first-winter); the initiator; the winner and loser; the time that the observation period started and finished; the date; the wind speed (recorded at either low or high water on the Beaufort scale); the flock size; the cause and form of the aggression. Data come primarily from the ebb, low water and flood periods, though some aggression during high water feeding on grass, algae, dead wrack and strand habitats was also recorded.

Turnstone aggressive interactions were placed in order of increasing intensity into the following categories: threat with tail down to tail up; threat with tails down; peck; chase; peck-chase and fight. Turnstone aggression postures have been described frequently before (*e.g.* Groves 1978, Cramp and Simmons 1983, Whitfield 1985a). The typical posture is one when the initiator's tail is depressed below the horizontal, though at varying degrees (tail down to up); the opponent may respond with a similar display (tails down). Pecks, chases, peck-chases (a combination of the previous two) and fights usually occur after an initial threat.

Purple Sandpiper aggression was categorised, also in order of increasing intensity, into: threat with wings in; threat with wings out to in; threat with wings out; peck; chase; peck-chase and fight. The typical Purple Sandpiper threat posture is one where the initiator lowers its body by crouching and points its head and beak aggressively towards its opponent. This may be developed into a wings-out posture (Fig. 4.1), where the wings are flicked out horizontally, or slightly lower, often with an associated call. This posture may occur whilst standing or during a short run at the opponent. If only the initiator holds its wings out, this is categorised as a 'wings out to in' threat; if the opponent responds with a similar display, then it is categorised as a 'wings out' threat. This wings-out display differs from the one- or two-wing-lift described previously in other studies, most of which were of breeding behaviour (Keith 1938, Feare 1966, Bengtson 1970), as in the latter display the wings are held vertically.

Fig.4.1. Purple Sandpiper in aggressive 'wings-out'posture



Aggression amongst birds in feeding flocks was caused either by encounters over food or feeding sites, or due to an infringement of individual distance (Conder 1949). Encounters over food and feeding sites were easily distinguishable as one bird was feeding before the encounter took place and as the winner took the food item or began feeding at the site immediately afterwards.

4.2.3. Individual return dates of Turnstones.

Only resident individuals were used to analyse variation in return dates. Individuals are assumed to have returned to the study area on the first day that they were seen there after the breeding season. As first-summer Turnstones often remain in their wintering quarters over summer or do not migrate fully to their breeding grounds (Thompson 1974, Cramp and Simmons 1983), these individuals were not used in analysis of return dates.

4.2.4. Home ranges.

To determine the low water home ranges of both individual Turnstones and Purple Sandpipers, flocks were searched for colour-ringed individuals during the once weekly low water counts of the study area and the position of any individuals sighted marked to the nearest 20m on a 1:10,000 scale map. Some individuals were sighted more than once during the observation period and in order that sightings were independent of each other, a minimum period of one hour had to elapse before an individual's position could be recorded again. Individuals were never recorded more than twice during a count. In order that the probability of detecting a colour-ringed individual was equal in all parts of the study area, the time spent searching each part of the coast was proportional to the number of birds found there, (for example, one hour was given to searching the area between Blackhall and Steetley and also one hour to Parton). Flocks of Turnstones and Purple Sandpipers were quickly and easily found in all parts of the study area and thus the time taken to detect a colour-ringed individual on a particular stretch of coast was simply dependent upon the number of birds present. Individuals were often sighted during the low water period outside of these counts, but their position was not recorded in these cases as sightings may then have been biased to particular areas.

Home ranges were calculated only for individuals that were resident on the 'Headland' in each year that they were known to be alive. 'West Harbour to North Gare' and 'North and South' residents were not used in the analysis as these birds may have used the offshore Long Scar rocks, which could not be surveyed, and thus the sizes of their home ranges would have been underestimated. Headland residents were seen only occasionally between West Harbour and North Gare and it is thought, hardly ever used Long Scar rocks. Data were taken from the whole of the period that individuals were present in the study area.

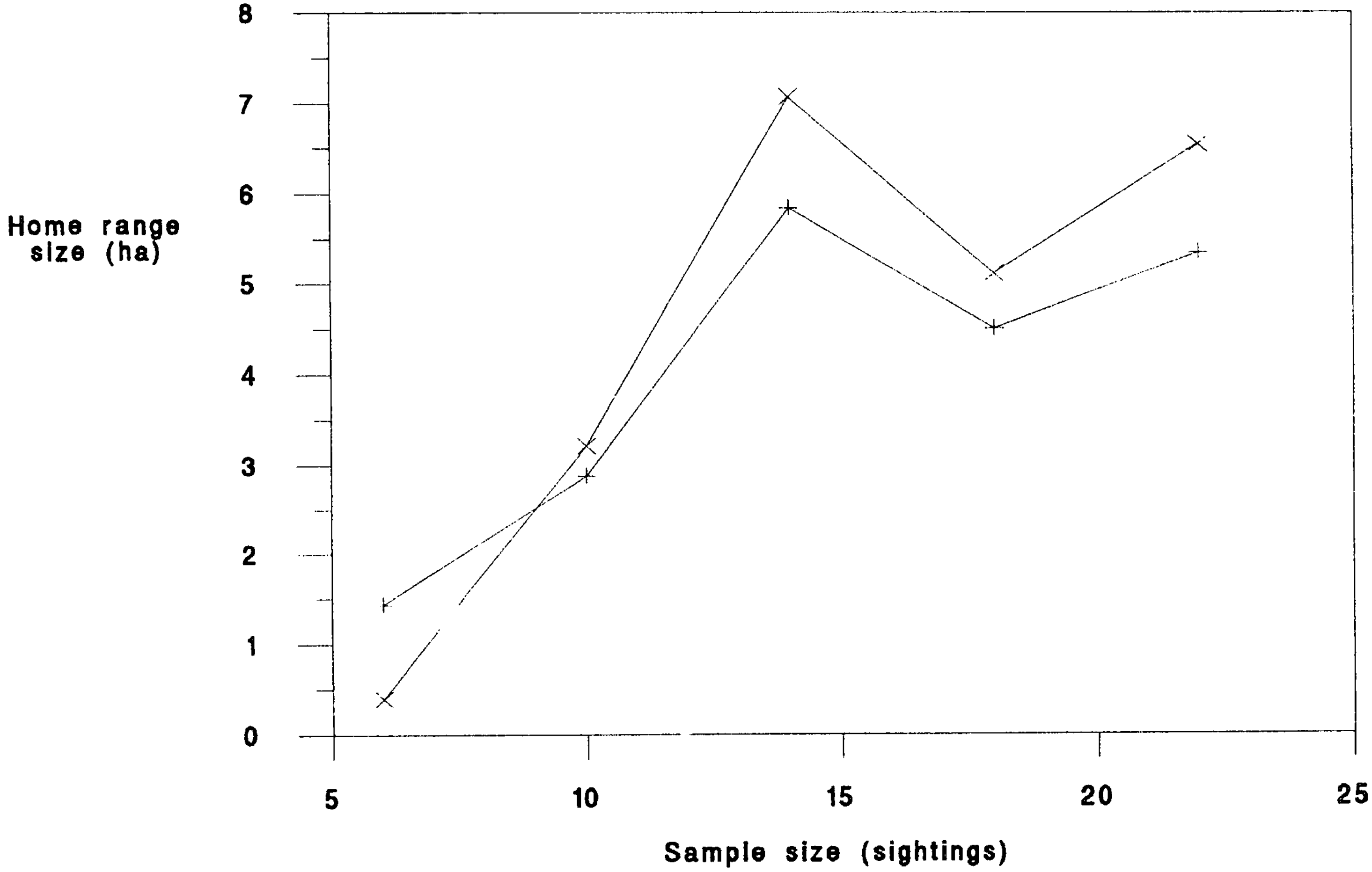
The method used to determine home ranges was the Harmonic Mean Measure (Dixon and Chapman 1980). This method has the advantage that it allows for ranges to be discontinuous, an important consideration for Turnstones and Purple Sandpipers, whose ranges may be split into more than one activity centre in disjunct areas of rocky shore. Other techniques for estimating home ranges, such as the maximum polygon method, in which the home range boundary is defined by extreme sightings (Sandersen 1966) and the probability circle or probability ellipse (see Sandersen 1966, Van Winkle 1975), do not allow for such discontinuity in ranges. The latter two probabilistic methods are also very sensitive to outlying points, and use predetermined geometric shapes to describe ranges. Such circles or ellipses may bear little relation to the actual shape of an animal's home range (MacDonald *et al.* 1980). The harmonic mean measure is less sensitive to outlying points, (due to the use of harmonic rather than arithmetic means) and has the additional advantage that centres of activity (Hayne 1949) are always within areas of activity and not between them.

The harmonic mean measure constructs a spatial distribution for the probability of seeing an individual, through the measurement of the distances between the sightings of an individual and the intersections of a grid superimposed on the map of sightings. In the present study, a grid of 200m (north-south) by 100m (east-west) was placed over a 8 km by 4 km map. One disadvantage of the method is that there is a bias towards sightings that lie on grid intersections, which leads to a distortion in the range's size and shape (Dixon and Chapman 1980). This problem was avoided by translocating sightings to grid cell centres (see Spencer and Barrett 1984).

In the present study, an individual's home range at low water was based on the area enclosed by the 90% probability isopleth (*i.e.* the area in which an individual spends 90% of its time). Such an area may enclose areas of habitat usually or completely unused by these species at low water, *e.g.* sandy shores (see 4.3.1.1.1 and 4.3.1.2.1), grass and areas of town above the mean high water line and sea below the mean low water line. To omit these areas, an individual's home range was thus defined as the area of rocky shore between the mean low water and mean high water lines that was enclosed within the 90% isopleth. The home ranges were calculated using the Ranges IV package (Kenward 1990), which provides for such habitat analysis.

The home range estimate is dependent upon the number of sightings used: if too few sightings are used, the size of the home range may be underestimated. Fig. 4.2 shows how the home range estimates of Turnstones (*n* = 10) and Purple Sandpipers (*n* = 9) varied with the size of the sample of sightings. The median home range estimate increased initially with sample size, but above 20 sightings stabilised. In order to calculate an estimate not biased by sample size, estimates were thus only produced for individuals that were sighted a minimum of 20 times.

Fig. 4.2. The relationship between home range size and the number of sightings in the sample for Turnstone (x) and Purple Sandpiper (+).



4.3. Results.

4.3.1. Species Behaviour.

4.3.1.1. Turnstone.

4.3.1.1.1. Low water feeding numbers and habitat use.

Fig. 4.3 shows the monthly maxima of Turnstones recorded feeding on Hartlepool Headland at low water, for each of the three years of study. Numbers rose over summer to a peak in autumn each year, before then stabilising over winter. No spring passage through the area was evident from the numbers observed in this area and numbers fell in April and May as birds migrated from the study area. The pattern is similar to that seen for Turnstones roosting at West Harbour and is a reflection of the actual changes in the population of the study area. Numbers here were not affected by seasonal changes in the use of different feeding areas: Fig. 4.4 shows that there were no significant seasonal changes in the proportion of times that Headland resident Turnstone were seen away from the Headland at low water (combining August and September, October and November *etc.*: $\chi^2 = 8.286$, d.f. = 4, n.s.).

Monthly maxima are not shown for Turnstones using the area between Inscar and North Gare breakwater as there was high variation in numbers here due to the tide (see below). At one small feeding site within this area, 'south Seaton pipe', it was however possible to see that Turnstone numbers decreased a little over the winter (Appendix 9; for 1991/2: $r_s = -0.619$, $n = 20$, $P < 0.01$; for 1992/93: $r_s = -0.701$, $n = 20$, $P < 0.001$). (Numbers here also tended to be lower in 1992/93 than the previous winter: Mann-Whitney $z = 1.592$, $P = 0.111$). In contrast to the pattern seen at Hartlepool Headland, Turnstone numbers in an area immediately south of the study area, Seal Sands, showed a marked increase in April and May and then again in July and August (Fig. 4.5), possibly as a result of small spring and early autumn passages (data from R. Ward). Observations at Seal Sands

Fig. 4.3. Turnstone monthly maxima on Hartlepool Headland at low water.

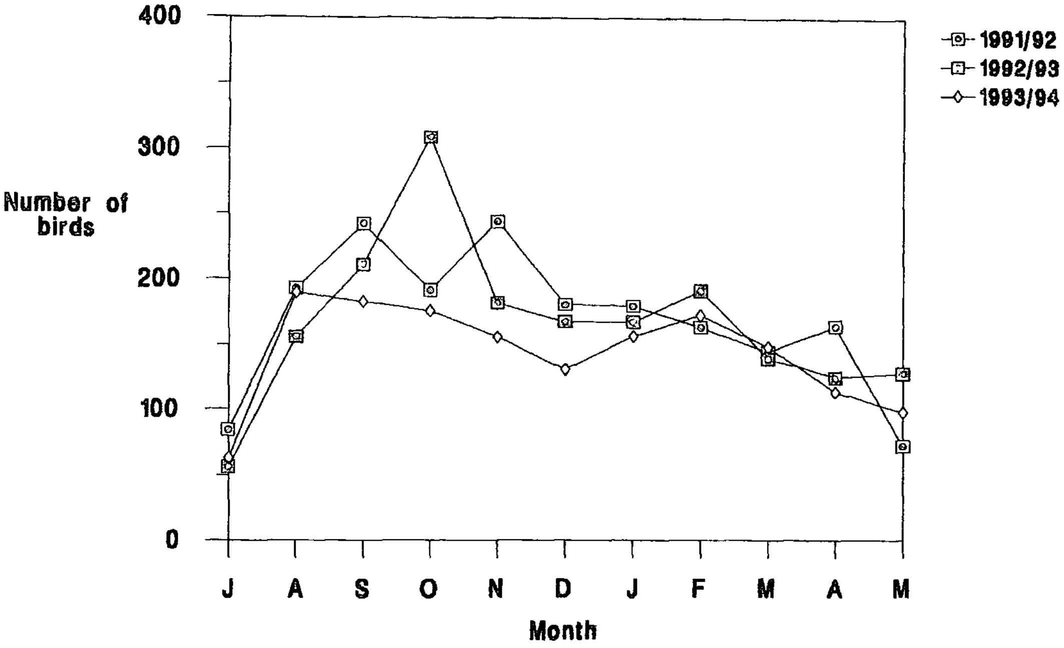


Fig. 4.4. The percentage of low water observations of Turnstones resident at Hartlepool Headland that were away from the Headland, in relation to season. The number of observations is shown adjacent to each point.

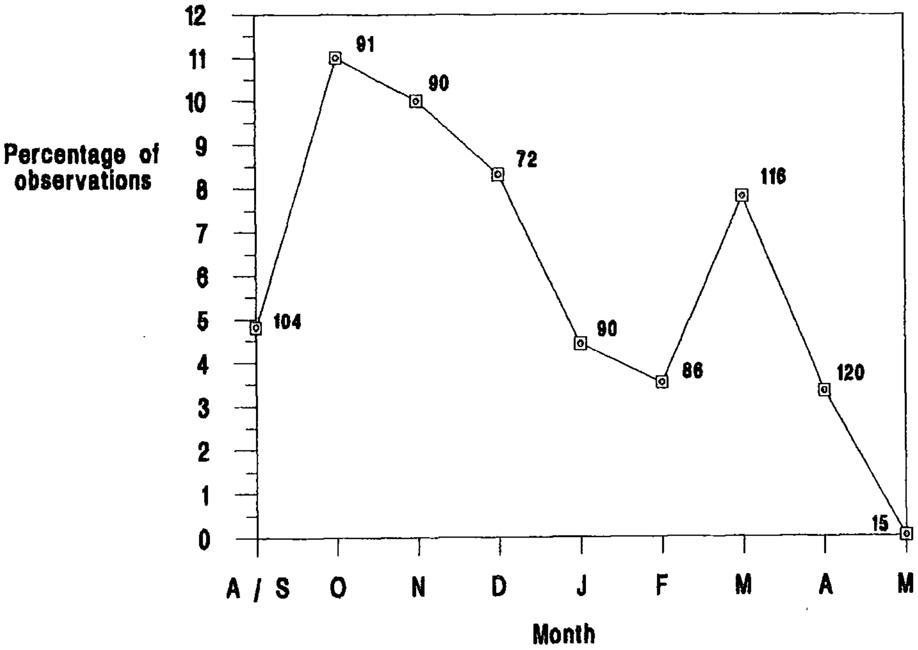
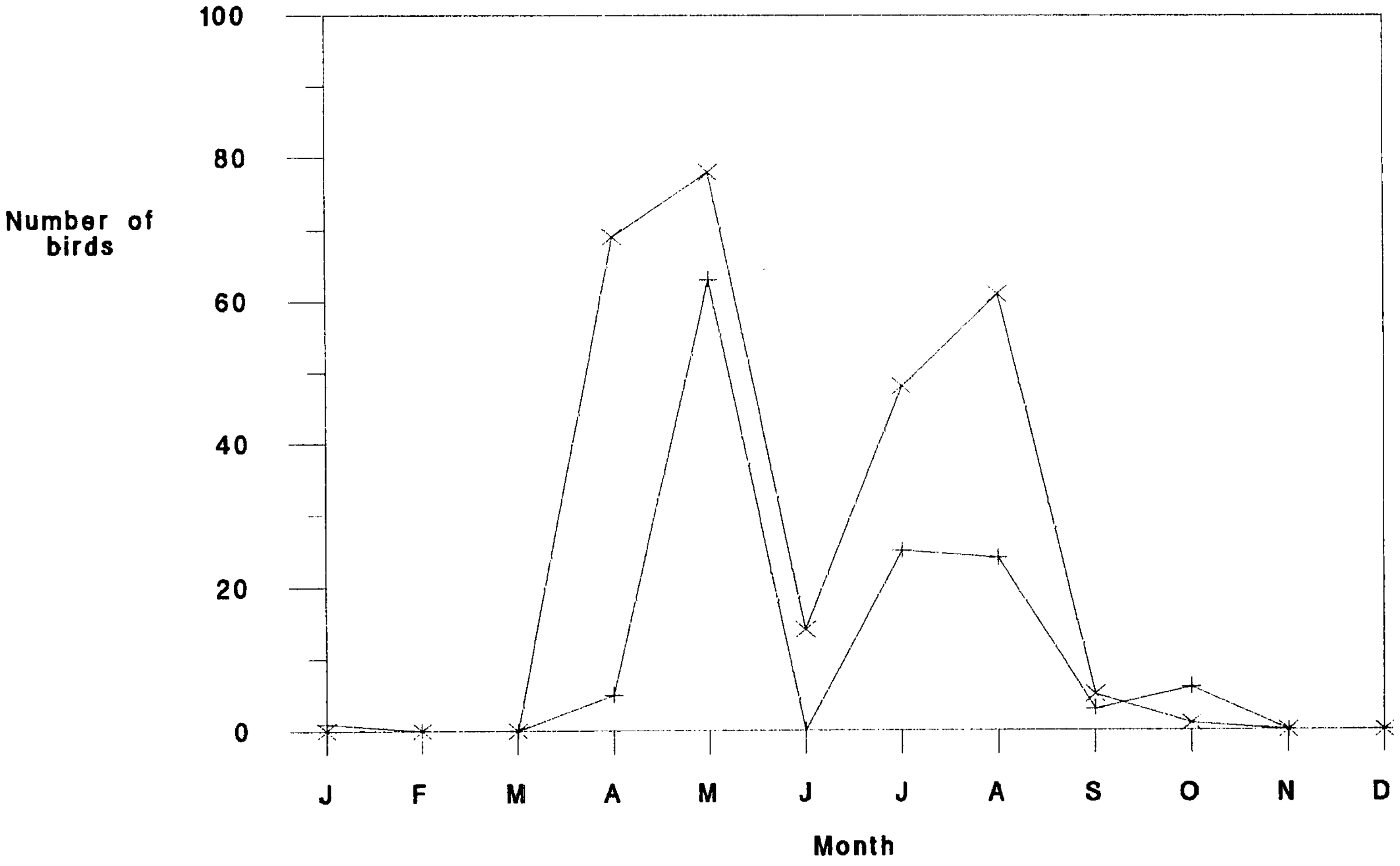


Fig. 4.5. Turnstone monthly maxima at Seal Sands at low water, during 1992 (x) and 1993 (+).



in summer 1992 of a number of colour-ringed first-summer Turnstones (R. Ward and M. Parsons pers. comm.), previously resident within the study area, suggest however that the increase in Turnstone numbers here in spring and summer may be partly due to the use of this mudflat by over-summering birds. The increased use of Seal Sands at this time of year may be a result of the Turnstones' attraction to the increased surface invertebrate life associated with the growth here of *Enteromorpha* algae. Low numbers in June may have been due to partial northward migration of these birds (see Thompson 1974).

Table 4.1 shows the maximum numbers of Turnstones recorded feeding at low water on Hartlepool Headland in each of the three winters of study, together with those of Purple Sandpiper and three other species. These figures give an indication of the change in size of the local populations of the species during the study period. They are of importance in understanding how numbers roosting at West Harbour may have changed as a result of its redevelopment and are discussed in reference to this in Chapter 7. Maximum winter Turnstone numbers on the Headland showed a steady decrease over the three years.

The pattern of use by Turnstones of one section of Hartlepool Headland, Parton (see Fig. 1.1), over a tidal cycle is shown in Fig. 4.6; (data from 2 September 1991). Numbers of Turnstones increased as the tide ebbed, peaking 2 hours before low water and then dropping slightly. Numbers increased a little after low water, as birds moved back from adjacent areas, before dropping as the tide flooded in.

The predicted height of low water was an important determinant upon the numbers of Turnstones seen feeding in each part of the study area (see Appendix 10 for graphs). During winter the numbers of Turnstones recorded at low tide on Hartlepool Headland were greatest on days when the low water level was in the middle of its range. Recorded numbers were lower on spring and neap tides, in the former case perhaps partly because of difficulty in seeing birds that were often distant and possibly hidden by rocks. On neap tides, many

Table 4.1. Yearly winter maxima of waders feeding at low water on Hartlepool Headland.

Species	1991/92	1992/93	1993/94
Turnstone	244 (19)	192 (18)	173 (20)
Purple Sandpiper	102 (16)	149 (15)	135 (18)
Oystercatcher	414 (18)	436 (10)	410 (5)
Knot	2650 (18)	1780 (6)	2210(5)
Redshank	119 (18)	80 (10)	81 (5)

Figures in parentheses are numbers of counts.

Table 4.2. Habitat use by Turnstones and Purple Sandpipers at low water.

Species	Musselbed	Exposed rock	Algae	Live wrack	Dead wrack	Strand	Grass
Turnstone	211	81	2	7	7	45	1
Purple Sandpiper	388	94	28	4	0	1	0

Figures represent the total number of observations of colour-ringed individuals in each habitat during low water surveys.

Fig. 4.6. Turnstone numbers at Parton over the low water period 2 September 1991.

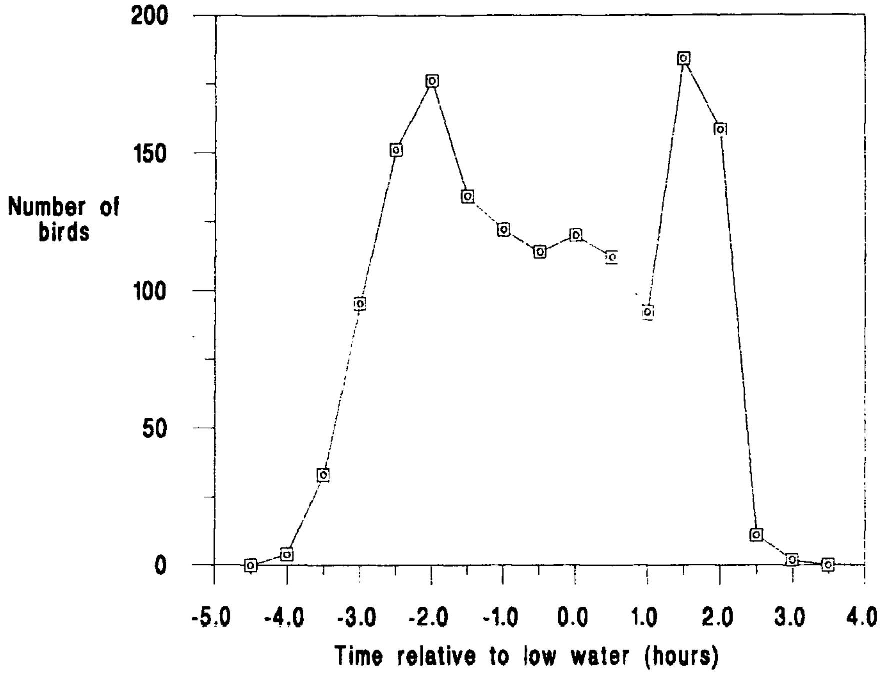
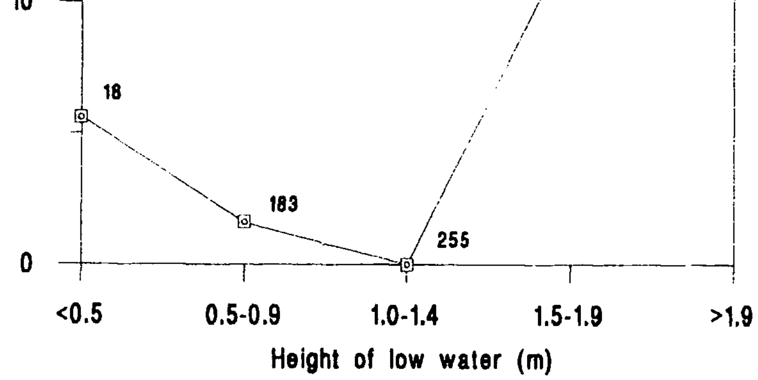


Fig. 4.7. The percentage of low water observations of Turnstones resident at Hartelepool Headland that were away from the Headland, in relation to the height of low water. The number of observations is shown adjacent to each point.



parts of the rocky intertidal at the Headland remained covered by water and this forced some birds to use other areas. Fig. 4.7 shows that Turnstones resident on the Headland were seen in areas away from the Headland on higher average low tide levels than when they were seen on the Headland (Mann-Whitney $z = 8.113$, $P < 0.001$). Numbers of Turnstones to the north of the Headland, between Steetley and Blackhall, were as a result greatest on neap tides and lowest on spring tides and a similar pattern was seen in the area between Inscar and North Gare breakwater. Although some of the increase on neap tides in the latter area can be attributed to the use of the area by Headland residents, (colour-ringed Turnstones usually resident at Parton and Throston were intermittently seen around West Harbour and Seaton Sands during winter), this was not the primary cause. The pattern more probably reflects the fact that the offshore Long Scar rocks (see Fig. 1.1), an alternative feeding area, remained largely flooded on neap low tides (and was completely covered on tides of over 2.2m) and that this forced birds to use the adjacent coast. It was, unfortunately, not possible to count birds on Long Scar rocks or to search them for colour-ringed individuals.

Over low water, Turnstones fed primarily on musselbeds (Table 4.2; data for Turnstones from 1991/92, for Purple Sandpipers from 1992/93 and 1993/94). Exposed rock and strand habitats were also used frequently, though live and dead wrack, algae and grass only occasionally. Algae and exposed rock are found higher up the shore and are thus not used so frequently at low water. Dead wrack is usually found at the high tide line and is thus normally used on flood, high or ebb tides. Figures are thus biased to habitats found primarily at the tide line during the low water period.

4.3.1.1.2. Pre-roosts, time of arrival at the West Harbour roost and post-roosts.

After low water, birds in many areas were forced to move from their low water feeding areas to other nearby sites by the rising tide. Such sites were used by both feeding and roosting birds and on neap tides, many birds remained over high water. On spring tides these sites were used by many individuals as 'pre-roosts' where individuals collected prior to moving to the main West Harbour roost. On Hartlepool Headland, three main areas acted as pre-roosts: the western edge of 'Throston'; the eastern edge of Lighthouse North' and Inscar (see Fig. 1.1). Fig. 4.8 shows how the number of Turnstones at Inscar increased on the flood tide and then decreased shortly before high water. The proportion of feeding birds decreased as high water approached (data from 6 September 1991).

Fig. 4.9 shows how the median time of arrival of Turnstones at the West Harbour roost varied according to the height of high water. Birds arrived on average, earliest relative to high water on spring tides and latest on neaps, though this trend was not significant ($r = 0.403$, d.f. = 11, $P < 0.10$ one-tailed):

$$\text{Time of Arrival} = -96.076 + 41.238 \text{ Height of High Water}$$

where time of arrival is in minutes before high water and the height of high water is in metres.

Taking this variation into account, there was some seasonal variation in the median time of arrival of Turnstones at the roost, though this was not significant (Fig. 4.10; $F_{3,9} = 1.82$, $P = 0.214$). Turnstones tended to arrive at the West Harbour roost early, relative to high water, in summer, but much later as autumn progressed. Arrival times were latest around midwinter. After midwinter, Turnstones again tended to arrive increasingly early relative to high water, though towards spring this trend became less clear.

Turnstones often did not move directly from West Harbour to their low water home ranges, but stopped to use 'post-roosts' or to feed in other areas prior to the uncovering of the lower shore. Post-roost sites were often the same as those used previously as pre-roosts. Fig. 4.11 shows how Turnstone numbers varied after high water at the post-roost site on the eastern edge of Throston; (data from 12 December 1991). Numbers increased to a peak two hours after high water, before decreasing to a stable level by one hour later. The proportion

Fig. 4.8. Numbers of Turnstones roosting and feeding at the Inscar 'pre-roost' 6 September 1991.

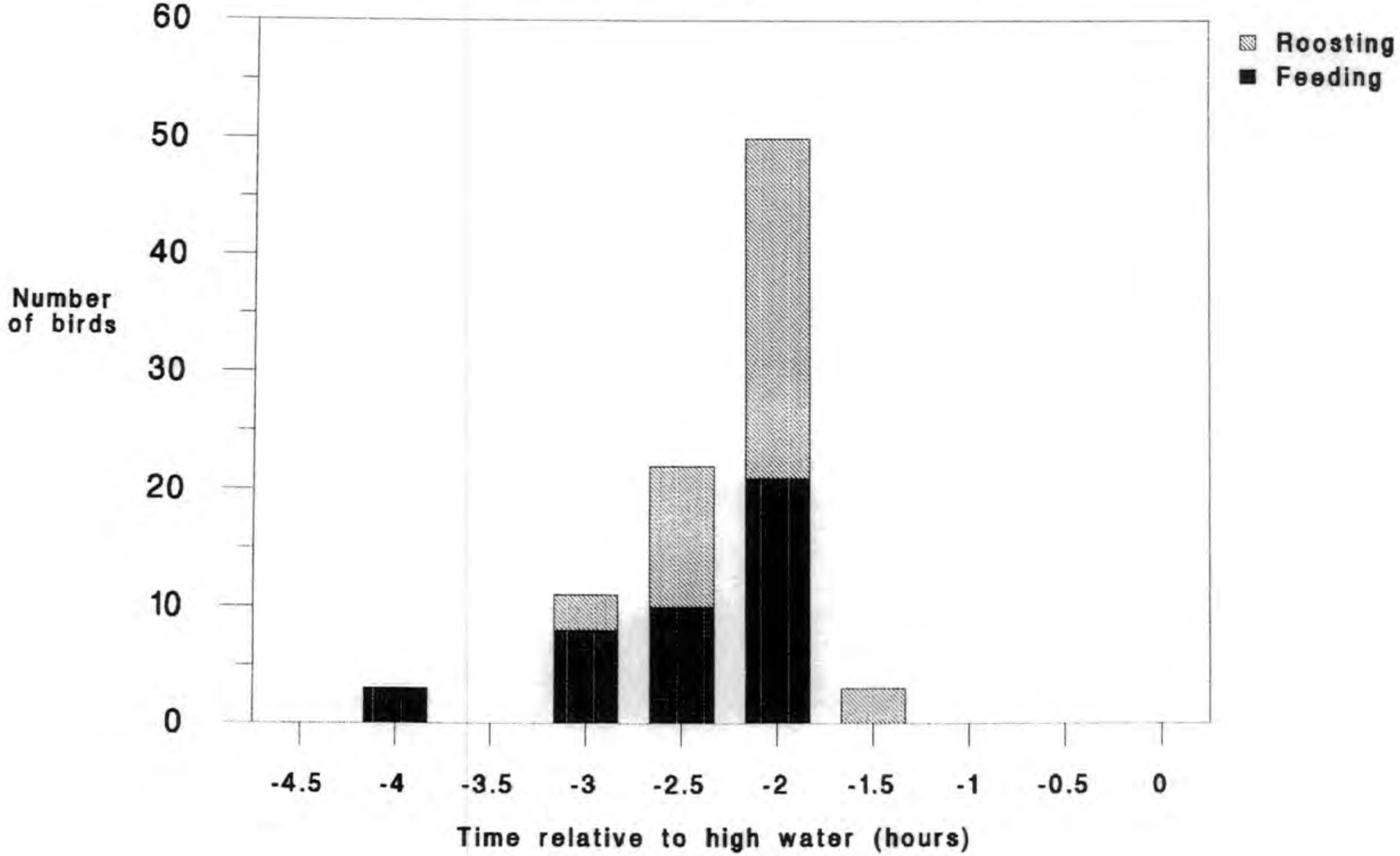


Fig. 4.9. The median time of arrival of Turnstones at the West Harbour roost in relation to the height of high water.

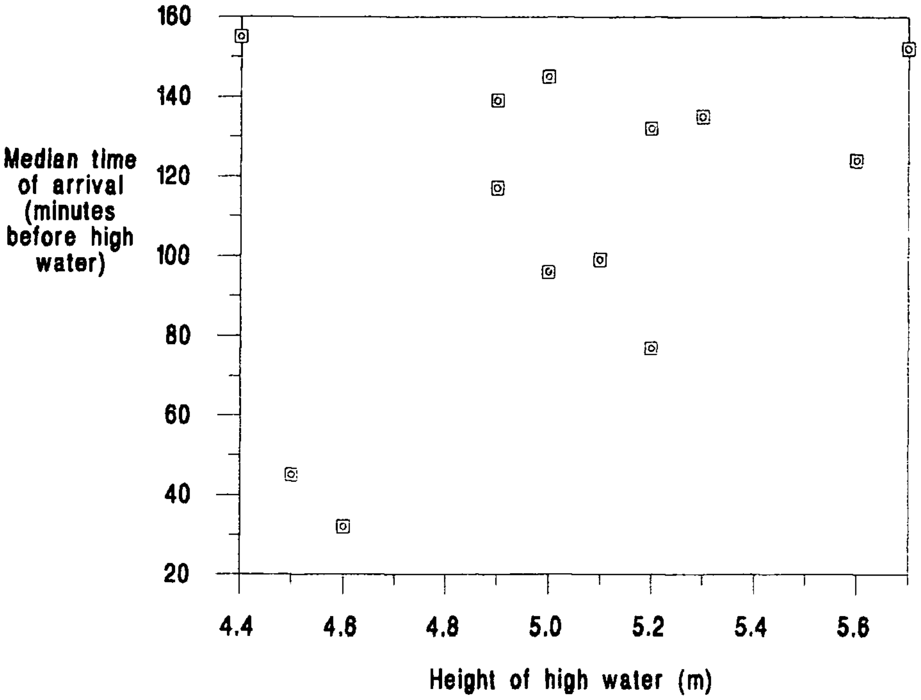


Fig. 4.10. The median time of arrival of Turnstones at the West Harbour roost in relation to season, using residuals from equation with height of high water.

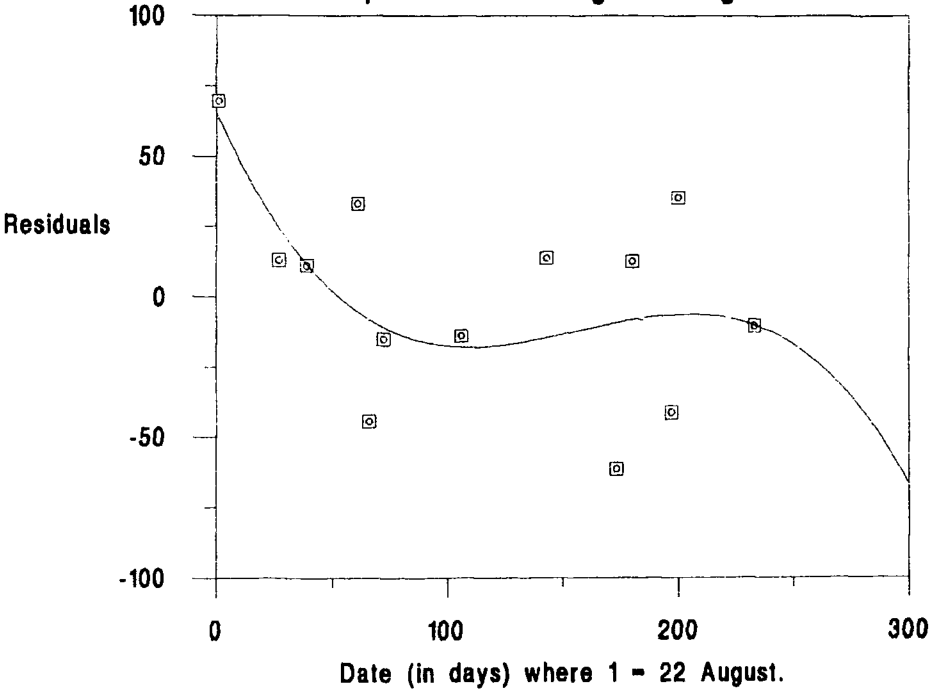
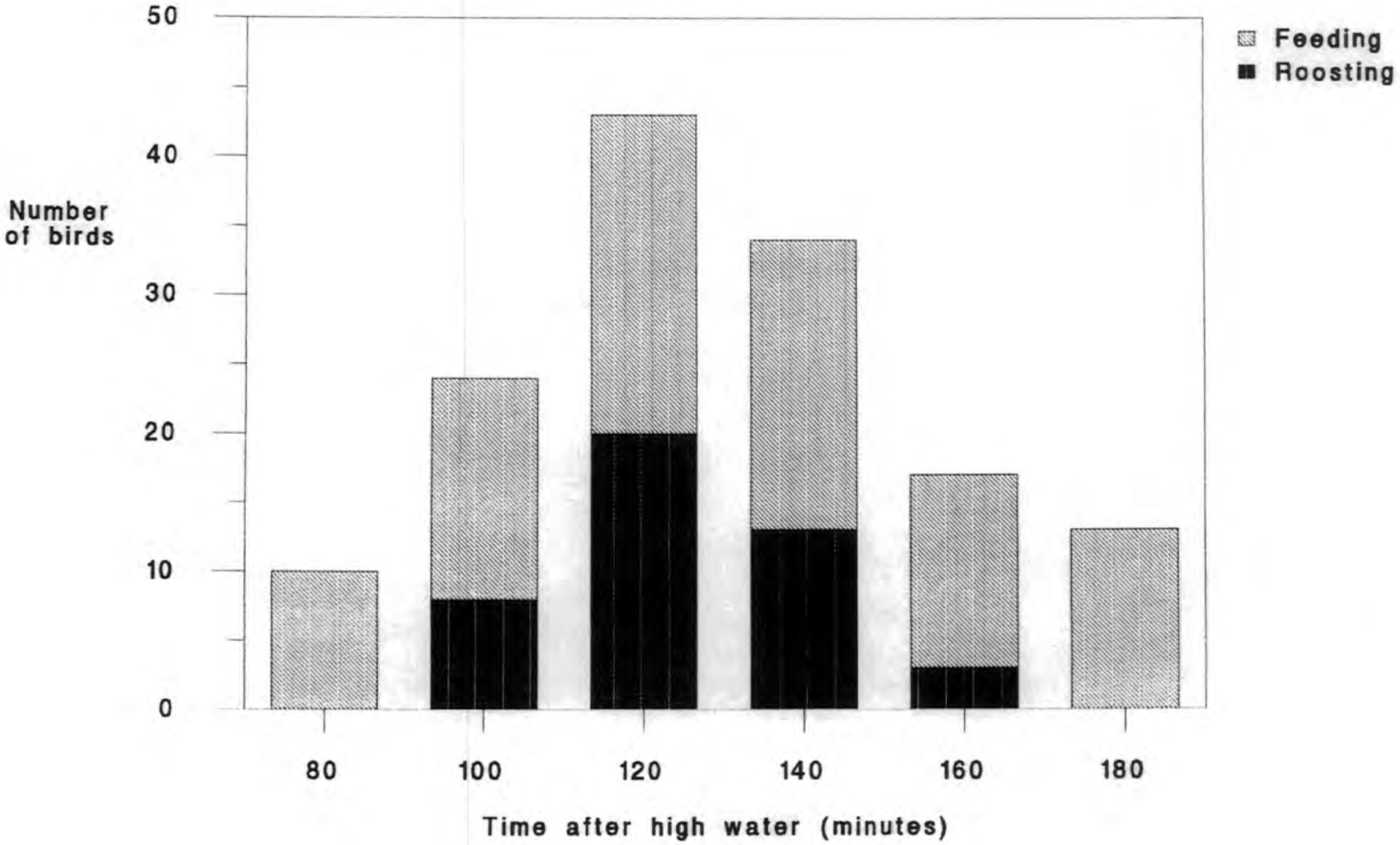


Fig. 4.11. Numbers of Turnstones roosting and feeding at the Throston 'post-roost' 12 December 1991.



of birds that were roosting also peaked two hours after high water. The birds that remained three hours after high water were all feeding.

4.3.1.2. Purple Sandpiper.

4.3.1.2.1. Low water feeding numbers and habitat use.

Fig. 4.12 shows the monthly maxima of Purple Sandpipers recorded feeding on Hartlepool Headland at low water, for each of the three years of study. As for Turnstones, the pattern seen is similar to that seen for birds roosting at West Harbour. A few (Norwegian) birds returned to the area in early summer, though numbers remained low until October and November when the majority of the wintering population arrived. Numbers remained stable until April and May when birds departed for their breeding quarters. Although no autumn or spring passages were evident from these feeding numbers, one colour-ringed passage bird was observed in spring. (This bird had been ringed in south-west Finland on autumn passage in 1972; other birds from this site have previously been recovered wintering on the continent, V. Vänskä pers. comm.). As with Turnstones, the monthly maxima of Purple Sandpipers seen at low water on Hartlepool Headland accurately reflect seasonal changes in total numbers. The proportion of times that Purple Sandpipers resident on the Headland were seen away from the Headland did not vary seasonally (Fig. 4.13; combining August to November, December to February and March to May: $\chi^2 = 1.169$, d.f. = 2, n.s.).

The maximum numbers of Purple Sandpipers recorded feeding over low water on Hartlepool Headland in each of the three winters of study is shown in Table 4.1. No trends were seen over this period. These figures are discussed later in Chapter 7 in reference to changes seen in roosting numbers at West Harbour.

Fig. 4.12. Purple Sandpiper monthly maxima on Hartlepool Headland at low water.

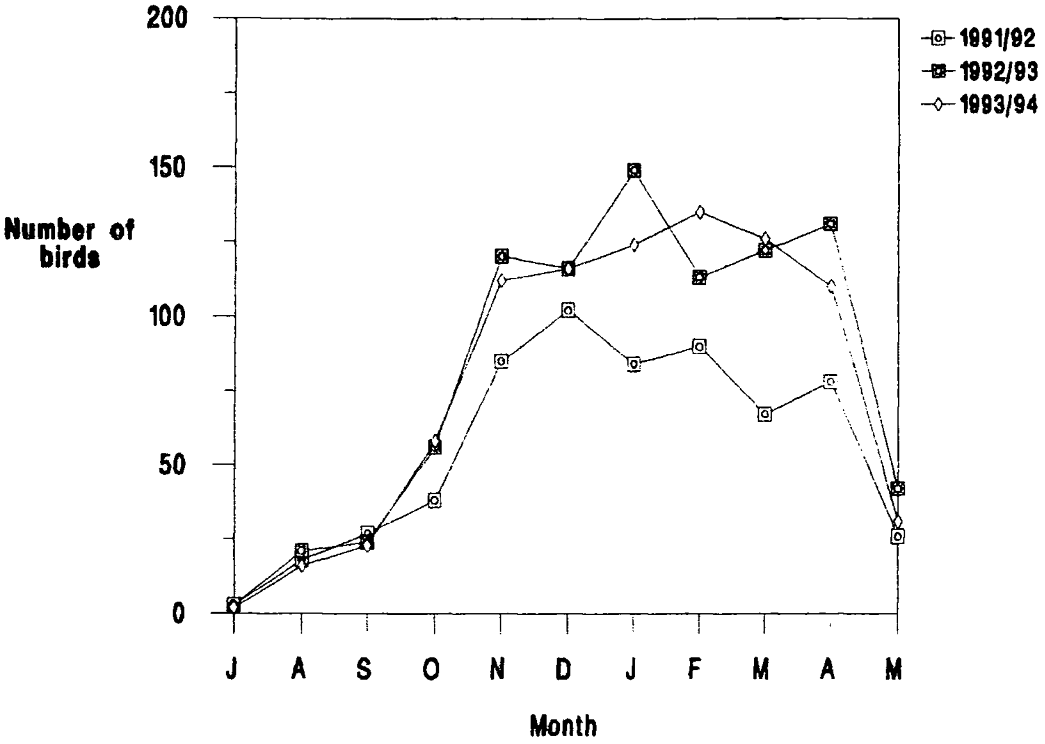


Fig. 4.13. The percentage of low water observations of Purple Sandpipers resident at Hartlepool Headland that were away from the Headland, in relation to season. The number of observations is shown adjacent to each point.

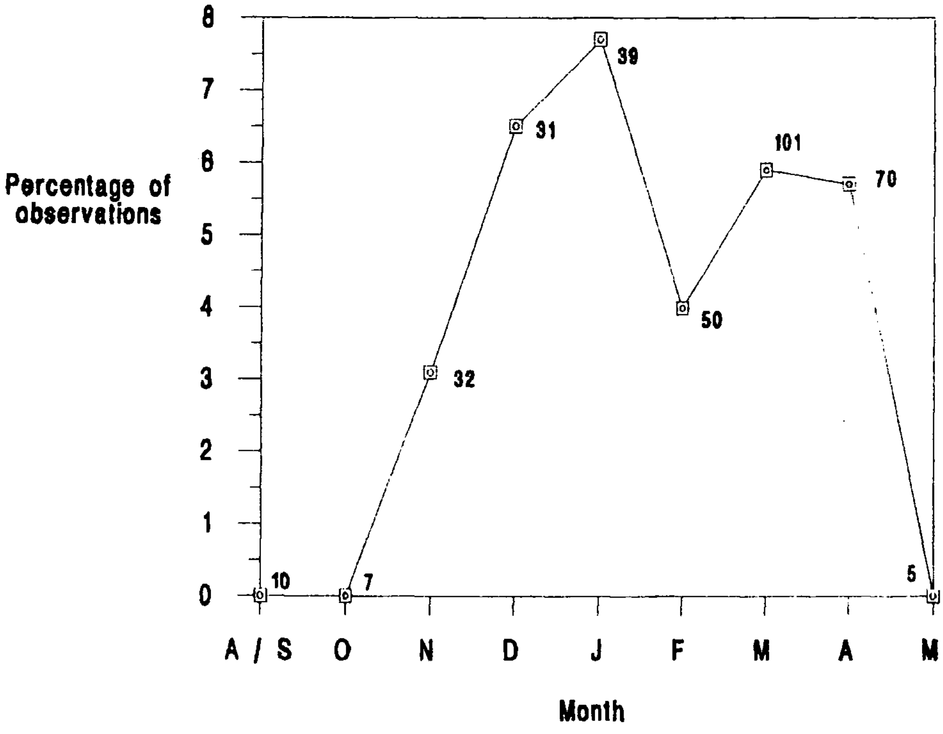


Fig. 4.14 shows the pattern of use by Purple Sandpipers of one part of the Headland, Parton, over a tidal cycle; (data from 26 November 1991). The pattern seen is similar to that shown by Turnstones: numbers rose as the tide ebbed, reaching a peak 2 hours before low water and then dropping slightly. Numbers again rose to a peak 1.5 hours after low water as birds moved in from adjacent areas; they then fell as the tide came in.

The numbers of Purple Sandpipers seen feeding at low water in each part of the study area were also largely determined by the height of low tide (see Appendix 10 for graphs). The numbers of Purple Sandpipers recorded at low water on Hartlepool Headland were, as with Turnstones, greatest when the low tide level was in the middle of its range. There was not such a pronounced decrease in numbers on neap tides however, particularly in winter 1992/93. In spite of this, Purple Sandpipers resident on the Headland were seen away from the Headland, during the low water period, on higher average low tide levels than when they were seen on the Headland (Fig. 4.15; $t = 2.401$, d.f. = 315, $P < 0.05$). The numbers of Purple Sandpipers recorded at low water between Inscar and North Gare breakwater were, as with Turnstones, greatest on neap tides when the offshore Long Scar rocks remained flooded. Few Purple Sandpipers were, in contrast recorded between Steetley and Blackhall.

Over low water Purple Sandpipers fed primarily on musselbeds, with rocks, algae, live wrack and strand only used infrequently (Table 4.2). Exposed rock and algae are found higher up the shore and are used more often on flood and ebb tides. There was a highly significant difference in habitat use at low water between Purple Sandpipers and Turnstones (combining live and dead wrack, strand and grass: $\chi^2 = 97.976$, d.f. = 4, $P < 0.001$). Purple Sandpipers were found more often on mussel beds and algae and Turnstones more often on dead and live wrack and strand (and grass).

Fig. 4.14. Purple Sandpiper numbers at Parton over the low water period 26 November 1991.

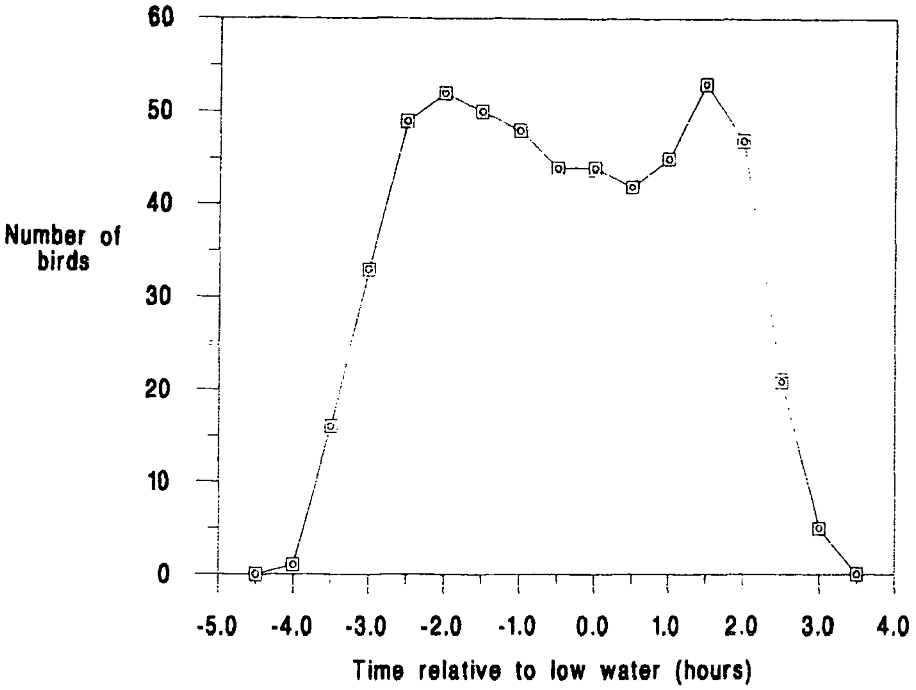
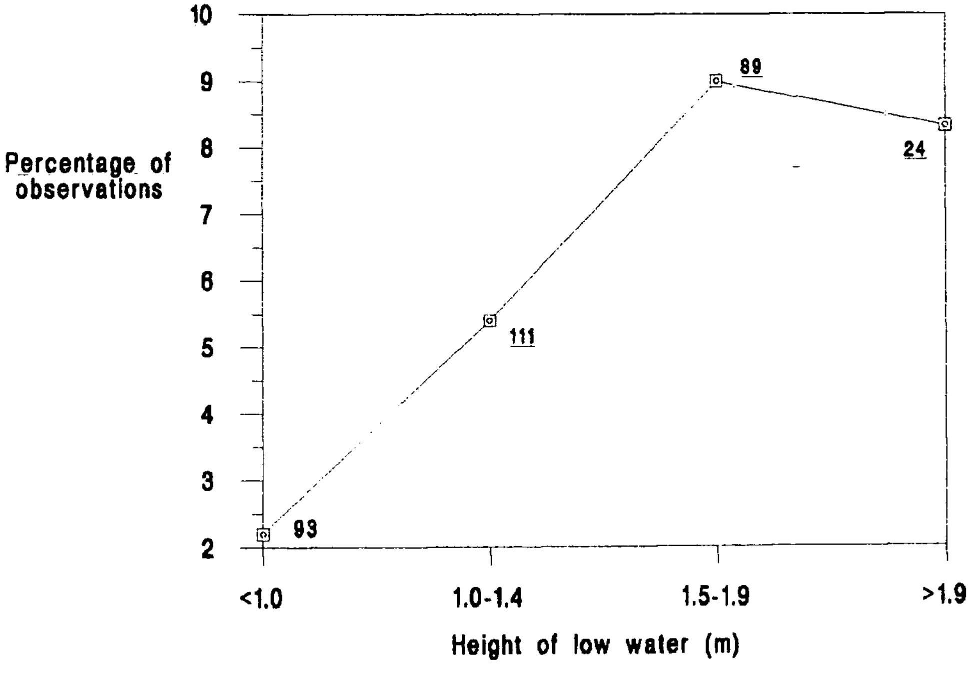


Fig. 4.15. The percentage of observations of Purple Sandpipers resident at Hartlepool Headland that were away from the Headland, in relation to the height of low water. The number of observations is shown adjacent to each point.



4.3.1.2.2. Time of arrival at the West Harbour roost and post-roosts.

After leaving feeding areas, some birds used pre-roosts (at the western edge of 'Throston', the eastern edge of 'Lighthouse north' and Inscar) before moving to West Harbour. Unfortunately, no quantitative data are available from these sites to indicate their pattern of use.

Fig. 4.16 shows how the median time of arrival of Purple Sandpipers at the West Harbour roost varied according to the height of high water. Birds arrived on average, earliest relative to high water on spring tides and latest on neaps ($r = 0.616$, d.f. = 14, $P < 0.01$ one-tailed):

Time of Arrival = -103.405 + 46.081 Height of High Water

where time of arrival is in minutes before high water and the height of high water is in metres.

After taking this variation into account, there was significant seasonal variation in the median time of arrival of Purple Sandpipers at the roost (Fig. 4.17; using a cubic equation between the residuals of the above equation and the date in days, where 1 = 22 August: $r^2 = 0.585$; $F_{3,12} = 5.63$, $P < 0.05$):

$$y = 34.187 - 1.971x + 0.021x^2 - 5 \times 10^{-5}x^3$$

where y is the time of arrival in minutes before high water and x is the date in days.

Purple Sandpipers arrived at the West Harbour roost early, relative to high water, in August, but much later as autumn progressed. Arrival times were latest around early November. After November, Purple Sandpipers again tended to arrive increasingly early relative to high water. From March, this trend reversed, with birds arrive increasingly late again.

Fig. 4.16. The median time of arrival of Purple Sandpipers at the West Harbour roost in relation to the height of high water.

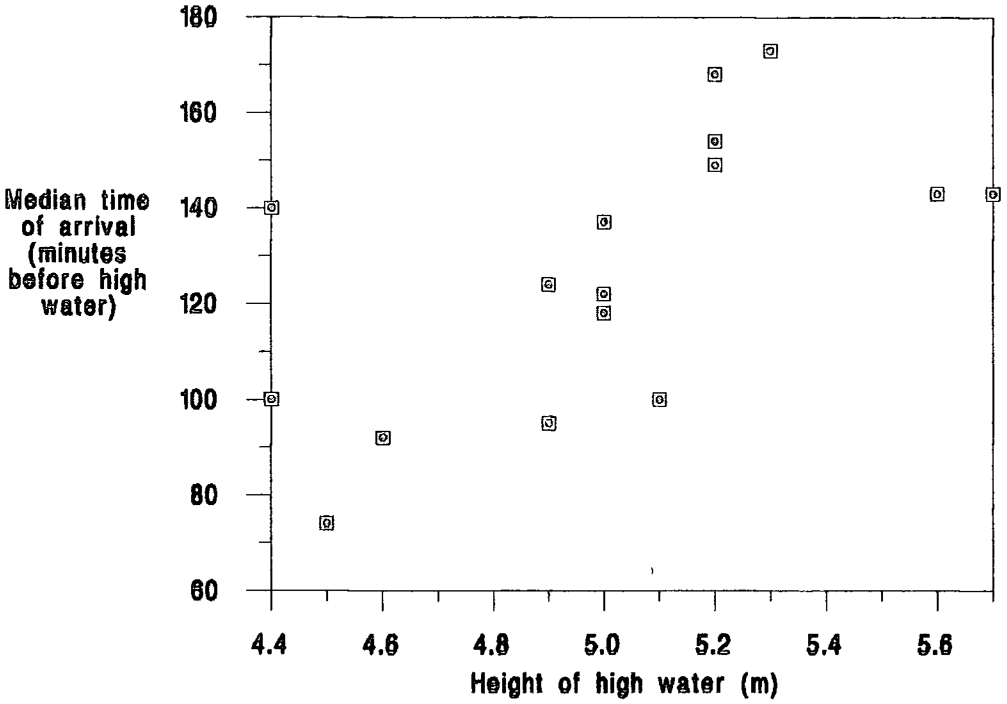


Fig. 4.17. The median time of arrival of Purple Sandpipers at the West Harbour roost in relation to season, using residuals from equation with height of high water.

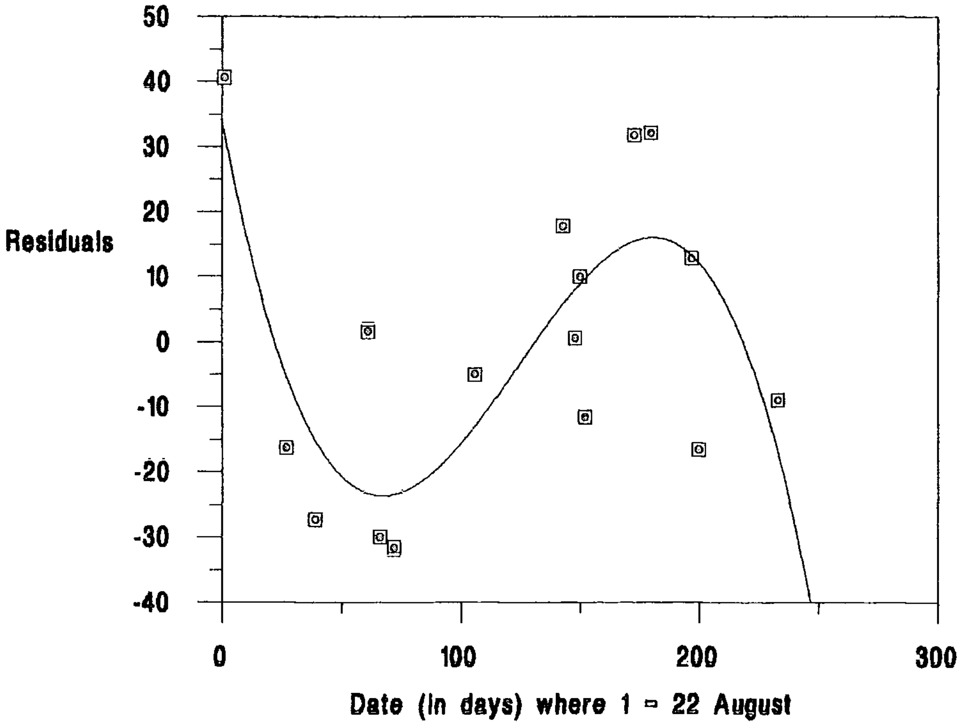
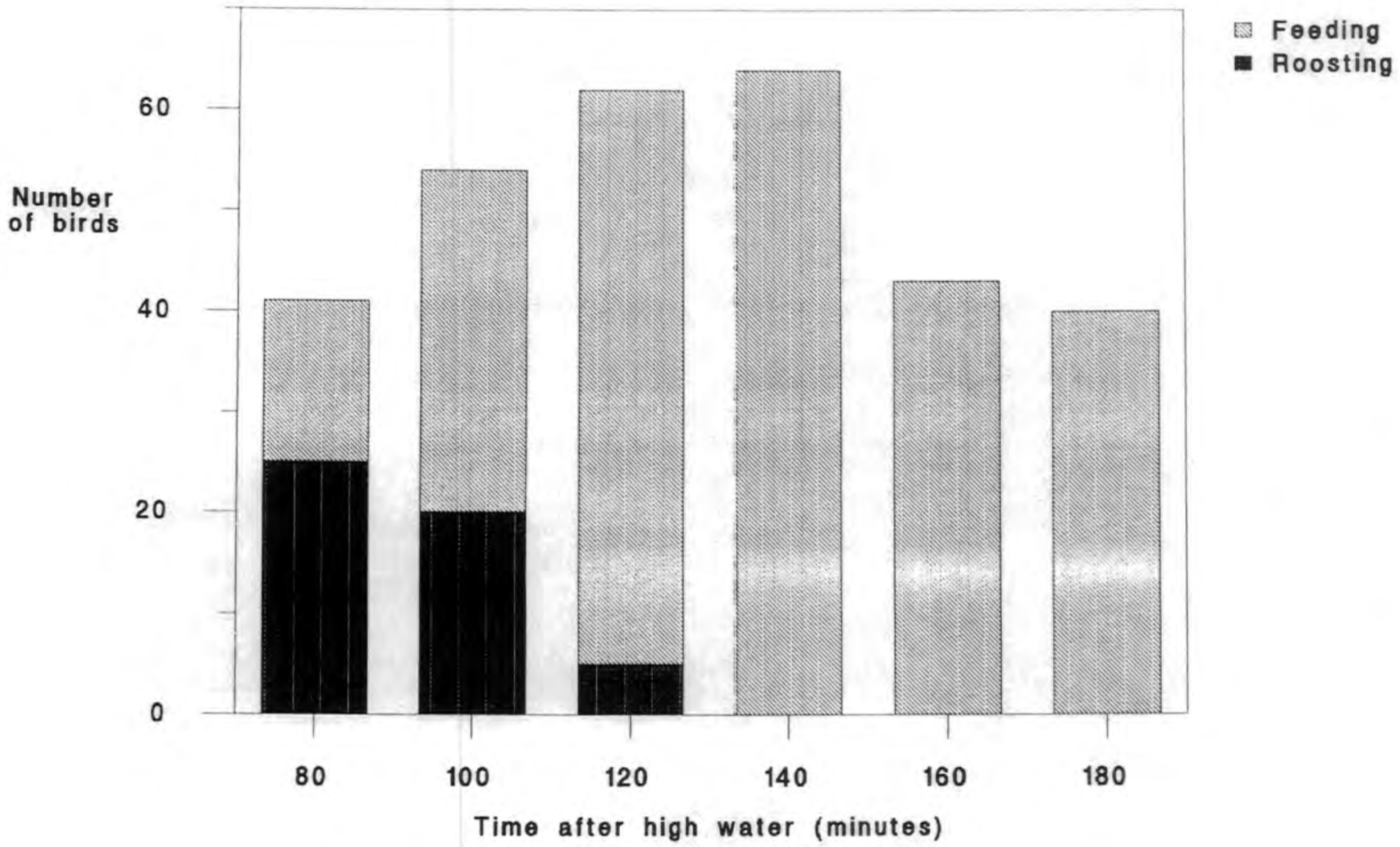


Fig. 4.18. Numbers of Purple Sandpipers roosting and feeding at the Throston 'post-roost' 12 December 1991.



Purple Sandpipers often did not move directly from West Harbour to their low water home ranges, but stopped to use 'post-roosts' or to feed in other areas prior to the uncovering of the lower shore. Post-roost sites were typically the same as those used previously as pre-roosts. Fig. 4.18 shows how Purple Sandpiper numbers varied after high water at the post-roost site on the eastern edge of Throston; (data from 12 December 1991). Numbers increased to a peak two hours after high water, before decreasing to a stable level by one hour later. The proportion of birds that were roosting was greatest closest to high water. The birds that remained three hours after high water were all feeding.

4.3.2. Individual behaviour.

4.3.2.1. Turnstone.

4.3.2.1.1. Intraspecific feeding aggression.

Encounters over food (either for items of food or for feeding sites) comprised 95.2% (n = 270) of all aggression recorded between Turnstones in feeding flocks (data from August 1993 to May 1994). The remaining 4.8% of encounters were due to infringements of individual distance.

The majority of encounters were simple threat displays; pecks and higher intensity displays, *i.e.* chases, peck-chases and fights were comparatively less frequent (Table 4.3). Only 5.5% (n = 1059) of encounters were lost by the initiator, but these included a higher than expected proportion of chases, peck-chases and fights (combining chases, peck-chases and fights as high intensity encounters: $\chi^2 = 10.312$, d.f. = 2, $P < 0.01$).

The intensity of aggression varied seasonally (Table 4.4; combining chases, peck-chases and fights: $\chi^2 = 35.569$, d.f. = 4, $P < 0.001$). Pecks were less frequent in autumn and more frequent in spring. The intensity of aggression also varied with feeding habitat (Table 4.5; combining algae and exposed rock; chases, peck-chases and fights: $\chi^2 = 41.867$, d.f. = 10, $P < 0.001$). Pecks were less frequent when Turnstones were feeding on the strand and

Table 4.3. The intensity of aggression of Turnstones in feeding flocks; (data from September 1991 to May 1994).

	Threat		Peck	Chase	Peck-chase	Fight
	Tail down to tail up	Tails down				
Initiator won	783	35	118	53	10	2
Initiator lost	0	44	4	6	1	3
Total	783 (73.9)	79 (7.5)	122 (11.5)	59 (5.6)	11 (1.0)	5 (0.5)

Figures represent frequencies of encounters recorded; figures in parentheses are percentages of the total number of encounters recorded.

Table 4.4.. The intensity of aggression of Turnstones in feeding flocks and season; (data from September 1991 to May 1994).

Season	Threat	Peck	Chase	Peck-chase	Fight
Autumn	313	28	25	7	3
Winter	417	49	25	3	2
Spring	132	45	9	1	0

Figures represent frequencies of encounters recorded.

Table 4.5. The intensity of aggression of Turnstones in feeding flocks and habitat; (data from September 1991 to May 1994).

Habitat	Threat	Peck	Chase	Peck-chase	Fight
Strand	202	15	10	0	1
Dead wrack	109	10	7	1	1
Live wrack	41	3	1	1	0
Musselbed	299	41	28	9	2
Grass	161	48	9	0	1
Algae	25	3	1	0	0
Exposed rock	19	2	2	0	0

Figures represent frequencies of encounters recorded. Within the study area, 'algae' typically occurred amongst areas of 'exposed rock' in the upper intertidal; due to the small sample sizes in both habitats, data from the two are combined in the analysis.

Table 4.6. The intensity and cause of aggression of Turnstones in feeding flocks; (data from August 1993 to May 1994).

	Threat	Peck	Chase	Peck-chase	Fight
Food	235	13	8	1	0
Individual distance	7	0	4	1	1

Figures represent frequencies of encounters recorded.

musselbeds and much more frequent when they were feeding on grass; chases, peck-chases and fights were more frequent when Turnstones fed on musselbeds. There were insufficient data to investigate whether the intensity of aggression varied between aggression over food and that caused by infringements of individual distance (Table 4.6).

The rate of intraspecific aggression resulting from encounters over food varied between 0 and 8 encounters per five minute period per individual Turnstone and increased as conspecific flock size became greater (Fig. 4.19; $r^2 = 0.092$; t (flock size) = 3.470, d.f. = 119, $P < 0.001$):

$$\ln(\text{Aggression Rate} + 1) = 0.544 + 0.017 \text{ Flock Size}$$

No significant trends were detected in multiple regression between the intraspecific rate of encounters over food and the date relative to midwinter ($t = 1.270$, $n = 113$, n.s.), the height of low tide ($t = -0.424$, n.s.), the time relative to low water ($t = 1.947$, n.s.) or wind speed ($t = 0.700$, n.s.).

Individual aggression rates in encounters over food varied according to habitat (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 16.830$, d.f. = 5, $P < 0.01$). Aggression rates were highest when Turnstones were foraging on the strand and dead wrack and lowest when Turnstones were foraging on algae.

The rate of intraspecific encounters resulting from infringements of individual distance varied between 0 and 3 encounters per five minute period per individual Turnstone and was correlated with date (Fig. 4.20; $r^2 = 0.065$; t (date) = -2.881, d.f. = 119, $P < 0.01$):

$$\ln(\text{Aggression Rate} + 1) = 0.028 - 7.6 \times 10^{-4} \text{ Date}$$

where the date was measured as days before (-) or after (+) midwinter.

Encounters caused by infringements of individual distance were more frequent in autumn and less frequent in spring. No significant trends were detected between the

Fig. 4.19. The relationship between the rate of intraspecific aggression over food per individual Turnstone and conspecific flock size.

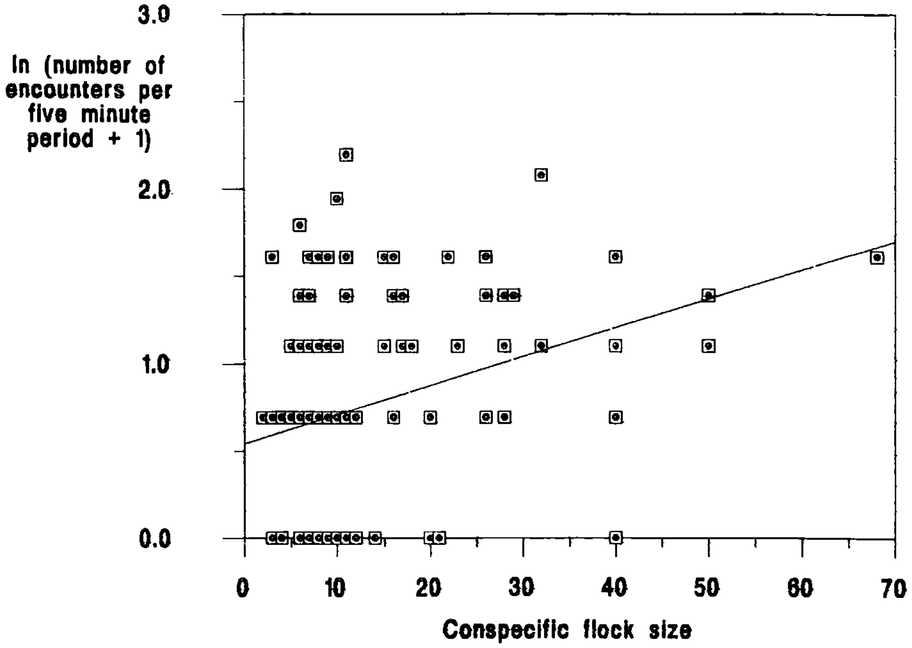
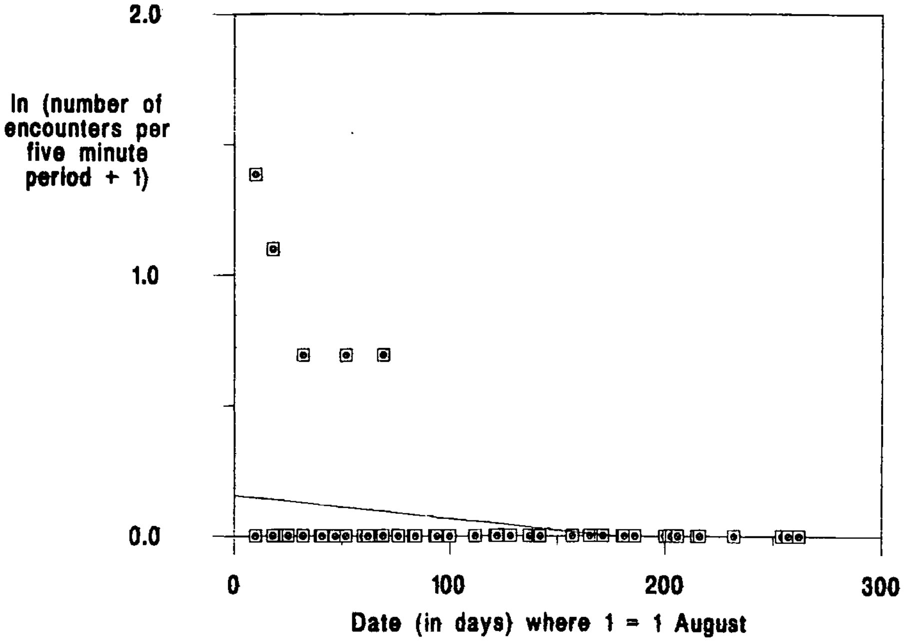


Fig. 4.20. The relationship between the rate of intraspecific aggression over infringements of individual distance per individual Turnstone and date.



intraspecific rate of encounters caused by infringements of individual distance and flock size ($t = 0.677$, $n = 113$, n.s.), height of low tide ($t = -1.384$, n.s.), time relative to low water ($t = -1.053$, n.s.) or wind speed ($t = -1.241$, n.s.).

The rate of encounters resultant from infringements of individual distance also varied according to habitat (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 11.590$, d.f. = 5, $P < 0.05$). Individual aggression rates were highest when Turnstones were feeding on dead and live wrack and lowest on rock and algae.

4.3.2.1.2. Turnstone dominance hierarchies on low water feeding areas.

Individual feeding dominance was calculated as the percentage of encounters won by an individual (Ens and Goss-Custard 1984). Data for each individual were taken from the ebb, low water and flood periods only and from autumn to spring each year. Dominance hierarchies were calculated for Turnstones in each of the two main feeding areas in the study site: Hartlepool Headland and the area between West Harbour and North Gare breakwater and are shown for each of the three years of study in Appendix 11. (Insufficient data were available for dominance hierarchy analysis in the latter area in 1993/94). On Hartlepool Headland in 1991/92, only 1 of 5 interactions between colour-ringed individuals went against rank order, in 1992/93, none of 10 and in 1993/94 only 5 of 21. Between West Harbour and North Gare in 1991/92, only 1 of 6 interactions between colour-ringed individuals went against rank order and in 1992/93, none of 11 (combining areas and years: Sign Test $x = 7$, $n = 53$, $P < 0.001$). Turnstone dominance hierarchies on feeding grounds were thus very stable within years. Between years, there was a positive, though insignificant, correlation between the dominance of individuals on their home feeding areas (for 1991/92 and 1992/93: $r_s = 0.347$, $n = 16$, $P < 0.10$ one-tailed; for 1992/93 and 1993/94: $r_s = 0.611$, $n = 8$, $P < 0.10$ one-tailed). As dominance hierarchies differed slightly between years, and as shown later, individuals tended to be of greater dominance in their second than first-winter (and increase in dominance with age), individual dominance was calculated separately for each year of study.

The dominance of individuals on their home feeding areas was independent of body mass (for 1991/92: $r_s = -0.338$, $n = 10$, n.s.; for 1993/94: $r_s = 0.090$, $n = 7$, n.s.) and wing-length (for 1991/92: $r_s = -0.311$, $n = 8$, n.s.; for 1993/94: $r_s = 0.200$, $n = 5$, n.s.). (Only individuals caught and measured on the same date were used in these analyses; data for 1991/92 are from 26 February 1992 and for 1993/94 from 23 September 1993).

The dominance ranks of residents can be compared to those of individuals that were classed as visitants to their area, (*e.g.* 'West Harbour to North Gare' and 'North and South' residents are classed as visitants to the Headland, in addition to the visitants to the study area as a whole). On Hartlepool Headland, residents were of higher rank than visitants in 1992/93 (Mann-Whitney $z = 2.005$, $P < 0.05$ one-tailed, n (residents) = 16, n (visitants) = 6), though not in 1991/92 ($z = 0.061$, n.s., n (residents) = 12, n (visitants) = 4) nor 1993/94 ($z = 0.486$, n.s., n (residents) = 17, n (visitants) = 9). Residents and visitants were of similar rank in the area between West Harbour and North Gare (for 1991/92: $z = 1.331$, n.s., n (residents) = 11, n (visitants) = 3; for 1992/93: $z = 0.848$, n.s., n (residents) = 10, n (visitants) = 3). Combining areas and years, colour-ringed residents won 10 of 14 interactions with visitants to their area (Sign Test $x = 4$, $n = 14$, $P < 0.10$). On Hartlepool Headland, adult resident Turnstones were of higher dominance rank than first-winter residents in 1993/94 (Mann-Whitney $z = 2.524$, $P < 0.01$ one-tailed, n (adults) = 14, n (first-winter) = 3), though not in late winter / early spring 1992 ($z = 0.280$, n.s., n (adults) = 9, n (first-winter) = 3). Between West Harbour and North Gare adult residents were of higher dominance rank than first-winter residents in late winter / early spring 1992 ($z = 1.944$, $P < 0.05$ one-tailed, n (adults) = 8, n (first-winter) = 3). Combining data from all years, first winter Turnstones won only 4 of 96 interactions with adults whilst feeding (Sign Test $P < 0.001$). The dominance of adults over first-winter birds may either be due to size differences between the two classes or the greater experience of adults in aggressive encounters. If experience is important and is only gained gradually, it is possible that second-winter birds may also be subordinant to older birds. Second-winter resident Turnstones however were of similar dominance rank to adult residents in 1992/93 on both the Headland (Mann-Whitney $z = 0.535$, n.s., n (adults) = 6, n (second-winter) = 9) and in the area between West Harbour and North Gare ($z = 0.457$, n.s., n (adults) = 7, n (second-winter) = 3) Individual Turnstones tended to be of greater dominance on their home feeding areas in their second winter than in their first, though not significantly so (Wilcoxon $T = 4$, $n = 6$, $P < 0.10$). Individual dominance on home feeding areas increased significantly with age (Appendix 12; $r_s = 0.381$, $n = 38$, $P < 0.01$).

There was no relationship between an individual's dominance on its home feeding area and whether it survived that winter (for 1992/93: Mann-Whitney $z = 0.428$, n.s.) or whether it returned after the following summer (for summer 1992: $z = 0.666$, n.s.; for summer 1993: $z = 0.143$, n.s.); (for data see Appendix 13).

4.3.2.1.3. Return dates of individual Turnstones.

Turnstones, (excluding first-summer individuals), returned to Hartlepool between late July and early October each year, with peak arrival in August (Fig. 4.21). There was no correlation between the arrival dates of individuals in 1992 and 1993 ($r_s = 0.170$, $n = 12$, n.s.). The median arrival date however did not differ between years (median arrival date in 1992 = 5 August, $n = 25$; median arrival date in 1993 = 10 August, $n = 25$; Mann-Whitney $z = 0.479$, n.s.).

In 1992, there was a correlation between an individual resident's dominance on its home feeding area the previous winter and its return date, with the most dominant individuals arriving back the latest (Fig. 4.22; $r_s = 0.622$, $n = 15$, $P < 0.05$). There was no such correlation in 1993 (Fig. 4.23; $r_s = 0.032$, $n = 15$, n.s.).

Fig. 4.21. The timing of the return of adult Turnstones to the study area after the breeding season. The figure shows the number of residents returned on certain dates as a percentage of the total number that returned.

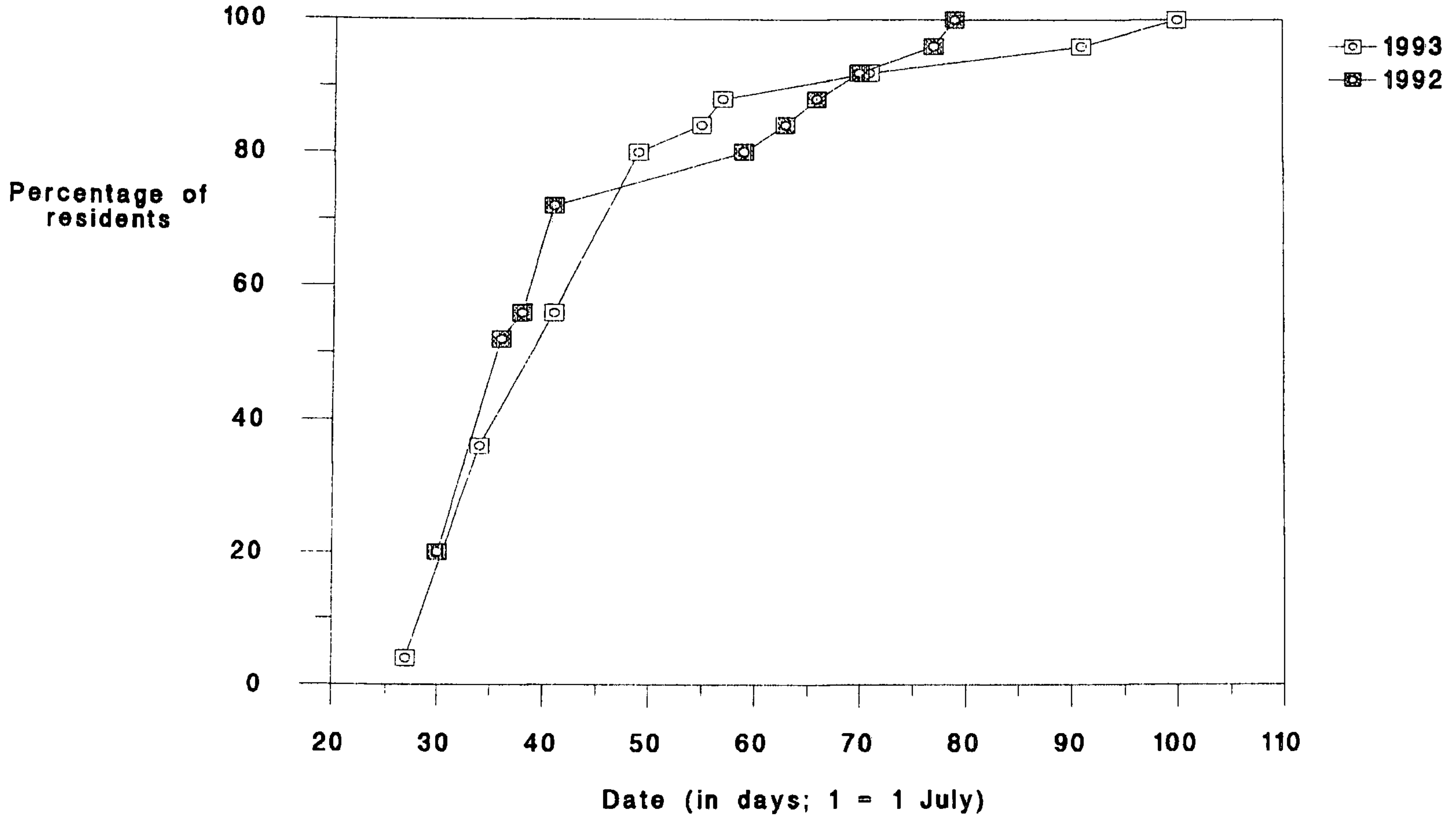


Fig. 4.22. The relationship between the return dates of adult Turnstones to Hartlepool in autumn 1992 and their dominance the previous winter.

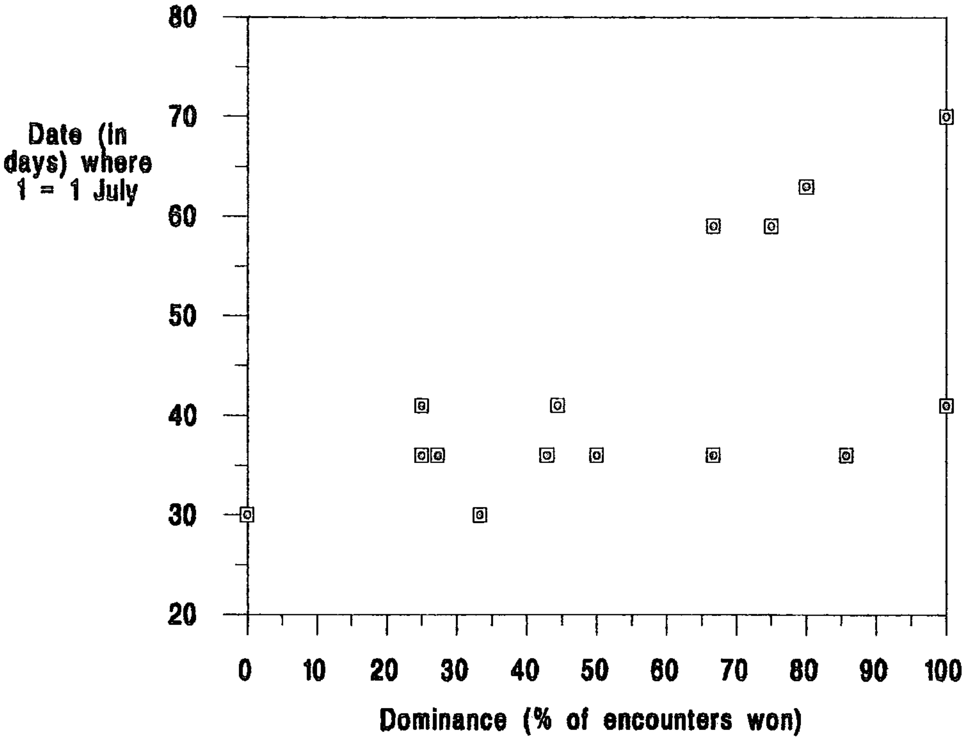
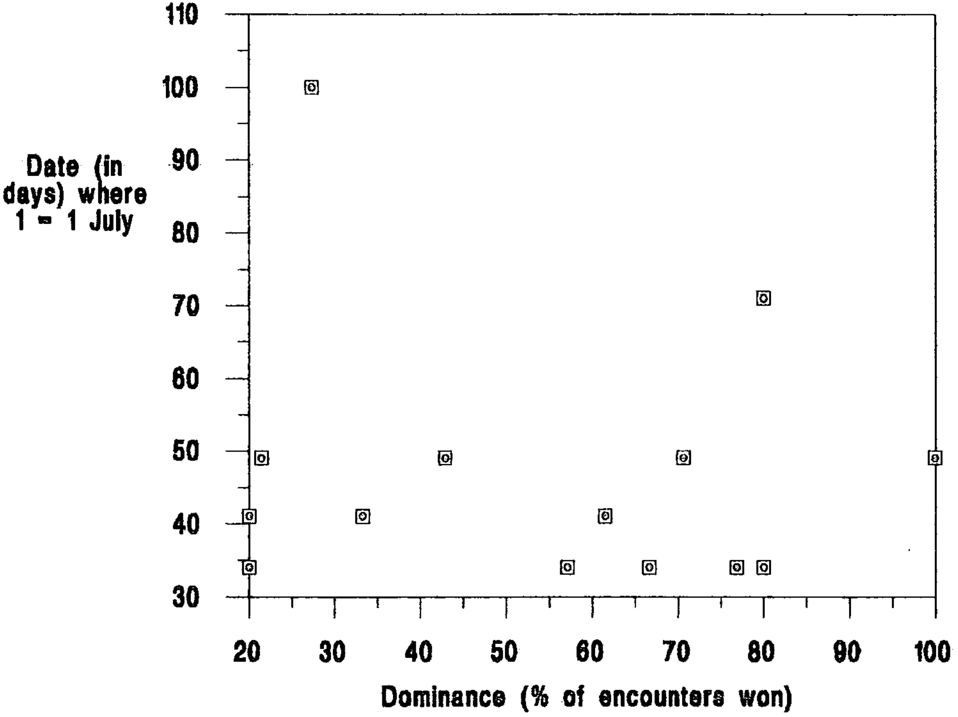


Fig. 4.23. The relationship between the return dates of adult Turnstones to Hartlepool in autumn 1993 and their dominance the previous winter.



4.3.2.1.4. Turnstone low water home ranges.

Home ranges were calculated for 13 Turnstones which were resident on Hartlepool Headland in each year that they were known to be alive and that were seen a minimum of 20 times on low water surveys of the study area. Data are combined for up to three years for each individual as there was no evidence that any of the individuals shifted their range between years. (Data for two individuals came from one year only however, one a first-winter individual). There was no correlation between the number of sightings of an individual (range of 23 to 70 sightings) and its estimated home range size ($r_s = 0.071$, $n = 13$, n.s.).

Fig. 4.24 shows the frequency distribution of home range sizes for Turnstones (together with that for Purple Sandpipers). Ranges varied from between 2.2 and 29.5ha in size, though the distribution was positively skewed with a median of only 6.6ha. The smallest range was that of the first-winter individual. Although most individuals were faithful to one small section of the coast, individuals were occasionally sighted away from the Headland, notably on neap tides (see section 4.3.1.1). The individuals with the largest ranges were those that were sighted away from the Headland most frequently, typically around West Harbour and Seaton Sands, although in one case an individual was seen on rocks by North Gare breakwater. An example of the distribution of low water sightings of one individual Turnstone is shown in Fig. 4.25. This individual's range centred on a cluster of sightings at Parton and Throston on the Headland, though it also included a smaller activity centre formed around sightings at West Harbour. The disjunct distribution of these sightings helps validate the use of the harmonic mean measure of home range estimation, as this technique may create more than a single activity centre.

The relationship between the home range size and feeding dominance rank of Headland resident Turnstones was investigated using data from 1992/93 and using only those individuals present throughout that winter. No correlation was found between home

Fig. 4.24. Home range sizes of Turnstones and Purple Sandpipers resident at Hartlepool Headland.

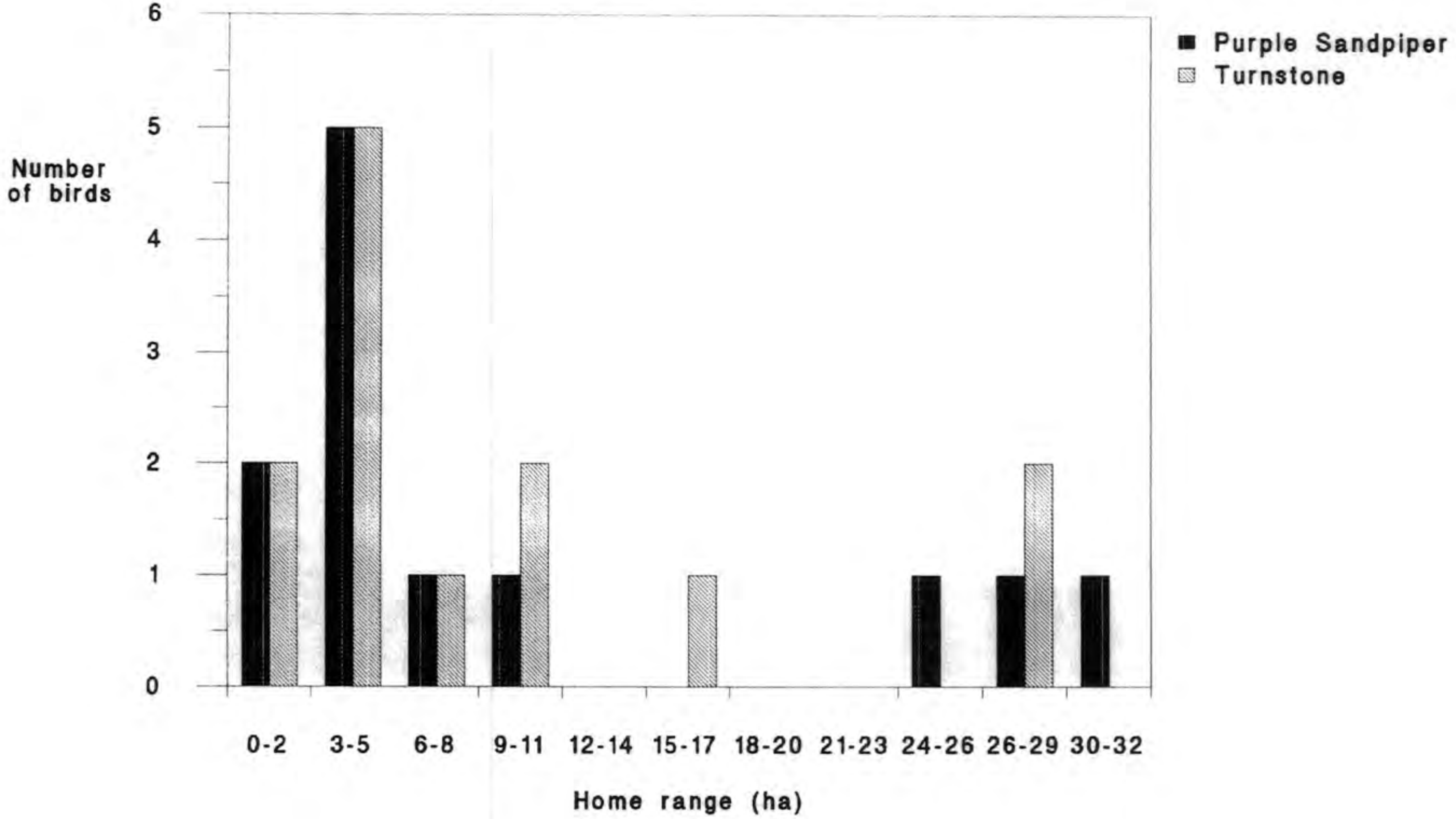


Fig.4.25. An example of the low water sightings of an individual Turnstone, used for the calculation of home range

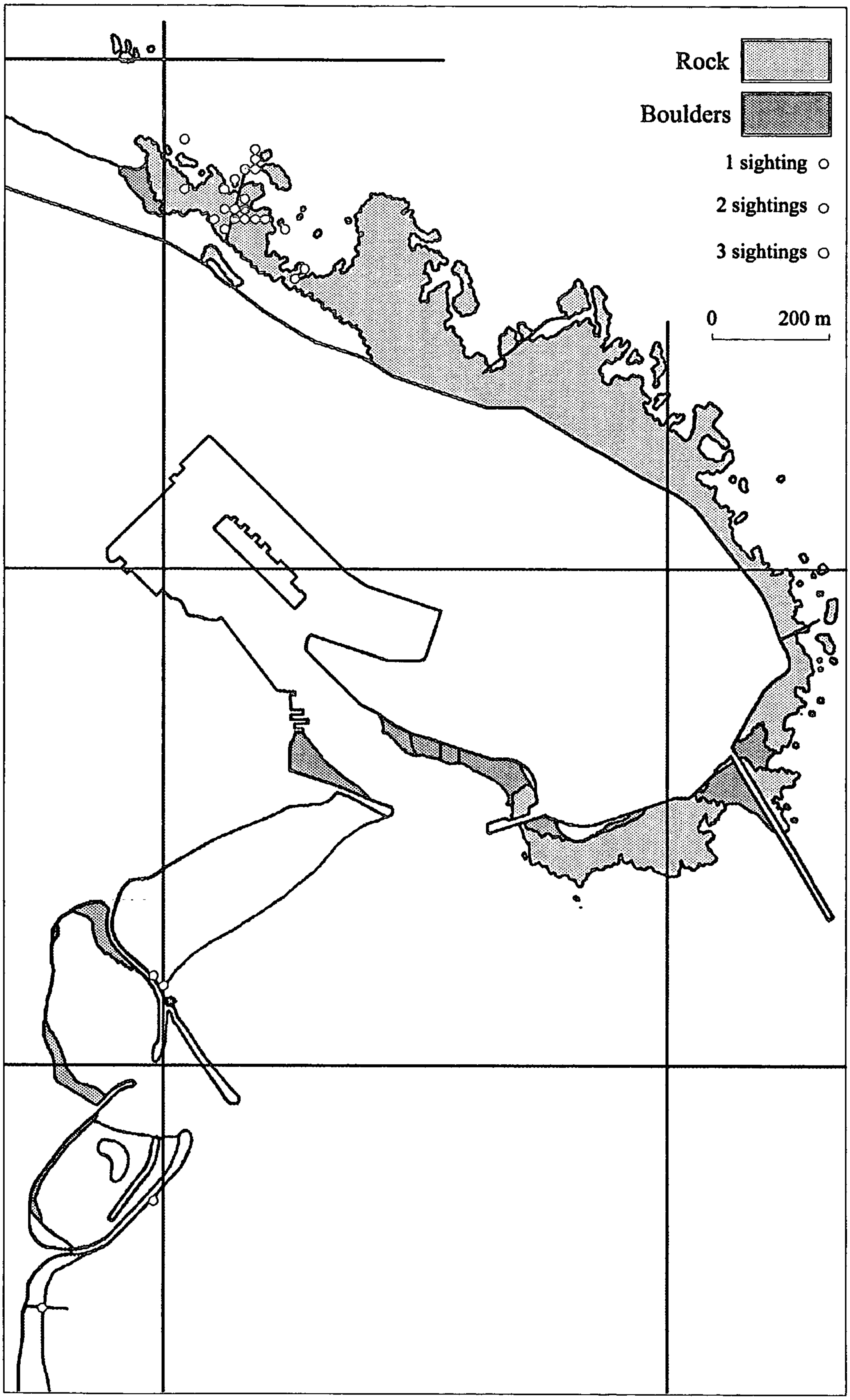
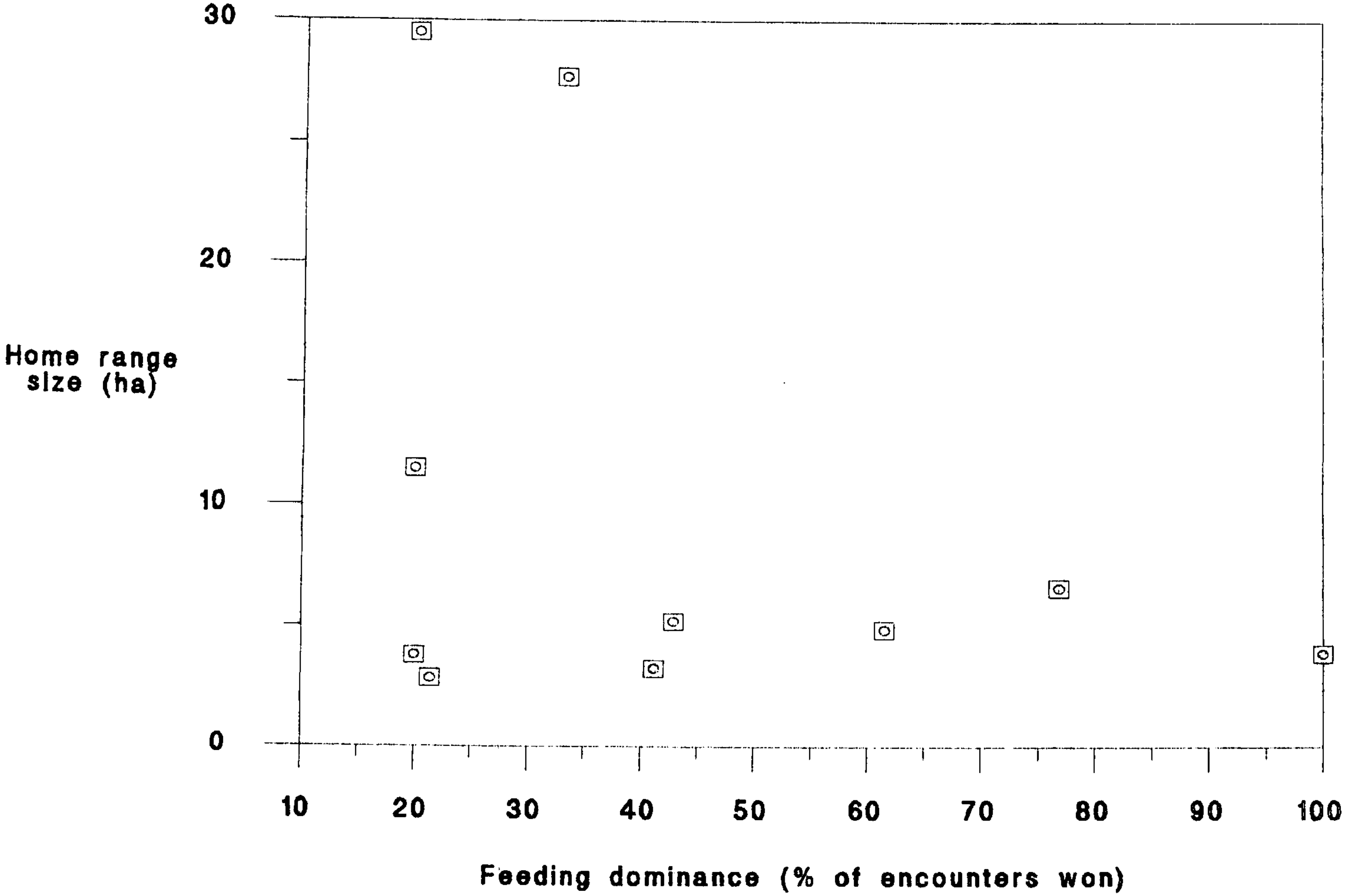


Fig. 4.26. Turnstone home range size and its relationship to dominance.



range size and feeding dominance for these individuals (Fig. 4.26; r_s = -0.178, n = 10, n.s.), though the three largest ranges were all of low ranked individuals.

4.3.2.2. Purple Sandpiper.

4.3.2.2.1. Intraspecific feeding aggression.

Encounters over food (either for items of food or for feeding sites) comprised 79.7% (n = 192) of all aggression recorded between Purple Sandpipers in feeding flocks. The remaining 20.3% of encounters were due to infringements of individual distance. The proportion of encounters attributable to individual distance was significantly higher for Purple Sandpipers than for Turnstones (χ^2 = 25.451, d.f. =1, $P < 0.001$). The reasons for this difference and the possible importance of density in determining the frequency of encounters over individual distance are discussed later.

The majority of encounters were simple threat displays with the wings held in (Table 4.7). Threats with the wings held out, and higher intensity displays, *i.e.* pecks, chases and peck-chases were comparatively less frequent and no fights were recorded. Only 1.6% of encounters were lost by the initiator (n = 387), a significantly lower proportion than for Turnstones (χ^2 = 9.422, d.f. = 1, $P < 0.01$).

There was no difference in the intensity of aggression recorded in encounters over food and those caused by an infringement of individual distance (Table 4.8; combining wings out to in and wings out as threats with wings out; pecks, chases and peck-chases as higher intensity displays: χ^2 = 0.065, d.f. = 2, n.s.). The intensity of aggression similarly did not vary seasonally (Table 4.9; combining wings out to in and wings out; pecks, chases and peck-chases; autumn and winter: χ^2 = 2.022, d.f. = 2, n.s.). The intensity of aggression did however vary according to foraging habitat (Table 4.10; combining wings out to in and wings out; pecks, chases and peck-chases; live wrack and mussels; algae and exposed rock: χ^2 = 9.491, d.f. = 2, $P < 0.01$). Threats with wings out, pecks, chases and peck-chases were more frequent when Purple Sandpipers were feeding on live wrack and musselbeds and simple threats with the wings held in more frequent on exposed rock and algae.

Table 4.7. The intensity of aggression of Purple Sandpipers in feeding flocks; (data from February 1992 to May 1994).

	Threat			Peck	Chase	Peck-chase	Fight
	Wings in	Wings out to in	Wings out				
Initiator won	282	13	3	69	12	2	0
Initiator lost	5	1	0	0	0	0	0
Total	287 (74.2)	14 (3.6)	3 (0.8)	69 (17.8)	12 (3.1)	2 (0.5)	0

Figures represent frequencies of encounters recorded; figures in parentheses are percentages of the total number of encounters recorded.

Table 4.8. The intensity and cause of aggression of Purple Sandpipers in feeding flocks; (data from August 1993 to May 1994).

	Wings in	Wings out to in	Wings out	Peck	Chase	Peck-chase
Food	109	6	1	37	0	0
Individual Distance	27	1	1	7	3	0

Figures represent frequencies of encounters recorded.

Table 4.9. The intensity of aggression of Purple Sandpipers in feeding flocks and season; (data from February 1992 to May 1994).

	Wings in	Wings out to in	Wings out	Peck	Chase	Peck-chase
Autumn	15	1	0	5	1	0
Winter	197	9	1	47	11	2
Spring	75	4	2	17	0	0

Figures represent frequencies of encounters recorded.

Table 4.10. The intensity of aggression of Purple Sandpipers in feeding flocks and habitat; (data from February 1992 to May 1994).

	Wings in	Wings out to in	Wings out	Peck	Chase	Peck-chase
Live wrack	10	0	0	3	0	0
Musselbeds	224	14	3	61	12	1
Algae	35	0	0	3	0	1
Exposed rock	18	0	0	2	0	0

Figures represent frequencies of encounters recorded. 'Algae' and 'exposed rock' are combined in the analysis for the reasons given in 4.3.2.1.1; live wrack typically occurred within musselbeds in the lower intertidal and the two habitats are also combined in the analysis.

The rate of intraspecific encounters over food, which varied between 0 and 3 encounters per five minute period per individual Purple Sandpiper, increased as flock size became greater (Fig. 4.27; $t = 3.501$, d.f. = 257, $P < 0.001$) and decreased with time relative to low water (Fig. 4.28; $t = -3.384$, d.f. = 257, $P < 0.001$):

ln (Aggression Rate + 1) = 0.157 + 0.015 Flock Size - 0.001 Time

where Time is in minutes before (-) or after (+) low water; ($r^2 = 0.090$).

No significant trends were detected in multiple regression between the intraspecific rate of encounters over food and the date relative to midwinter ($t = 0.252$, $n = 252$, n.s.), the height of low water ($t = -0.868$, n.s.) or wind speed ($t = 1.318$, n.s.).

The aggression rate over food was not dependent upon habitat (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 1.288$, d.f. = 2, n.s.). If flock size and time relative to low water were taken into account, there was also no difference in the aggression rate over food between individuals of small, medium and large bill-length size classes (Kruskal-Wallis $\chi^2 = 2.186$, d.f. = 2, n.s.). (If flock size and time relative to low water were not taken into account however, there was a tendency for the aggression rate to be greatest for medium size classed individuals and less for small and large size classed individuals: Kruskal-Wallis $\chi^2 = 4.728$; d.f. = 2, $P < 0.10$).

The rate of intraspecific encounters resulting from an infringement of individual distance varied between 0 and 3 encounters per five minute period per individual Purple Sandpiper. No correlations were found in multiple regression between this rate and flock size ($t = 1.331$, $n = 260$, n.s.), the date relative to midwinter ($t = -0.656$, n.s.), the height of low water ($t = -1.502$, n.s.), the time relative to low water ($t = 1.807$, n.s.) or wind speed ($t = -0.485$, n.s.). The individual rate of aggression resultant from infringements of individual distance did not vary with habitat (Kruskal-Wallis $\chi^2 = 2.930$, d.f. = 2, n.s.) or according to an individual's bill-length size class (Kruskal-Wallis $\chi^2 = 1.340$, d.f. = 2, n.s.).

Fig. 4.27. The relationship between the rate of intraspecific aggression over food per individual Purple Sandpiper and conspecific flock size.

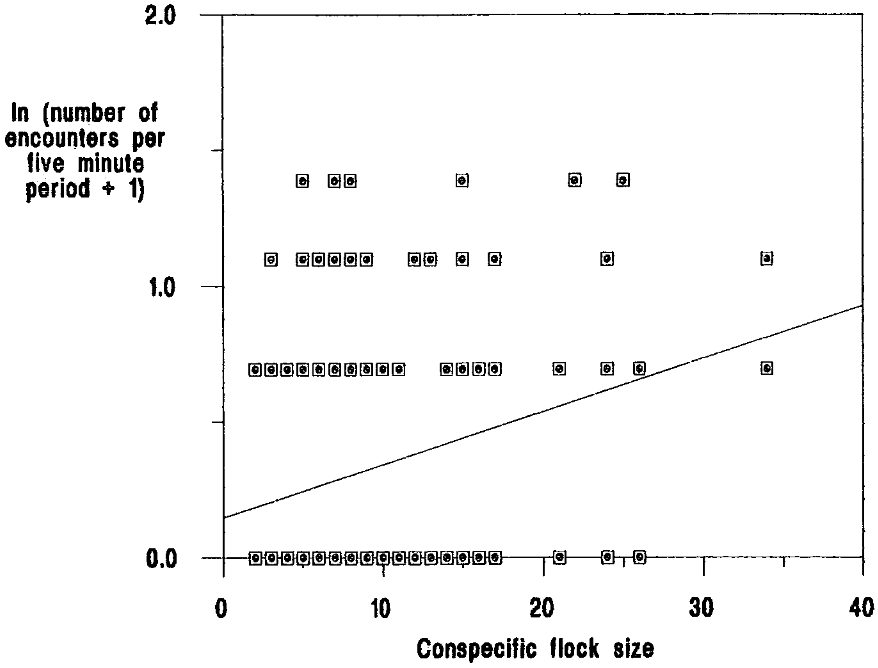
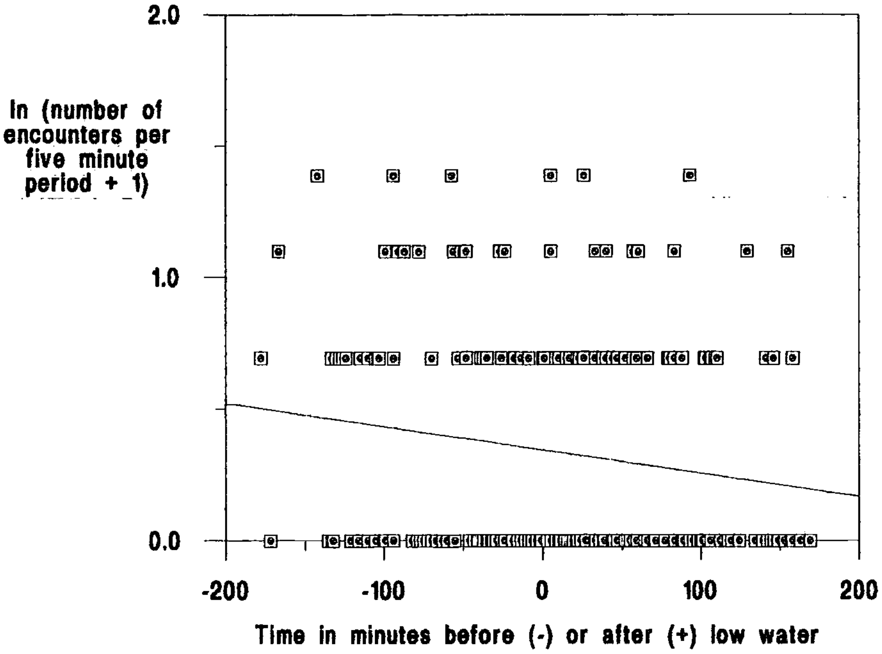


Fig. 4.28. The relationship between the rate of intraspecific aggression over food per individual Purple Sandpiper and time.



4.3.2.2.2. Purple Sandpiper dominance hierarchies on low water feeding areas.

Dominance hierarchies were calculated for Purple Sandpipers in both 1992/93 and 1993/94 in each of the two main feeding areas in the study area: Hartlepool Headland and the area between West Harbour and North Gare breakwater and are shown in Appendix 11. Data were collected from the ebb, low water and flood periods and from only winter and spring each year when the proportions of the two populations of Purple Sandpipers present at Hartlepool were stable. Prior to this, in autumn, the Norwegian population was more abundant in the area (see 3.3.1.1.2 for definition of seasons).

On Hartlepool Headland in 1993/94 none of 7 interactions between colour-ringed individuals went against rank order. Between West Harbour and North Gare, similarly, none of 6 interactions between colour-ringed individuals went against rank order in 1992/93 and only 3 of 18 in 1993/94 (combining areas and years: Sign Test $x = 3$, $n = 31$, $P < 0.001$). Dominance hierarchies were thus very stable within years. Between years there was a positive, though insignificant, correlation between an individual's dominance on its home feeding area ($r_s = 0.667$, $n = 7$, $P < 0.10$ one-tailed). As dominance hierarchies did differ slightly between years, and as shown later for roosting hierarchies, individuals may change dominance between their first and second winter, individual dominance was calculated separately for each year of study.

For Purple Sandpipers, the relationship between body size and dominance was investigated using bill-length size classes. In the present study, bill-length size class was highly significantly positively correlated to body mass and wing-length (see also Summers 1988, Summers *et al.* 1992). For Headland residents in 1992/93, feeding dominance was positively correlated with bill-length size class (Kruskal-Wallis $\chi^2 = 7.443$, d.f. = 2, $P < 0.05$, n (small) = 2, n (medium) = 6, n (large) = 3): individuals of the large bill-length size class were of highest rank and individuals of the small bill-length size class were of lowest rank. In 1993/94 no differences in dominance rank were seen between small and medium size-classed individuals resident on the Headland (Mann-Whitney $z = 0.558$, n.s., n (small) $= 3$, n (medium) $= 9$). Dominance rank was independent of bill-length size class for resident Purple Sandpipers between West Harbour and North Gare in both 1992/93 (Mann-Whitney $z = 0.000$, n.s., n (medium) $= 6$, n (large) $= 2$) and 1993/94 (Kruskal-Wallis $H_{c\ 3,3,1} = 2.370$, n.s.). Combining areas and years, larger size classed individuals won 7 of 14 interactions with smaller size classed individuals (Sign Test n.s.). Within the medium bill-length size class, feeding dominance on home feeding areas was positively correlated with bill-length in 1993/94 ($r_s = 0.587$, $n = 12$, $P < 0.05$ one-tailed), though insignificantly so in 1992/93 ($r_s = 0.491$, $n = 12$, $P < 0.10$ one-tailed). No such relationships were found within the large bill-length size class in 1992/93 ($r_s = 0.5$, $n = 5$, n.s.), nor within the small bill-length size class in 1993/94 ($r_s = 0.029$, $n = 6$, n.s.).

No differences were found in the dominance ranks of residents and visitants on either Hartlepool Headland (for 1992/93: Mann-Whitney $z = 0.726$, n.s., n (residents) $= 11$, n (visitants) $= 1$; for 1993/94 $z = 0.825$, n.s., n (residents) $= 12$, n (visitants) $= 2$) or in the area between West Harbour and North Gare (for 1992/93: $z = -0.257$, n.s., n (residents) $= 8$, n (visitants) $= 4$; for 1993/94: $z = -0.192$, n.s., n (residents) $= 7$, n (visitants) $= 4$). Residents won 8 of 10 encounters with visitants to their area however (Sign Test $P < 0.10$ one-tailed). There was no difference in the dominance of individual Purple Sandpipers on their home feeding areas and in areas away from home (combining data from years: Wilcoxon $T = 7$, $n = 9$, n.s.). One individual with 100% dominance on its home feeding area, however, was seen to lose all of 4 encounters away from home.

There was no difference in the dominance ranks of adult and first-winter Purple Sandpipers resident between West Harbour and North Gare in 1992/93 (Mann-Whitney $z = 0.600$, n.s., n (adult) $= 5$, n (first-winter) $= 3$). Combining areas and years adult Purple Sandpipers won 17 of 26 interactions with first-winter individuals (Sign Test, n.s.). Second-winter resident Purple Sandpipers were of similar dominance rank to older resident adults both on the Headland (Mann-Whitney $z = 0.820$, n.s., n (adult) $= 8$, n (second-winter)

= 3) and between West Harbour and North Gare (z = 1.273, n.s., n (adult) = 6, n (second-winter) = 1). Colour-ringed adult Purple Sandpipers won all of 11 interactions with colour-ringed second winter Purple Sandpipers however (Sign Test $P < 0.001$).

There was a tendency for Purple Sandpipers of high winter feeding dominance not to return after summer, particularly in 1993 (for data see Appendix 13; for summer 1993: Mann-Whitney $z = -1.802$, $P < 0.10$; for summer 1994: $z = -1.025$, n.s.).

4.3.2.2.3. Purple Sandpiper low water home ranges.

Home ranges were calculated for 12 Purple Sandpipers which were resident on Hartlepool Headland in each year that they were known to be alive in the study area and that were seen a minimum of 20 times on low water surveys of the study area. Data are combined for up to three years for each individual as there was no evidence that any of the individuals shifted their range between years. (Data for one individual came from one year only however, its first-winter). As for Turnstones, there was no correlation between the number of sightings of an individual (range of 20 to 45 sightings) and its estimated home range size ($r_S = 0.307$, $n = 12$, n.s.).

The frequency distribution of home range sizes is shown in Fig. 4.24, together with that for Turnstones. Ranges varied from between 1.5 and 32.1ha in size, though the distribution was positively skewed, with a median of only 5.6ha. The range of the first-winter individual was 3.5ha. There was no difference in the home range sizes of Purple Sandpipers and Turnstones (Mann-Whitney $z = 0.136$, n.s.). As with Turnstones, the largest ranges were those of individuals sighted away from the Headland most frequently, all between West Harbour and Seaton Sands. These three individuals all had their main activity centre around sightings at Parton and Throston; individuals resident on Lighthouse north or Breakwater north (see Fig. 1.1) were never seen away from the Headland. An example of the distribution of low water sightings of one individual Purple Sandpiper is shown in Fig. 4.29. Sightings are mainly spread between Lighthouse north and Breakwater north; the one

Fig.4.29. An example of the low water sightings of an individual Purple Sandpiper, used for the calculation of home range

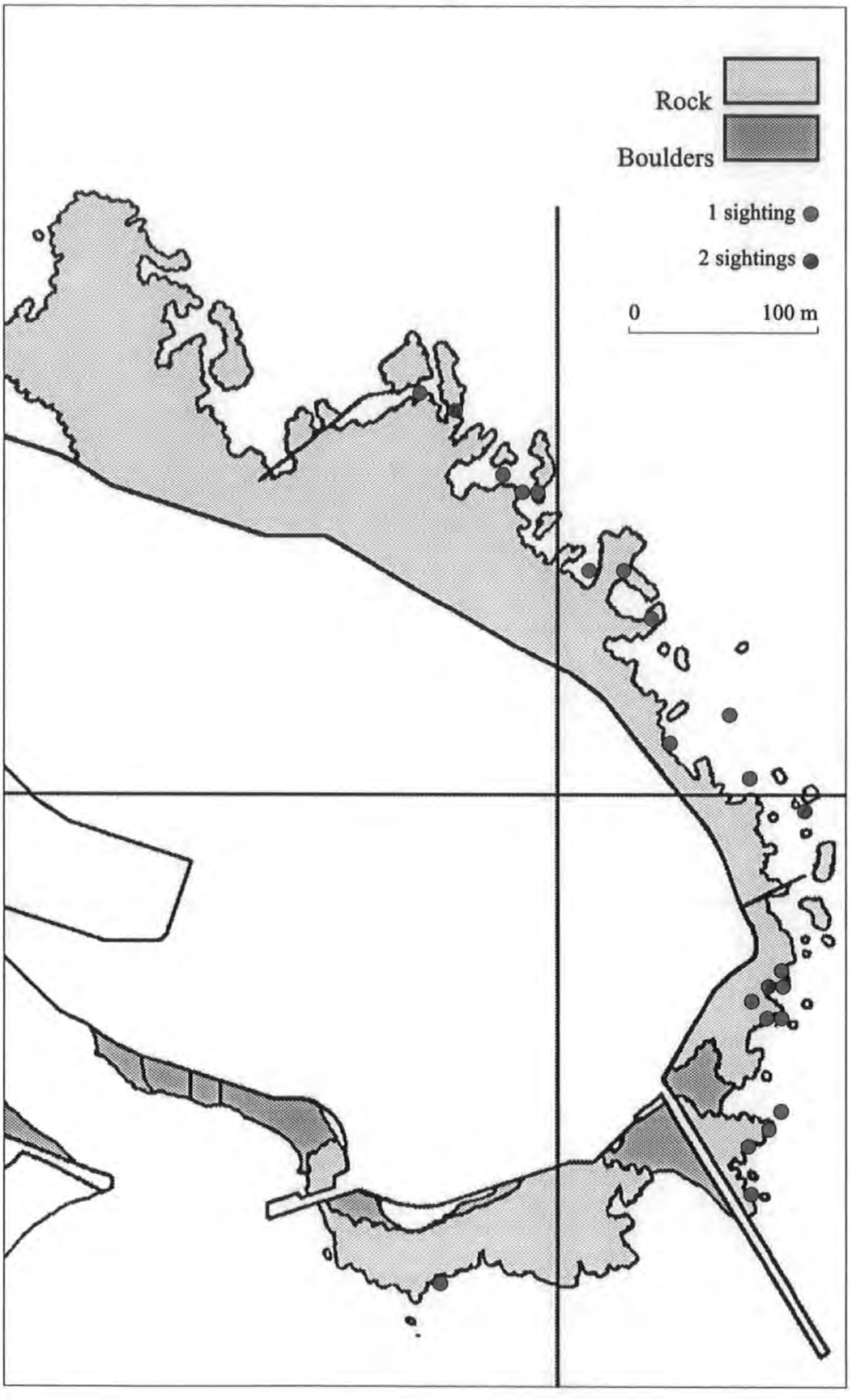


Fig. 4.30. Purple Sandpiper home range size and its relationship to bill-length.

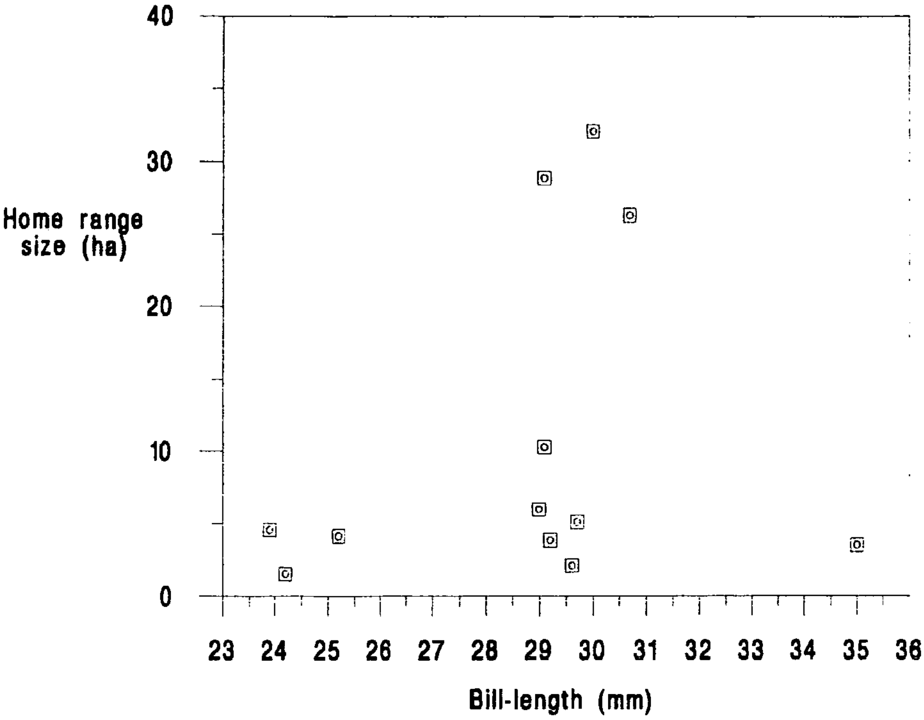
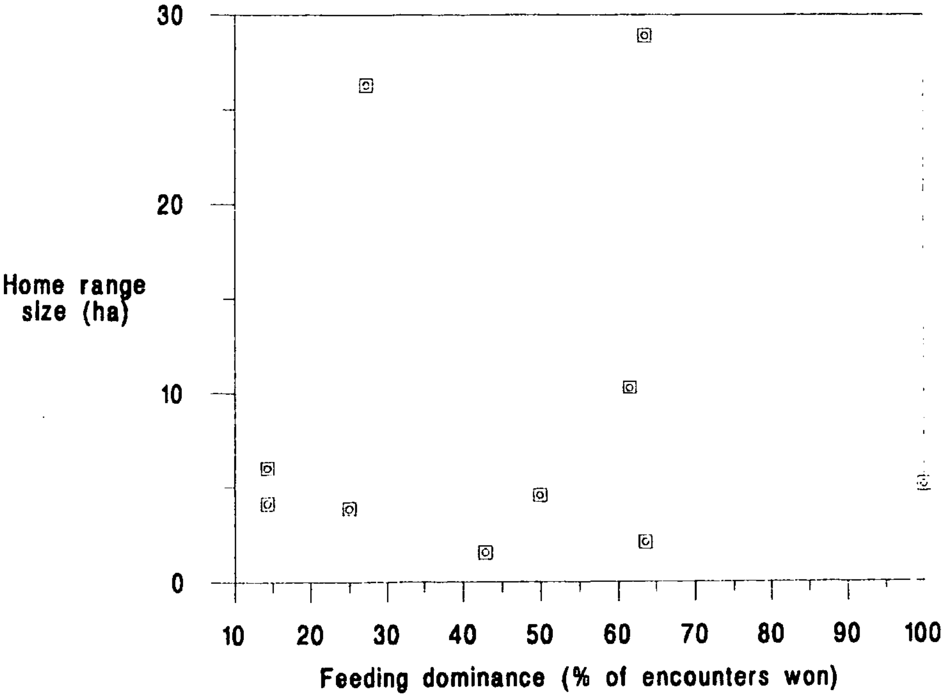


Fig. 4.31. Purple Sandpiper home range size and its relationship to dominance.



sighting outside this area, on Inscar rocks, occurred on a neap tide with high winds, when much of the individual's usual range was flooded and unavailable.

The home ranges of Purple Sandpipers varied in size between individuals of different bill-length size class, though not significantly (Fig. 4.30; Kruskal-Wallis χ^2 = 3.548, d.f. = 2, n.s.). The three largest ranges were all of individuals of the medium bill-length size class.

The relationship between the home range size and feeding dominance of Headland resident Purple Sandpipers was investigated using data from 1993/94. No correlation was found between home range size and feeding dominance for these individuals (Fig. 4.31; r_s = 0.146, n = 10, n.s.).

4.3.2.3. Interspecific aggression.

Table 4.11 summarizes all the interspecific aggressive encounters recorded within feeding flocks of birds involving colour-ringed Turnstones or Purple Sandpipers; (data from July 1993 to May 1994). Only 2 of 40 interactions were won by the smaller species (Sign Test $P < 0.001$), and all encounters were won by the initiator.

Interspecific aggression accounted for 9.3% of all the feeding aggression recorded for Turnstones (n = 301) and 2.4% of all feeding aggression recorded for Purple Sandpipers (n = 206); (data from 1993/94). Only 2 (6.1%) of 33 interspecific encounters involving Turnstones were due to infringements of individual distance, though 6 (42.9%) of 14 encounters involving Purple Sandpipers.

Interspecific feeding encounters were of equal intensity to intraspecific feeding encounters for Turnstones (Table 4.12; combining pecks, chases, peck-chases and fights as high intensity encounters: χ^2 = 2.589, d.f. = 1, n.s.). Insufficient data were available for a similar analysis for Purple Sandpipers (Table 4.13).

Table 4.11. Interspecific aggression in feeding flocks; (data from July 1993 to May 1994).

Winner	Loser	*n*
Turnstone	Purple Sandpiper	7
Turnstone	Sanderling	10
Turnstone	Dunlin	1
Turnstone	Knot	1
Oystercatcher	Turnstone	11
Black-headed Gull	Turnstone	2
Herring Gull	Turnstone	1
Purple Sandpiper	Knot	1
Knot	Purple Sandpiper	5
Oystercatcher	Purple Sandpiper	1

Figures represent numbers of encounters recorded.

Table 4.12. The intensity of intra- and interspecific feeding aggression involving Turnstones.

	Threat	Peck	Chase	Peck-chase	Fight
Interspecific	31	2	0	0	0
Intraspecific	862	122	59	11	5

Figures represent numbers of encounters recorded.

Table 4.13. The intensity of intra- and interspecific feeding aggression involving Purple Sandpipers.

	Threat	Peck	Chase	Peck-chase	Fight
Interspecific	12	2	0	0	0
Intraspecific	304	69	12	2	0

Figures represent numbers of encounters recorded.

4.4. Discussion.

4.4.1. Seasonal and tidal changes in the numbers of birds recorded over low water and the low water habitat preferences of Turnstones and Purple Sandpipers.

The seasonal changes in Turnstone and Purple Sandpiper numbers recorded at low water on Hartlepool Headland reflect, as do the numbers at the West Harbour roost, the arrival and departure of the local populations. Numbers of Turnstones increased sharply in August with the return of local residents and increased further in September and early October as passage birds also used the area. The stability of numbers during winter reflects the site fidelity of individual Turnstones at this time of year (the present study, Cramp and Simmons 1983, Metcalfe and Furness 1985, Whitfield 1985a). No spring passage of Turnstones was evident from low water counts on the Headland, though there was some evidence of the use by passage birds of the mudflats of Seal Sands just to the south of the study site.

Low water numbers of Purple Sandpipers on Hartlepool Headland followed a similar seasonal pattern to the numbers recorded at high water at West Harbour. The first individuals from the Norwegian population returned from mid-July, but numbers remained low until October and November, when the remaining Norwegian birds returned together with those from the probable Greenland / Canada population (Nicoll *et al.* 1988). Numbers remained stable over winter, again reflecting this species' site fidelity at this time of year (the present study, Atkinson *et al.* 1978, Metcalfe 1984a, Summers *et al.* 1990b, K-B. Strann pers. comm.). Although no spring passage of Purple Sandpipers was evident from low water numbers on the Headland, one colour-ringed bird, originally ringed in Finland, was observed foraging on the Headland during both April 1992 and 1993. Additional observations (R. Ward pers. comm.) suggest that an area a few kilometres south of the study site, the 'German Charlies' adjacent to South Gare breakwater, may be used for feeding by

Purple Sandpipers on spring passage; (unfortunately it is not possible to census this site accurately).

There was no evidence that the numbers of Turnstones and Purple Sandpipers recorded at low water on Hartlepool Headland fluctuated during winter due to a change in birds' feeding sites, either because of prey depletion or the availability of a new food source. At one smaller site, 'south Seaton pipe', maximum Turnstone numbers were, however, lower at the end of winter than earlier and numbers were slightly lower in 1992/93 than 1991/92, suggesting that prey might have been depleted at this (musselbed) site. A high rate of predation of dogwhelks by Purple Sandpipers has been recorded elsewhere in north-east England (Feare 1970) and Marshall (1981) found that prey depletion by Turnstones may lead to low food abundance in late March and early April. Several studies have found that Oystercatchers deplete food supplies of mussels during winter to levels that reduce their intake rate (*e.g.* O' Connor and Brown 1976, Goss-Custard 1980, Zwarts and Drent 1981).

Turnstones are often found feeding on larvae, pupae and flies in beds of wrack and algae washed up during storms (Groves 1978, Whitfield 1990), though such behaviour in Purple Sandpipers is usually confined to the high water period (Gibb 1956, Summers *et al.* 1990a). Such wrack deposits are most likely to occur after storms and high winds in mid-winter and Turnstone numbers may vary along the coast at these times as birds take advantage of the resultant food supply. Although Turnstones were frequently found feeding at wrack deposits during the present study, these deposits were often near their usual feeding grounds - most notably at Parton and Throston - and so numbers on the Headland were not affected. Metcalfe (1986) also found that Turnstones were seen away from their home ranges most infrequently at this time of year.

The numbers of both Turnstones and Purple Sandpipers that were found feeding on different parts of the coast were largely dependent upon low tide levels. Numbers on the Headland were low on neap tides when some individuals' usual feeding grounds remained flooded. Between Inscar and North Gare, numbers were higher on neap tides as a result of an influx of birds that would normally have fed on the offshore Long Scar rocks. The lower numbers of both species recorded on the Headland on spring tides partly reflect the difficulties of surveying distant birds on rocky coasts (Summers *et al.* 1975, da Prato and da Prato 1979). The use by both species of Long Scar rocks at low water on all but the highest neap tides meant, however, that in contrast to da Prato and da Prato (1979), low water counts were less accurate for estimating the sizes of the local Turnstone and Purple Sandpiper populations than those taken at high water.

Over low water, Turnstones were seen to use a greater variety of habitats than Purple Sandpipers, reflecting their generalist and opportunistic foraging habits (Harris 1979, McKee 1982, Cramp and Simmons 1983, Summers *et al.* 1988b, Whitfield 1990). Turnstones occurred more frequently than Purple Sandpipers on exposed rock, strand and live and dead wrack habitats. Purple Sandpipers were found almost entirely on musselbeds, in contrast to McKee's (1982) findings that they favoured barnacle and algae covered rocks and 'pools'. At Hartlepool these habitats were found more commonly further up the shore profile (see also Dierschke 1993) and therefore were likely to be favoured on ebb and flood tides.

In both the present and McKee's (1982) study, however, Purple Sandpipers were seldom found away from rocky shores over low water, in contrast to Turnstones. At more northerly latitudes, Purple Sandpipers are less restricted to rocky shores and may be found on a greater range of habitats, including soft-substrate shores (Summers *et al.* 1988b, Strann and Summers 1990, Leinaas and Ambrose 1992). This is possibly a result of lack of competition from other waders, notably perhaps Dunlin.

4.4.2. Arrival to and departure from low water feeding areas, pre-roosts, arrival to and departure from the West Harbour roost and post-roosts.

Flocks of both Turnstones and Purple Sandpipers formed at a number of sites after their departure from their main low water feeding areas and before their arrival at their roosts, and again after their departure from these roosts and before arrival back at their main feeding areas. In the present study, flocks at such sites contained both feeding and roosting birds. The occurrence of pre-roost and post-roost flocks of birds has been recorded in a number of studies (Hoffman 1968, Zahavi 1971, Swingland 1976, Siegfried *et al.* 1977, Ydenburg *et al.* 1983) and their function has commonly been interpreted as one of 'information-centres', where individuals are able to gather information concerning the location of food resources (Ward and Zahavi 1973). As most individual Turnstones and Purple Sandpipers are restricted to small home ranges during winter and are thus likely to be highly familiar with the location of resources available to them, and as food resources on rocky shores are typically highly reliable and available (Becuwe 1973, Dierschke 1993), the importance of such gatherings for these species may not be primarily in their use as information-centres. It seems unlikely that an exchange of information about food would occur in flocks where a high proportion of individuals were in fact feeding at the time. It seems probable that the flocks may form firstly due to the lack of foraging space available to the waders on flood and ebb tides. The early formation and late dispersal of large flocks may also be advantageous to these birds due to the reduction of the risk of being taken by a predator, through increased vigilance (*e.g.* Powell 1974, Siegfried and Underhill 1975), decreased individual risk (Hamilton 1971, Fox *et al.* 1994) or increased predator confusion (Neill and Cullen 1974, Fox *et al.* 1994). As feeding opportunities are limited around mid-tide, the possible increase in competition for food resultant from such an increase in flock size (*e.g.* Recher and Recher 1969, Metcalfe and Furness 1987) would not be as significant as it would at low water.

The use of areas between low water feeding areas and roost sites for pre-and post-roosting and for feeding presents difficulties in interpreting the variation in a species' arrival times at the roost. Nevertheless some trends are apparent. Both Purple Sandpipers and Turnstones arrived at the West Harbour roost latest on neap tides and earliest on springs, This may have occurred either because individuals were able to feed for longer on neap tides or because they needed to. On spring tides more extensive low water feeding areas are available, offering more varied and possibly better feeding opportunities. Energetically, individuals may thus fulfil their feeding requirements more quickly on spring tides than on neaps and thus return to roosts earlier as a consequence.

Turnstones tended, though not significantly, to arrive at the roost latest at midwinter. As Turnstones do not feed at night (Evans 1976a, Marshall 1981), they will need to feed for a higher proportion of the daylight hours when the daylength is short in midwinter and thus for proportionally more of each tidal cycle. Energetic needs are often greatest in January and February during cold weather, but a number of wader species peak in mass before this (Johnson 1985, Summers *et al.* 1992, Norman and Coffey 1994). Turnstones may spend more time feeding around midwinter in order to put on this mass. In Purple Sandpipers, the peak in mass occurs early in November and December (Summers *et al.* 1992), and it is thus unsurprising that Purple Sandpipers arrive latest at the roost, relative to high water, around early November. In February, Purple Sandpipers again arrive early at the roost, but from mid-March they come progressively later, presumably as a result of increased time spent feeding in order to put on mass for their spring migration (Summers *et al.* 1992) Such a change in behaviour was less clear for Turnstones. Robinson (1992), however, recorded that both species left their low water feeding grounds and arrived at the West Harbour roost progressively later through spring.

4.4.3. Causes, rates and intensity of aggression whilst foraging.

Aggression in foraging flocks of waders is caused primarily by encounters over food and feeding sites (*e.g.* Feare 1966, Recher and Recher 1969, Groves 1978, Burger *et al.* 1979, Ens and Goss-Custard 1984, Metcalfe and Furness 1987), though it may also be a result of an infringement of individual distance (*e.g.* Smith and Bleakney 1966, Metcalfe and Furness 1987). In the present study, encounters over food and feeding sites were the primary cause of intraspecific aggression in both Turnstones and Purple Sandpipers though, as Metcalfe and Furness (1987) also found, Purple Sandpipers were involved in a higher proportion of 'non-food' encounters. This difference may relate to the food of the two species: Purple Sandpipers rely more on tactile foraging than Turnstones, taking smaller, less visible prey items (McKee 1982, Cramp and Simmons 1983) and are perhaps therefore less likely to be enticed into stealing food from other individuals. Burger *et al.* (1979) similarly found that wader species that used visual cues to find prey had higher 'aggression indices' than those that fed on subsurface prey.

For both Turnstones and Purple Sandpipers, the rate of intraspecific aggression over food and feeding sites increased with conspecific flock size. Several previous studies of waders have also found increases in aggression rate with either flock size or density (Recher and Recher 1969, Goss-Custard 1977, Burger *et al.* 1979, Fleischer 1983, Metcalfe and Furness 1987). In contrast the rate of intraspecific aggression over infringements of individual distance was not related to conspecific flock size for either species - flock density would perhaps have been a more useful measure. If density was important in determining the frequency of encounters over individual distance, then the greater importance of such forms of encounter in Purple Sandpiper aggression could be explained by this species having higher density flocks: this was not thought to be the case however. For Purple Sandpipers, the intraspecific aggression rate over food and feeding sites was highest early in the low water period, shortly after roosting when individuals were most in need of food. Purple Sandpipers do not have to feed for as much of the day during winter as other waders (Dierschke 1993) and later in the low water period, competition for food may be less severe. For Turnstones the rate of intraspecific aggression over infringements of individual distance was greatest in autumn, probably as numbers (and thus densities) of Turnstones were at a peak at this time.

The large number of unfamiliar passage birds at this time may also lead to increased aggression rates, as individuals may be unsure of each other's dominance status. Marshall (1981) similarly found high aggression rates amongst Turnstones in both the autumn and spring passage seasons.

The rates and intensity of aggression of Turnstones both over food and feeding sites and over infringements of individual distance varied with habitat. Rates of aggression were greatest on dead wrack (and to a lesser extent on live wrack and the strand) and lowest on algae (and to a lesser extent on exposed rock). Pecking was most frequent on grass and chases and fights on musselbeds. For Purple Sandpipers, aggression intensity, but not rates, varied with habitat: higher intensity encounters occurred on musselbeds and live wrack than on exposed rock or algae. The variation in aggression intensity and rates may relate to the food available in each habitat or the physical nature of each habitat. Dierschke (1993) found that rates of assimilated energy intake in Purple Sandpipers were highest on dead wrack beds and piers (in effect, rocky shores) and aggression over food is likely to be greatest for both species in these and other habitats of high food availability (such as grass in spring for Turnstones). For both species, aggression over food was found to be of low intensity and rate on algae, a habitat of low intake rate for Purple Sandpipers (Dierschke 1993). The high aggression rates and intensity of Turnstones feeding on dead wrack beds and on grass, and the high intensity aggression of Purple Sandpipers feeding on musselbeds (and live wrack) may also be a result of the more visible prey available in these habitats.

Aggression rates on rock, algae and musselbed habitats may also be lower because individuals are less able to see each other than when feeding on flat strand, dead wrack and grass habitats. Metcalfe and Furness (1987) found that intraspecific aggression rates of Turnstones and Purple Sandpipers were more affected by the density of visible conspecifics than by the actual densities. Some habitats may also be limited in space - for example piers - and this may cause an increase in flock density. Burger *et al.* (1979) found that aggression rates were highest on a beach habitat limited in size and used primarily shortly after high water and thus when flock densities were high. Turnstone aggression rates over infringements of individual distance also varied according to habitat. The formation of high density flocks around particular food sources - at dead wrack beds for example - may result not only in high rates of aggression over food, but also in frequent aggression between individuals that have come too close to each other. Mallory and Schneider (1979), studying Short-billed Dowitchers *Limnodromus griseus*, found that aggression rates increased when birds were in high density flocks as a consequence of feeding on patchily distributed *Limulus* eggs.

Although both Turnstones and Purple Sandpipers often fed in mixed-species flocks in the study site, behaviour which is common amongst wintering waders (Recher and Recher 1969, Burger *et al.* 1979, Stawarczyk 1984, Metcalfe and Furness 1987), interspecific aggression involving either species was infrequent. Recher and Recher (1969) and Metcalfe and Furness (1987) similarly found that interspecific aggression was infrequent in flocks of foraging waders and Metcalfe (1989) suggested that mixed-species flocks were of advantage to Turnstones due to their low aggression rates. As in other studies (Stawarczyk 1984, Metcalfe and Furness 1987), the majority of interspecific encounters were initiated and won by the larger species. Burger et al. (1979) found that larger wader species were more aggressive interspecifically than smaller species, presumably as they were more able to win encounters with other species. Though Recher and Recher (1969) and Metcalfe and Furness (1987) both found that interspecific encounters in feeding wader flocks were of lower intensity than intraspecific encounters, such a difference was not found in the present study for Turnstones.

4.4.4. Individual dominance on feeding grounds.

Dominance hierarchies of both Turnstones and Purple Sandpipers on their feeding grounds were particularly stable: only a few encounters went against rank order and most encounters were won by the initiator. Dominance may be related to age (adults dominating younger birds), sex and body-size or mass, though these factors are often inter-related (*e.g.* Patterson 1977, Van der Mueren 1977, Ketterson 1979, Jönsson 1987, Piper and Wiley 1989). In the present study, age was an important determinant of the outcome of encounters between Turnstones on their feeding grounds, though not so important for Purple Sandpipers. Adult Turnstones were of higher dominance than first-winter individuals in two of three hierarchies and won almost all encounters with first-winter birds. Whitfield (1985a) and Groves (1978) have also found that adult Turnstones dominate first-winter birds in foraging encounters; (though the results from the former study are for combined roosting and feeding aggression). A number of previous studies of other waders have also found that adults dominate first-winter individuals whilst foraging (*e.g.* Harrington and Groves 1977, Goss-Custard *et al.* 1982a). Dominance of adults over first-winter birds may be a result of two factors: the inexperience of first-winter individuals in aggressive interactions (Groves 1978, Whitfield 1985a) or the greater body size or mass of adults (*e.g.* for Turnstones: Summers *et al.* 1976, the present study), though the greater body mass of adults may be a result of improved feeding through their dominance. The dominance of adult Turnstones over second-winter individuals suggests that the experience of individuals may be important in determining the outcome of encounters even after the first year. The lack of difference seen in the dominance rank of adult and first-winter Purple Sandpipers on feeding grounds in late winter / early spring 1993 may be due either to the similarity of these age groups in size and mass at this time (Chapter 2; though see Summers *et al.* 1992), the fact that first-winter individuals may have lost their inexperience in aggressive encounters by this time, or simply due to small sample sizes.

Purple Sandpiper dominance rank on feeding grounds was, to some extent, positively correlated with body-size (as expressed by bill-length size class). Purple Sandpipers are sexually dimorphic in size, with females larger than males (Tatarinkova 1977) and they also vary in size according to geographical origin (Summers *et al.* 1992). Within a population therefore, females are likely to dominate males, whilst within a sex, individuals from the probable Greenland / Canada population are likely to dominate those from the Norwegian population. It is not clear however, whether females dominate males due to their sex or simply due to the size difference. There is some evidence that dominance may indeed be related just to size, as within the medium bill-length size class (*i.e.* females from the Norwegian population and males from the probable Greenland / Canada population) feeding dominance was positively correlated with size, as expressed by bill-length. In contrast however, Whitfield (1985a) found that male Turnstones, which are only marginally larger than females in body size (Cramp and Simmons 1983, Whitfield 1985a), were of higher dominance in aggression on roosting and feeding areas combined.

The subordination of individuals of the small bill-length size class to individuals of larger classes may not necessarily hamper them while attaining their daily energy requirements. Individuals of small body size will require less food than larger birds to maintain their energy balance and as Dierschke (1993) found, Purple Sandpipers may anyway have to forage for only 50% of daylight hours to meet their energy needs, even in midwinter. Summers *et al.* (1990a) found that Purple Sandpipers with longer bills take larger food than those with shorter bills and it may be that competition for food occurs mainly between individuals of the same bill-length size class rather than between individuals of different classes. This may partly explain why encounters over food and feeding sites accounted for a relatively small proportion of Purple Sandpiper aggression and why encounters over infringements of individual distance were, relative to Turnstones, more important.

Turnstones resident on the Headland in 1992/93 were of significantly higher rank than visitants to that area, suggesting that residence and familiarity with an area were important determinants of dominance. Although no such relationships were observed amongst Purple Sandpipers, it was noted that one individual with 100% dominance on its home feeding area, lost all of four encounters when feeding in a different area. Sandell and Smith (1991), studying dominance relationships in captive Great Tits *Parus major*, found that without a difference in prior residency, age was an important determinant of dominance rank. However, juveniles often became dominant over adults if they had the advantage of prior residence. Similar results have also been found by Nilsson and Smith (1988) and Yasukawa and Bick (1983). Whitfield (1985a) found that amongst wintering Turnstones, an individual's status waned with increased distance from its home feeding area and that 'home' birds initiated and won more encounters than 'away' birds. Lowered status away from home resulted in lowered intake rates in Whitfield's study. By remaining faithful to an area of shore during winter, Turnstones and Purple Sandpipers are likely to have greater intake rates than if they were more nomadic and they also have the chance to become highly familiar with the area's resources.

The stability of dominance hierarchies on feeding grounds suggests that individuals are able to recognise birds of different status. Individuals may be differentiated by varying size, by plumage characteristics related to age or sex (see Prater *et al.* 1977) or by individual variation in plumage. Such individual variation may help to either signal status (Rohwer 1975, Balph *et al.* 1979, Fugle *et al.* 1984, Järvi and Bakken 1984) or aid individual recognition (Collias 1943). Ewald and Rohwer (1980) have, for example, found that the defence costs of non-breeding Anna and Black-chinned Hummingbirds (*Calypte anna* and *Archilochus alexandri*) vary with plumage colour, suggesting that colour may signal status. Barnard and Burk (1979), however, have emphasised the difficulties in distinguishing assessment of rank by individual recognition from that involving simpler cues, such as plumage.

Individual Turnstones vary in plumage in the breeding season (Ferns 1978) and Whitfield (1986, 1987) has found that individuals are able to recognise neighbours at this time. Although winter plumage is less distinct, the relative stability and small size of groups of Turnstones on feeding grounds (Whitfield 1985a, Metcalfe 1986) may facilitate individual recognition at this time. Metcalfe (1984a) suggested that Purple Sandpipers were more mobile within winter than Turnstones and that individual recognition and thus stable hierarchies would be less common due to a greater mixing of the population. In the present study, individual Purple Sandpipers were however seen more frequently than Turnstones on low water feeding grounds and had similar home ranges, suggesting equal or greater site fidelity. Individuals were thought to associate with only a small number of other birds and dominance hierarchies were thus very stable. Individual recognition may be possible in this species too. Amongst less site faithful wader species, dominance heirarchies are likely to be less stable due to a greater mixing of unfamiliar birds. Myers (1983), for example, showed that amongst wintering Sanderlings flocks were of random composition (see also Roberts and Evans 1993) and that little dominance structuring existed.

4.4.5. Dominance and survival; return to wintering grounds.

Subordination may be viewed either as an alternative strategy to dominance, but one with equal fitness (Rohwer and Ewald 1981), or as a temporary strategy for 'hopeful dominants' (West Eberhard 1975). The smaller body mass often apparent in subordinates (*e.g.* Lundberg 1985, Piper and Wiley 1990) might be a result of their lower rank or in the former theory be associated with a transient rather than resident strategy in which smaller body mass would be an advantage (*e.g.* Senar *et al.* 1992). Ekman and Askenmo (1984) in a study of social dominance amongst Willow Tit *Parus montanus* groups, found that access to resources was greatest for dominants and 'that fitness in terms of survival was correlated with access to preferred feeding sites'. They concluded that subordination in this case was not an alternative strategy to dominance, but one of hopeful dominants. Senar *et al.* (1990) similarly found that resident Siskins *Carduelis spinus* were dominant over transients and had preferential access to food resources, whilst Kikkawa (1980) found that the winter survival of Silvereyes *Zosterops lateralis* was related to dominance, probably as a consequence of their feeding advantages over others.

In the present study, the winter feeding dominance of Turnstones was not related to either over-winter survival or to the return of individuals after the following summer.

Whitfield (1985a) however provided some evidence that subordination may increase an individual's likelihood of death during winter and thus concluded also that subordination was compatible with the hopeful dominants hypothesis.

Although no individually marked Purple Sandpipers died during the winter at Hartlepool, return rates over summer for this species were comparatively low, particularly in 1993 (see Chapter 2). Interestingly there was a greater tendency for subordinates to return after summer 1993 than for dominants to do so. This trend may have been caused partly by a change in the wintering grounds of some more dominant individuals, rather than by their death: two individuals are known, for example, to have changed their wintering quarters between 1992/93 and 1993/94 (see Chapter 2). Whether dominance, sex or geographical origin, (dominance may be related to both the latter factors), affected the likelihood of an individual's return or whether the low return rate of both dominants and individuals of the large bill-length size class was merely due to chance is however unclear. As a consequence of the relationship between dominance and size (and the high variation in size) in this species, it is possible that larger individuals may be able to move to new areas without a great risk of loss of status, but it is not clear why they should do so.

The suggestion that dominance over winter may correlate to survival over summer is dependent upon correlations between winter and summer dominance and between summer dominance and survival. As well as affecting summer survival, dominance during the breeding season may also help an individual gain a territory (Parker 1974) and Whitfield (1985a) has hypothesised that dominance during winter may be used to predict the breeding success of Turnstones. In the present study, in 1992, dominant Turnstones, as predicted, arrived back at Hartlepool later than subordinates, thus reflecting their possible better breeding success. No such relationship occurred in 1993. Whitfield (1985a) himself, in contrast, found no clear relationship, even though he analysed the sexes separately to take into account the earlier departure of females from their breeding areas (Nettleship 1973).

The relationship, in Turnstones, between winter and summer dominance and thus between winter dominance and breeding success would still, therefore, appear to be tenuous.

4.4.6. Home ranges.

Both individual Turnstones and Purple Sandpipers were highly sedentary during the non-breeding season, each individual typically occupying a stretch of coast only a few 100m's long throughout autumn, winter and spring. Home range sizes were similar to those recorded for Turnstones by Metcalfe (1986) in a study in south-west Scotland, though his methods differed slightly; (he used a grid of 100m by 100m squares over his map and only moved points at grid intersections so that they were at least 10m from the intersections). There was no evidence that either species at Hartlepool was more mobile in autumn or spring, in contrast to Metcalfe's (1986) findings on Turnstones. Movements in autumn have been recorded in other wader species, for example Sanderling (Myers 1984), and Metcalfe suggested that Turnstones may behave similarly in autumn in order to sample different areas adjacent to their home area. The majority of Turnstones return to the same home range each winter however (Metcalfe 1986, the present study) and the same is true for Purple Sandpipers.

Metcalfe (1986) suggested that the increased mobility in late spring shown by the Turnstones in his study was not due to birds being forced to look elsewhere for food on account of prey depletion during winter, as the lowest food abundance levels probably occurred earlier, in late March and early April (Marshall 1981). The spring mobility seen in his study may have been a result of individual Turnstones trying to stay in flocks as numbers in the area decreased, whilst flocking became more important at this time as individual vigilance decreased prior to migration (Metcalfe and Furness 1984). (A similar decrease in individual vigilance in spring has also been seen for Purple Sandpipers: Robinson 1992).

The home ranges of Turnstones and Purple Sandpipers at Hartlepool Headland were similar in size. As individual Purple Sandpipers were seen more frequently at low water than Turnstones, it would seem that Purple Sandpipers, in this study, were probably at least as sedentary as Turnstones during the non-breeding season. Purple Sandpipers are more specialised to rocky shores than Turnstones. They use a smaller range of habitats (McKee 1982, the present study) and take a smaller range of prey (Cramp and Simmons 1983) and so their sedentary behaviour is perhaps unsurprising. Metcalfe (1984a), using rather limited data on Purple Sandpipers, has in contrast suggested that Purple Sandpipers may be more mobile than Turnstones in the non-breeding season. The sedentary nature of both species reflects the reliability and availability of their usual rocky shore food resources (Becuwe 1973, Dierschke 1993). The site fidelity of both species during the non-breeding season is discussed in greater detail in Chapter 2.

There was no clear relationship between home range size and dominance rank amongst either Turnstones or Purple Sandpipers, in contrast to Metcalfe's (1986) findings that subordinate Turnstones had larger ranges. Metcalfe suggested that subordinate Turnstones, on account of low intake rates resulting from interference by dominants, may range more widely in order to search for alternative less densely occupied feeding areas (see also Ens and Goss-Custard 1984). Whitfield (1985a) using a different method to calculate home ranges (Anderson 1982) found, however, in agreement with the present study, that Turnstone home ranges were not related in size to an individual's status.

There is some evidence that home range size may differ between Purple Sandpipers of different bill-length size class, with medium classed individuals having on average, slightly larger ranges. This situation might be caused by competition. As individuals of different bill-length take different sized prey (Summers *et al.* 1990a), competition for food should be greatest between individuals of a similar size. Whilst individuals of the medium size class may receive competition from birds of both small and large size classes, there would be less competition between individuals of the small and large size classes.

Individuals of the small and large classes may therefore suffer less competition overall than individuals of the medium class (as suggested in 4.3.2.2.1), and as a consequence of the lack of prey depletion and interference, may not need to forage over such large areas.

Summary.

1). Maximum winter numbers of Turnstones recorded feeding at low water on Hartlepool Headland declined over the three year study period. The maximum numbers of Purple Sandpipers showed no clear trend.

2). During winter, the height of low water determined the numbers of birds seen feeding in each part of the study area. Numbers of both species on the Headland were greatest on days when low water was in the middle of its range; numbers on the shore between West Harbour and North Gare were greatest on neap tides, when the offshore Long Scar rocks remained largely flooded.

3). At low water, Turnstones used a variety of habitats: they were mainly found on musselbeds, but also used exposed rock, strand and dead and live wrack habitats. Purple Sandpipers were confined to rocky shore habitats: musselbeds were most important, but Purple Sandpipers also used exposed rock and (non-wrack) algae habitats.

4). Both Turnstones and Purple Sandpipers used pre-roosts before flying to West Harbour and post-roosts afterwards. Both species arrived at the West Harbour roost later relative to high water on days of neap high tides. Both species also arrived at the roost relatively early in summer, late in the period of winter mass increase (around midwinter for Turnstones and early in November for Purple Sandpipers) and again late in spring, prior to migration.

5). Encounters over food were the main cause of intraspecific aggression for both Turnstones and Purple Sandpipers; encounters over infringements of individual distance were relatively infrequent. The intensity of aggression varied between habitats: chases were more frequent for both species on musselbeds and for Purple Sandpipers, simple threats more frequent on exposed rock and non-wrack algae habitats; aggression rates for Turnstones were greatest when feeding at dead wrack. Aggression intensity and rate were thus greatest on habitats that offered the most visible food and where bird densities were likely to be greatest. For both species, the intraspecific rate of aggression resultant from encounters over food increased with flock size. Interspecific aggression was, in comparison, infrequent for both species.

6). Dominance hierarchies on low water feeding areas were stable for both species within years. The dominance of individuals was positively, though insignificantly, correlated between years; Turnstone dominance increased with age. Residents were of higher dominance rank than visitants to their area in just one of five cases for Turnstones, but of similar rank in all other cases; resident and visitant Purple Sandpipers were of similar dominance rank. Adult resident Turnstones were of higher dominance rank than first-winter residents; no such difference was found for Purple Sandpipers. For Purple Sandpipers, dominance was positively correlated with bill-length size class; within the medium bill-length size class, dominance was also positively correlated with bill-length. Dominance during winter was not correlated with winter survival for Turnstones, or for summer survival for either species; few high ranked Purple Sandpipers tended to return to Hartlepool after summer 1993 however.

7). Individuals of both species were resident on small low water home ranges during winter; home range size did not differ between species. Home range size was not correlated with dominance for either species. For Purple Sandpipers, the largest ranges were those of individuals of the medium bill-length size class.

Chapter 5.

Individual Roosting Behaviour.

5.1. Introduction.

Three main hypotheses aim to explain the advantages to an individual of communal roosting during the non-breeding seasons. These are the reduction of the risk of predation (Lack 1966, 1968), the micro-climate theory, which suggests that roosts and their sites offer birds energetic advantages (*e.g.* Francis 1976, Tast and Rassi 1973, Ormerod and Tyler 1990), and the information-centre hypothesis, which proposes that information concerning the location of food resources is exchanged at roosts (Ward and Zahavi 1973). These hypotheses are not mutually exclusive however, and Weatherhead (1983) proposed that roosting offered different advantages to individuals of different dominance rank. In his theory, subordinate individuals use roosts in order to gain information about food resources, whilst dominant individuals use roosts in order to gain preferential sheltered and safe positions in the middle of flocks at the expense of these subordinates.

This chapter documents the behaviour and social structuring of individuals in the roosting flocks of Turnstones and Purple Sandpipers at West Harbour. Previous studies have found that stable dominance hierarchies exist amongst foraging Turnstones (Marshall 1981, Metcalfe 1984a, Whitfield 1985a) and the present study aimed to establish if such hierarchies also existed amongst roosting Turnstones and Purple Sandpipers. As discussed in the previous chapter, dominance may be related to sex, age or body-size and amongst foraging Turnstones, adults have been found to dominate first-winter birds (Groves 1978, Whitfield 1985a) and males to dominate females (Whitfield 1985a). Through competition for roosting sites, such dominance relationships are likely to be reflected in the social structuring of roosting flocks. Middle positions are likely to be preferable to those at the edge as they offer protection from predators (Kus *et al.* 1984) and shelter from poor weather (Whitlock 1979); birds may, however, also shelter from the wind by using the leeward edge of flocks. Structuring according to age, sex, body-size and body-mass has been found (Swingland 1977, Weatherhead and Hoysak 1984, Still *et al.* 1987, Summers *et al.* 1987, Ruiz *et al.* 1989 and Jenni 1993) and in some species, sexes may be segregated entirely, within or even between roosts (Orians 1961, Meanley 1965). In this study, the structuring of flocks is investigated in relation to whether individuals were residents or visitants, to their age, size (for Purple Sandpipers) and dominance status. Residents, adults, larger birds and dominants are predicted to roost more often in the middle of flocks and at higher conspecific densities. Aggression is predicted to occur at a higher rate in denser parts of flocks and aggression over roosting sites at a higher rate in the middle of flocks and when wind speed is high. Rates are predicted to be highest before high water when birds are arriving at the roost.

Amongst non-breeding waders, fidelity to high water roost sites is often high (*e.g.* Furness and Galbraith 1980a, Hockey 1985), though individuals may vary considerably in how often they use particular sites. This variation may result from competition within or for preferential roost sites, (*i.e.* those that are sheltered, relatively predator-free, or that are close to feeding areas *e.g.* Swennen 1984) or from the varying need for additional feeding over the high water period (*e.g.* Goss-Custard and Durell 1983). Birds that are dominant at a preferred roost may, for example, be expected to use that roost more frequently than those that are more subordinate. High water foraging is most likely to be needed by individuals, notably first-winter birds, that are subordinate whilst foraging at other stages of the tidal cycle, and will be accentuated during periods of stress, for example in winter or during severe weather (Heppleston 1971, Goss-Custard *et al.* 1977, Davidson 1981). Where the areas available for foraging over low water have been reduced by industrial development, subordinate individuals may be put under additional stress (Goss-Custard and Durell 1990) and in such areas, high water feeding at peripheral sites assumes additional importance (Davidson and Evans 1986). Seasonal and individual variations in roost attendance were investigated in the present study at two sites: West Harbour and Hartlepool Headland. At high water, West Harbour is used primarily for roosting (Chapter 3); numbers of both Turnstone and

Purple Sandpiper are at their greatest there on spring tides. Hartlepool Headland consists of a number of smaller sites, some limited in their availability by tidal height, and is primarily used on neap tides (Chapter 3). At high water, feeding is a more prominent activity here, for both Turnstones and Purple Sandpipers, than at West Harbour (Chapter 3). For the individuals that use them, these two sites offer different advantages therefore: West Harbour is a larger, perhaps safer and microclimatically favourable site, whilst Hartlepool Headland provides greater foraging opportunities over high water and is also closer to the low water feeding areas. Individuals that are dominant whilst feeding or at the West Harbour roost are expected to frequent the West Harbour roost more often than those that are subordinate. Individuals resident on the Headland, that are subordinate whilst feeding or whilst roosting at West Harbour are expected to occur on Hartlepool Headland more often over high water, either due to the need for high water feeding or due to avoidance of the West Harbour roost. Individuals that are subordinate whilst feeding are also expected to attend the West Harbour roost only on spring tides, when they are unable to feed over high water (see 3.3.4).

5.2. Methods.

5.2.1. Segregation within the roost.

The intraspecific segregation of groups of individuals roosting at West Harbour was studied by means of 'nearest neighbour' analysis. A focal (colour-ringed) individual was chosen at random by scanning the roosting flocks with a telescope, its individual colour-ring combination recorded and then that of its nearest (conspecific) colour-ringed neighbour. Data were collected only if there was another colour-ringed individual within 2m of the focal bird. Data were also taken only in winter and spring, when the proportions of different groups of individuals present amongst the colour-ringed population were most stable, so that the probability that an individual of one group should be a focal bird's nearest neighbour should have been constant throughout the period of data collection, if group composition had not changed.

5.2.2. Aggression at the roost.

Aggression was recorded at the West Harbour roost only for focal birds that were colour-ringed. Whenever possible, individuals were watched for five minute periods in order to calculate aggression rates. The following information was recorded: the colour-ring identity of the focal bird and that of the opponent if that bird was also colour-ringed; the species of the opponent; the age of both birds, if possible (adult or first-winter); the initiator; the winner and loser; the time that the period of observation started and finished; the date; the wind speed (recorded at high water on the Beaufort scale); the roost position and conspecific roost density of the focal bird (see 5.2.3); the cause of the aggression and the form of the aggression. Turnstone aggressive interactions were placed, in order of increasing intensity, into the following categories: threat with tail down to tail up; threat with tails down; peck; chase; peck-chase and fight (see 4.2.2). Purple Sandpiper aggression was categorised, also in order of increasing intensity, into: threat with wings in; threat with wings out to wings in; threat with wings out; peck; chase; peck-chase and fight (see 4.2.2).

Aggression at West Harbour was recorded only between individuals that were roosting. (Aggression also occurred between individuals in encounters over food, feeding sites and bathing positions - see also Whitfield 1985a - though this was uncommon). Aggression at the roost was caused either by encounters over roosting sites or due to an infringement of individual distance (Conder 1949). These were distinguished as follows: interactions over roosting sites were initiated by an individual moving through the flock, with the winner remaining at the site of the encounter; interactions caused by an infringement of individual distance were initiated by individuals in a stationary position in the flock and were directed towards individuals that had moved too close to them.

5.2.3. Structuring within flocks: position in the roost and conspecific roost density.

Colour-ringed individuals were recorded as being in the middle or the edge of flocks, or for birds on the steep-sided island at West Harbour, at the bottom of flocks. Individuals were recorded as being at the edge if they were the outer birds in that part of the flock; inside of this outer ring they were classed as being in the middle. Individuals on the West Harbour island were classed as being at the bottom of flocks if they were outer birds at the base of the flock, nearest the water.

Conspecific roost densities were calculated by counting the number of conspecifics within a 0.6m radius ring around the focal bird. A smaller ring than this would have contained too few birds to give an accurate representation of the density in that part of the flock; individuals beyond this distance, however, are unlikely to be involved in encounters with the focal bird. Bird-lengths were used to estimate the 0.6m distance: Turnstones are 23cm in length and Purple Sandpipers 21cm (Cramp and Simmons 1983). Densities were categorised as Low (0 - 3 other conspecifics), Medium / Low (4 - 7 conspecifics), Medium (8 - 11 conspecifics), Medium / High (12 - 15 conspecifics) and High (16^+ conspecifics). In some analyses these categories have been assigned values, ranging from 1 (Low) to 5 (High). Data were collected as close as possible to high water when the numbers of birds were at their maximum. In order to investigate the effect of roost size on individual roost position and conspecific density, the number of conspecifics at the roost was recorded at high water.

For Turnstones, data were collected in both 1991/92 and 1992/93 and additional data for flocks on the flat top of the inner pier (where flocks had only a middle and an edge) in August and September 1993. For Purple Sandpipers, data were collected only in 1992/93.

5.2.4. Attendance at the West Harbour roost and Hartlepool Headland high water sites.

To establish the frequency with which individuals used particular roost and high water sites, flocks were scanned by telescope or binoculars so that, if possible, all the colour-ringed individuals present were seen and their identities recorded. West Harbour was searched once a week and the Headland high water sites, once or twice a fortnight.

Data for Turnstones were obtained primarily from autumn and winter 1992/93. For Purple Sandpipers, data were collected in late winter / early spring 1993 from West Harbour alone and in winter 1993/94 from both sites.

5.3. Results.

5.3.1. Turnstone.

5.3.1.1. Segregation within the roost.

This first section aims to establish if different groups of individuals were segregated at the roost. A distinction is made here between segregation and structuring within roost flocks. Segregation occurs when groups of individuals occupy different areas of flocks, as a consequence, for example, of a lack of mixing after groups of birds have initially arrived at the roost. Aggression between individuals results in social structuring in the roost, as birds are separated into the middle, edge and bottom of flocks.

To find out whether Turnstones mixed freely together at the West Harbour roost, or whether they segregated into groups from different feeding areas, data from winter and spring 1992/93 were analysed. Tests for biases in the data are shown in Appendix 14.

Table 5.1 shows that individuals from one area were the nearest neighbours of individuals from the same area significantly more often than expected (combining West Harbour to North Gare residents with North and South residents: $\chi^2 = 11.153$, d.f. = 1, $P < 0.001$). Some segregation between groups from different feeding areas clearly therefore exists.

5.3.1.2. Intraspecific aggression at the roost.

Encounters over roosting sites comprised 50.2% (n = 233) of the aggression recorded between Turnstones at West Harbour (data from 1993/94). The remaining 49.8%

Table 5.1. Nearest colour-ringed neighbours of focal Turnstones from different areas.

		Nearest Neighbour		
		H	WH	N + S
	H	41	7	7
Focal Bird	WH	4	7	4
	N + S	6	6	2

Where H = Headland residents; WH = West Harbour to North Gare residents and N + S = North and South residents.

of encounters were due to an infringement of individual distance. The proportion of encounters over roosting sites became greater as wind speed increased (Table 5.2; $\chi^2 = 21.021$, d.f. = 5, $C = 0.288$, $P < 0.001$).

The majority of encounters were simple threat displays (Table 5.3); pecks and higher intensity displays, *i.e.* chases, peck-chases and fights were comparatively infrequent. Only 5.4% ($n = 792$) of encounters were lost by the initiator, but these included a higher than expected proportion of fights and chases (chases, peck-chases and fights are combined as high intensity displays: $\chi^2 = 8.152$, d.f. = 2, $P < 0.05$). In comparison to aggression amongst feeding Turnstones, there were more pecks than expected in roosting aggression, but fewer chases and peck-chases (combining chases and peck-chases: $\chi^2 = 37.135$, d.f. = 3, $P < 0.001$).

There was no difference in the intensity of aggression in encounters over roosting sites and over individual distance (Table 5.4; combining pecks, chases, peck-chases and fights due to paucity of data: $\chi^2 = 0.020$, d.f. = 1, n.s.).

The form of aggression seen between roosting Turnstones at West Harbour did not change seasonally (Table 5.5; combining chases, peck-chases and fights: $\chi^2 = 3.547$, d.f. = 6, n.s.). There was, however, a tendency for the intensity of aggression to become greater as wind speed increased (Table 5.6; combining chases, peck-chases and fights: $\chi^2 = 14.614$, d.f. = 8, $C = 0.135$, $P < 0.10$).

The rate of encounters over roosting sites, which varied between 0 and 4 per five minute period, per individual Turnstone, also increased with wind speed (Fig. 5.1; $t = 5.509$, d.f. = 168, $P < 0.001$ one-tailed):

$$\ln(\text{Aggression Rate} + 1) = -0.062 + 0.120\ \text{Wind Speed (Beaufort)}$$

$(r^2 = 0.153;\ F_{1,168} = 30.346,\ P < 0.001)$.

Table 5.2. The cause of encounters between Turnstones at the West Harbour roost and the relationship with wind speed; (data from August 1993 to May 1994).

	Wind Speed (Beaufort)					
	1	2	3	4	5	6
Roosting Site	3	27	29	27	3	28
Individual Distance	12	38	26	27	6	7

Figures represent frequencies of encounters recorded.

Table 5.3. The frequencies of different forms of aggressive interaction recorded between Turnstones roosting at West Harbour; (data from October 1991 to May 1994).

	Threat		Peck	Chase	Peck-chase	Fight
	Tail Down to Up	Tails Down				
Initiator won	569	21	142	14	1	2
Initiator lost	2	31	6	1	0	3
Total	571 (72.1)	52 (6.6)	148 (18.7)	15 (1.9)	1 (0.1)	5 (0.6)

Figures represent frequencies of encounters recorded; figures in parentheses are percentages of the total number of encounters recorded.

Table 5.4. The intensity and cause of encounters between Turnstones at the West Harbour roost; (data from August 1993 to May 1994).

	Threat	Peck	Chase	Peck-chase	Fight
Roosting Site	96	19	0	2	0
Individual Distance	95	15	5	1	0

Figures represent frequencies of encounters recorded.

Table 5.5. The intensity of encounters between Turnstones at the West Harbour roost and its relationship with season; (see 3.3.1.1.1 for definition of seasons; data from October 1991 to May 1994).

Season	Threat	Peck	Chase	Peck-chase	Fight
Autumn	332	72	7	4	0
Winter	178	42	6	1	0
Spring	76	23	1	0	0
Summer	37	11	1	0	1

Figures represent frequencies of encounters recorded.

Table 5.6. The intensity of encounters between Turnstones at the West Harbour roost and its relationship with wind speed; (data from October 1991 to May 1994).

Wind speed (Beaufort)	Threat	Peck	Chase	Peck-chase	Fight
1	111	24	1	0	1
2	227	45	2	1	0
3	84	24	1	2	0
4	83	25	4	2	0
5	61	19	2	0	0
6	41	8	0	0	0
7	14	3	5	0	0

Figures represent frequencies of encounters recorded.

Fig. 5.1. The relationship between the rate of intraspecific aggression over roosting sites per individual Turnstone and wind speed.

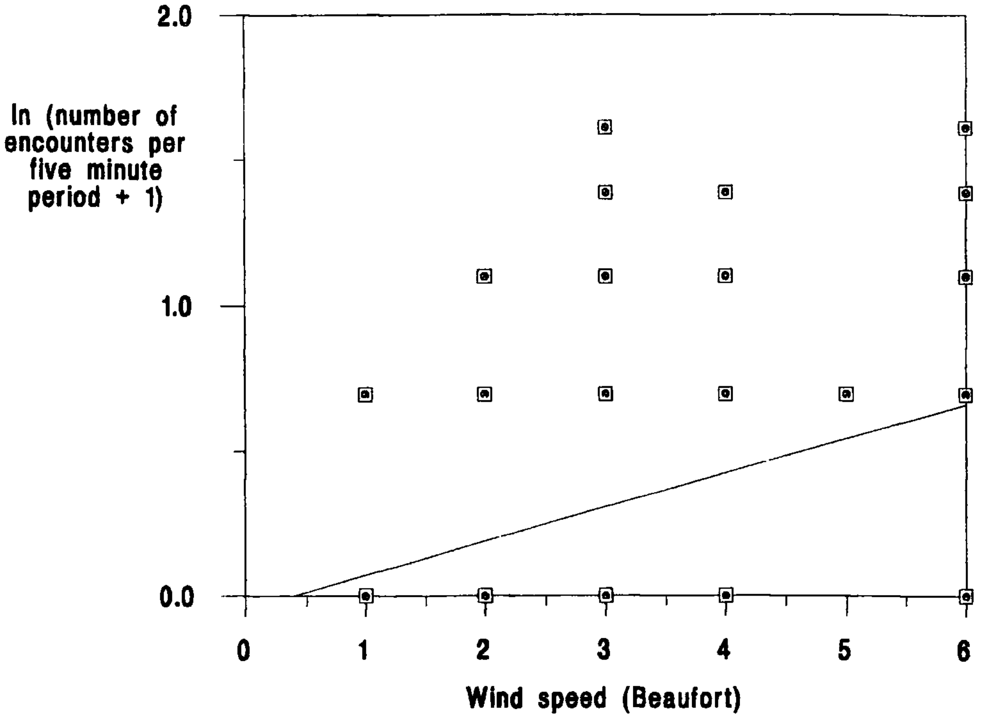
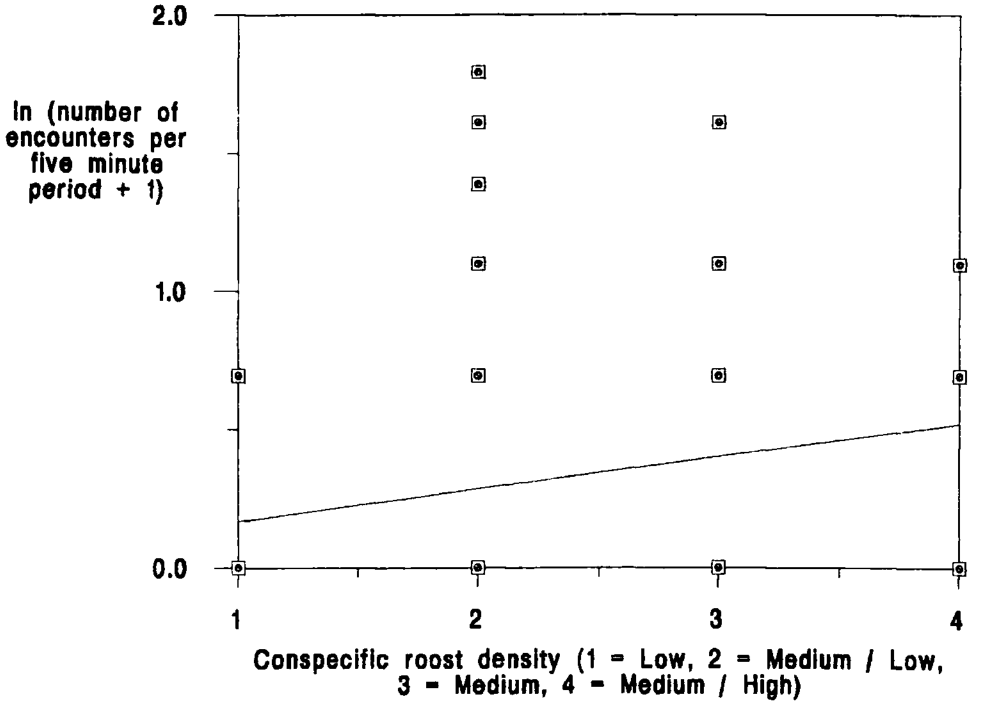


Fig. 5.2. The relationship between the rate of intraspecific aggression over infringements of individual distance per individual Turnstone and conspecific roost density.



No significant trends were detected in multiple regression between the rate of encounters over roosting sites and intraspecific roost density ($t = 1.308$, $n = 129$, n.s.), time relative to high water ($t = 0.182$, n.s.) or date relative to midwinter ($t = 0.338$, n.s.). Similarly the rate of encounters over roosting sites was not affected by roosting position, *i.e.* middle, edge or bottom (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 0.316$, d.f. = 2, n.s.).

In contrast, the rate of intraspecific encounters resulting from infringements of individual distance, which varied between 0 and 5 per five minute period, per individual Turnstone, increased as conspecific roost density increased (Fig. 5.2; $t = 2.271$, d.f. = 127, $P < 0.05$ one-tailed):

$$\ln(\text{Aggression Rate} + 1) = 0.052 + 0.115\ \text{Conspecific Roost Density}$$

$$(r^2 = 0.039;\ F_{1,127} = 5.159,\ P < 0.05).$$

No significant trends were detected in multiple regression between the rate of encounters over infringements of individual distance and wind speed ($t = -0.288$, $n = 129$, n.s.), time relative to high water ($t = 0.140$, n.s.) or date relative to midwinter ($t = 0.892$, n.s.). Similarly the rate of encounters over infringements of individual distance was not related to roosting position (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 2.480$, d.f. = 2, n.s.).

5.3.1.3. Turnstone dominance hierarchies at the West Harbour roost.

Individual roosting dominance was calculated, as for feeding dominance, as the percentage of encounters won by an individual (Ens and Goss-Custard 1984).

Dominance hierarchies for Turnstones roosting at West Harbour are shown for each winter (data from autumn, winter and spring) and for summer 1992 in Appendix 15 (see 3.3.1.1.1 for definition of seasons). In 1992/93, only one of 21 interactions between colour-ringed Turnstones went against rank order and in 1993/94, none of 17 interactions went against rank order (combining all three winters and summer 1992: Sign Test $n = 44$, $x = 1$, $P < 0.001$). Turnstone dominance hierarchies at the roost were thus very stable within years. There was a significant positive correlation between the dominance of individuals at the West Harbour roost in 1991/92 and 1992/93 ($r_s = 0.636$, $n = 10$, $P < 0.05$ one-tailed); however the correlation between individual dominance in 1992/93 and 1993/94 was not so significant ($r_s = 0.479$, $n = 11$, $P < 0.10$ one-tailed). As dominance hierarchies did differ slightly between years, and as shown later, individuals tended to increase in dominance with age, individual dominance was calculated separately for each year of study.

Dominance rank at the West Harbour roost was independent of body mass (for 1991/92: $r_s = -0.278$, $n = 8$, n.s.) and wing-length (for 1991/92: $r_s = -0.5$, $n = 5$, n.s.). (Only data from individuals caught and measured on 26 February 1992 were included in this analysis). Similarly, dominance rank was not dependent upon whether individuals were classed as residents or visitants (for 1991/92: Mann-Whitney $z = 0.501$, n.s., n (residents) = 16, n (visitants) = 5; for 1992/93 $z = 0.431$, n.s., n (residents) = 30, n (visitants) = 8; for 1993/94 $z = 1.135$, n.s., n (residents) = 19, n (visitants) = 7). Visitant colour-ringed Turnstones, however, won a greater proportion of aggressive encounters between the two classes at the West Harbour roost (Sign Test $n = 18$, $x = 3$, $P < 0.01$). Resident Turnstones did not differ significantly in rank according to their 'home' feeding areas, *i.e.* Headland, West Harbour to North Gare or North and South (for 1991/92: Kruskal-Wallis $\chi^2 = 2.099$, d.f. = 2, n.s.; for 1992/93: $\chi^2 = 0.989$, d.f. = 2, n.s.; for 1993/94: $\chi^2 = 0.179$, d.f. = 2, n.s.).

Adult resident Turnstones were not, on average, of higher dominance rank at the West Harbour roost than first-winter residents (for 1991/92: Mann-Whitney $z = 0.770$, n.s., n (adult) = 13, n (first-winter) = 2; for 1993/94: $z = 1.243$, n.s., n (adult) = 16, n (first-winter) = 3). During 1993/94 however, first-winter Turnstones were seen to win only four of 28 encounters with adults at the roost (Sign Test $P < 0.001$). The dominance of adults over first-winter birds in these recorded encounters may either be due to size differences between the two classes or the greater experience of adults in aggressive encounters. If experience is important and is only gained gradually, it is possible that second-winter birds may also be subordinant to older birds. In 1992/93, second-winter resident Turnstones were indeed found to be of lower dominance at the West Harbour roost than older residents (Mann-Whitney $z = 2.843$, $P < 0.01$ one-tailed, n (adult) = 16, n (second-winter) = 11). Colour-ringed second-winter individuals won only two of twelve interactions at the roost with older, colour-ringed adults (Sign Test $P < 0.05$ one-tailed). Individual dominance at the West Harbour roost was also found to increase with age (Appendix 12; $r_s = 0.459$, $n = 33$, $P < 0.01$).

The dominance of individual Turnstones at the West Harbour roost was positively correlated to their feeding dominance (on 'home' feeding areas) in 1991/92 ($r_s = 0.777$, $n = 8$, $P < 0.05$ one-tailed) and 1993/94 ($r_s = 0.578$, $n = 11$, $P < 0.05$ one-tailed), though not significantly so in 1992/93 ($r_s = 0.349$, $n = 20$, n.s.). Three 'pairs' of colour-ringed Turnstones were seen interacting both whilst roosting at West Harbour and whilst feeding. In two of these cases the outcome of the interaction was different when roosting than when feeding, and in one case the same.

Dominance was also recorded for Turnstones in 1991/92 on the high water feeding area at Seaton Sands (see Fig. 1.1 and Appendix 15). Only one of nine interactions went against rank order (Sign Test $P < 0.05$ one-tailed) and adults were found to be of higher rank than first-winter birds (Mann-Whitney $z = 2.412$, $P < 0.01$ one-tailed, n (adult) = 9, n (first-winter) = 3). High water feeding dominance at Seaton Sands was also positively correlated with low water feeding dominance ($r_s = 0.886$, $n = 6$, $P < 0.05$ one-tailed).

5.3.1.4. Position at the roost and conspecific roost density.

Both individual roost position and conspecific roost density were affected by the number of conspecifics at the roost. As roost size increased, the proportion of colour-ringed Turnstones observed in the middle, edge and bottom of flocks varied (Table 5.7; $\chi^2 = 15.211$, d.f. = 4, $P < 0.01$), whilst densities of conspecifics became greater (Table 5.8;

Table 5.7. The relationship between Turnstone individual roost position and roost size; (data are from observations of colour-ringed birds in 1991/92).

	Roost Size (number of conspecifics)		
	0 - 99	100 - 399	400+
Middle	23	29	29
Edge	25	64	27
Bottom	2	10	14

Table 5.8. The relationship between Turnstone conspecific roost density and roost size; (data are from observations of colour-ringed birds in 1991/92).

	Roost Size (number of conspecifics)			
	0 - 99	100 - 249	250 -399	400+
Low	12	7	12	10
Medium / Low	28	6	25	13
Medium	13	17	14	26
Medium / High	2	10	24	19
High	0	2	6	4

combining Medium / High and High: $\chi^2 = 39.462$, d.f. = 9, $C = 0.369$, $P < 0.001$). In order to reduce the influence of roost size on calculations involving roost position and conspecific density, data in all subsequent analyses have been taken solely from days on which the roost contained between 100 and 399 conspecifics inclusive.

There was, notably, a high correlation between roost position and conspecific roost density: middle positions were of higher density than both edge and bottom positions (data from observations in 1993/94: Kruskal-Wallis $\chi^2 = 41.124$, d.f. = 2, $P < 0.001$).

Resident and visitant colour-ringed Turnstones were found in similar positions within roosting flocks (Table 5.9; $\chi^2 = 4.341$, d.f. = 2, n.s.). There was similarly no difference in the roost positions of adult and first-winter Turnstones in 1991/92 (Table 5.10; combining edge and bottom: $\chi^2 = 0.165$, d.f. = 1, n.s.). In August and September 1993 however, adult Turnstones roosting on the inner pier within West Harbour, were found more often in the middle of flocks and first-winter birds more often at the edge of flocks (Table 5.11; $\chi^2 = 20.842$, d.f. = 1, $P < 0.001$).

The proportion of times that an individual was recorded in the middle of flocks was positively correlated to its dominance (data from 1992/93; Fig. 5.3; $r = 0.341$, d.f. = 35, $P < 0.05$ one-tailed), whilst the proportion of times that an individual was seen at the edge of flocks fell with increased dominance (Fig. 5.4; $r = -0.287$, d.f. = 35, $P < 0.05$ one-tailed). There was no relationship between individual dominance and the proportion of times that individuals were seen at the bottom of flocks (Fig. 5.5; $r = -0.147$, d.f. = 35, n.s.).

Resident and visitant Turnstones roosted at similar conspecific densities at West Harbour (Table 5.12; combining Medium / High with High: $\chi^2 = 0.472$, d.f. = 3, n.s.). Adult Turnstones, however, roosted at higher conspecific densities than first-winter Turnstones (Table 5.13; combining Medium / High with High: $\chi^2 = 52.197$, d.f. = 2, $P < 0.001$).

Table 5.9. Individual roost positions of resident and visitant Turnstones; (data are from observations of colour-ringed birds in 1992/93).

	Roost Position		
	Middle	Edge	Bottom
Resident	113	224	41
Visitant	41	52	8

Table 5.10. Individual roost positions of adult and first-winter Turnstones; (data are from observations of colour-ringed birds in 1991/92).

	Roost Position		
	Middle	Edge	Bottom
Adult	18	42	7
First-winter	5	17	3

Table 5.11. Individual roost positions of adult and first-winter Turnstones; (data are from observations of colour-ringed birds in August and September 1993).

	Roost Position	
	Middle	Edge
Adult	49	73
First-winter	12	89

Table 5.12. Conspecific roost densities of resident and visitant Turnstones; (data are from observations of colour-ringed birds in 1991/92 and 1992/93).

	Conspecific Roost Density				
	L	M / L	M	M / H	H
Resident	112	182	112	43	8
Visitant	28	48	26	14	1

L = Low, M / L = Medium / Low, M = Medium, M / H = Medium / High and H = High.

Table 5.13. Conspecific roost densities of adult and first-winter Turnstones; (data are from observations in 1991/92 and August and September 1993).

	Conspecific Roost Density				
	L	M / L	M	M / H	H
Adult	29	80	61	29	5
First-winter	59	47	13	4	3

Fig. 5.3. The relationship between the percentage of observations of individual Turnstones that were in the middle of roosting flocks and their dominance.

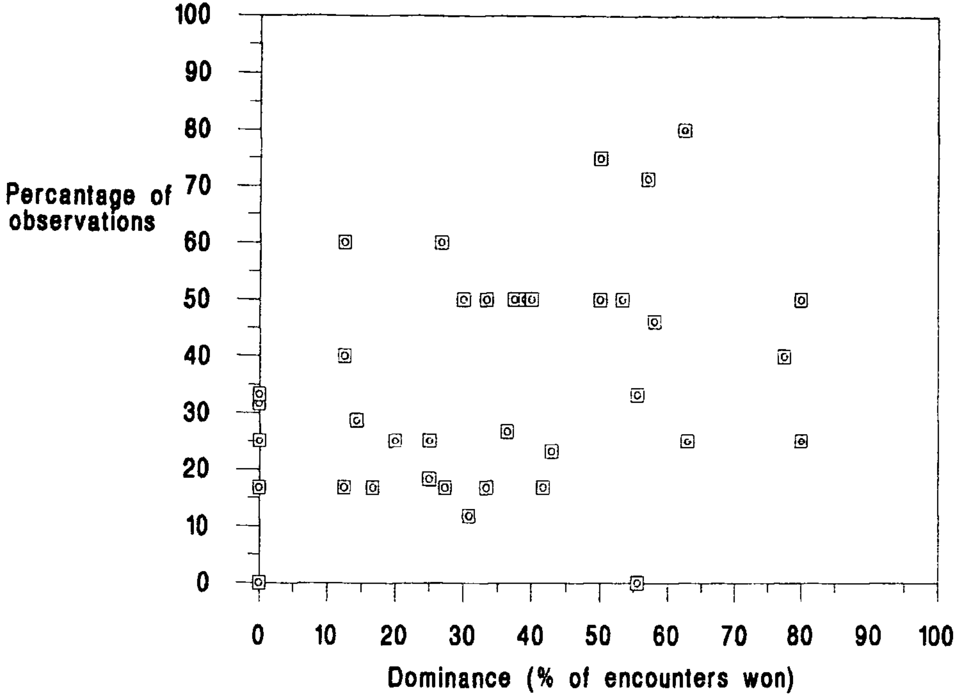


Fig. 5.4 The relationship between the percentage of observations of individual Turnstones that were at the edge of roosting flocks and their dominance.

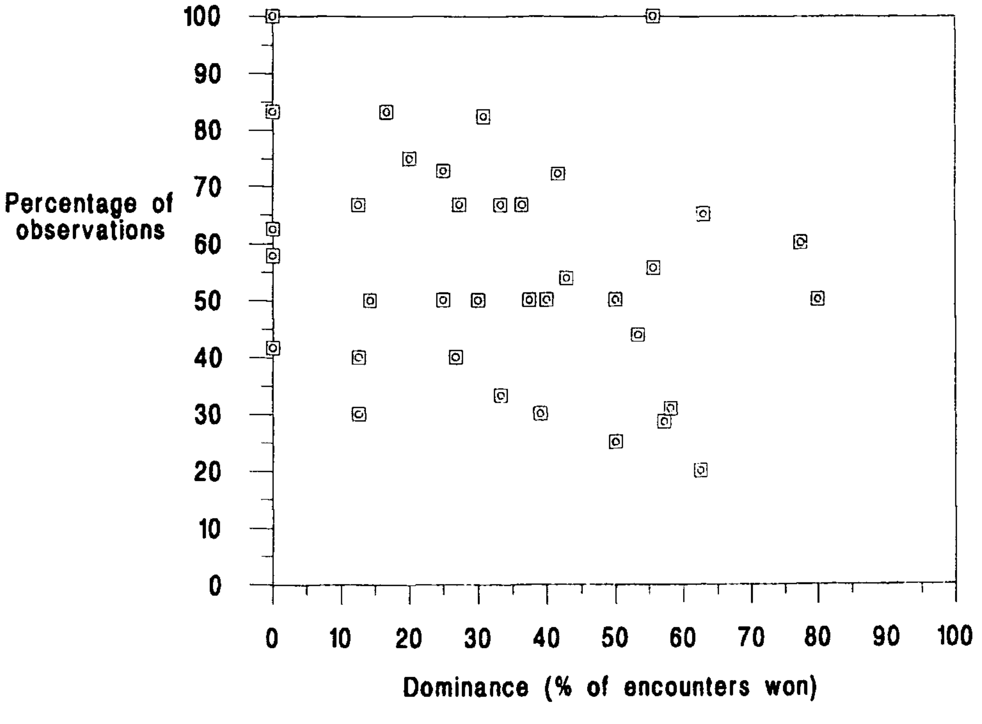


Fig. 5.5. The relationship between the percentage of observations of individual Turnstones that were at the bottom of roosting flocks and their dominance.

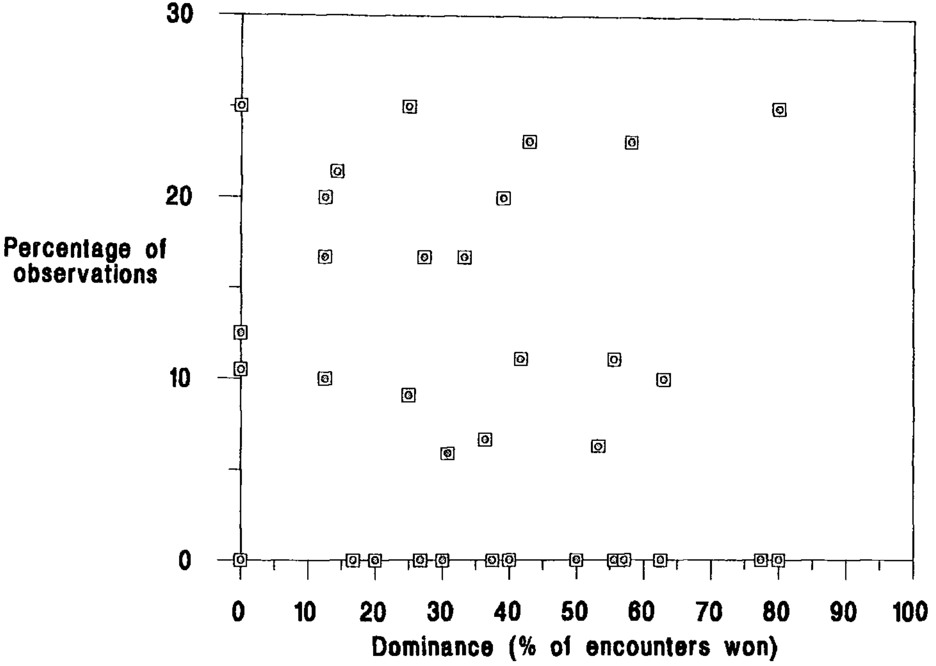
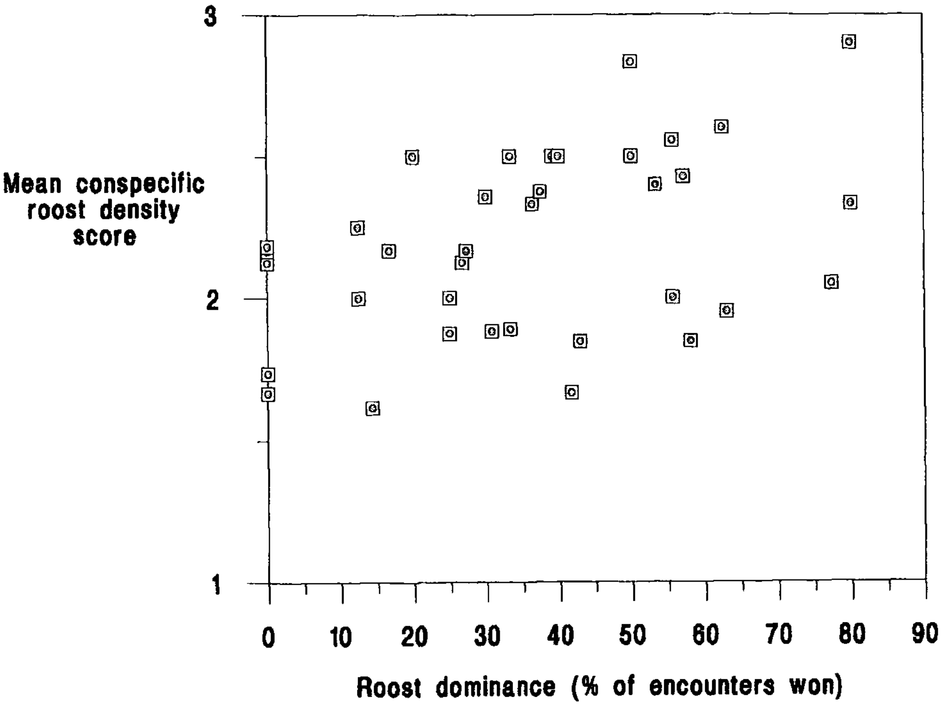


Fig. 5.6. The relationship between Turnstone dominance and individual conspecific roost density.



The mean conspecific density that an individual was seen roosting at was positively correlated to its dominance (Fig. 5.6; data from 1992/93; $r_s = 0.362$, $n = 37$, $P < 0.05$).

5.3.1.5. Attendance at the West Harbour roost and Headland high water sites.

Individual resident Turnstones were seen at the West Harbour roost proportionally less frequently in winter than autumn (Appendix 16; Wilcoxon $T = 58$, $n = 32$, $P < 0.001$). In spring however, individuals were seen at West Harbour as frequently as in either winter ($T = 42$, $n = 15$, n.s.) or autumn ($T = 43.5$, $n = 13$, n.s.).

Individual Turnstones resident on the Headland were correspondingly seen at Headland high water sites more frequently in winter than autumn (Appendix 16; $T = 6$, $n = 11$, $P < 0.01$ one-tailed). Insufficient data were available to analyse individual use of Headland high water sites in spring.

Headland residents were seen as many times at the West Harbour roost during winter 1992/93 as West Harbour to North Gare residents, though less often than North and South residents (one-way ANOVA $F_{2,18} = 4.394$, $P < 0.05$). In winter 1993/94 however, there was no such difference in the number of times that individuals from different areas visited the roost ($F_{2,16} = 0.117$, n.s.).

In 1992/93, the proportion of first-winter birds in roosting flocks of Turnstones was similar at West Harbour and at Inscar beach on Hartlepool Headland (Wilcoxon $T = 7$, $n = 7$, n.s.). In 1993/94, however, first-winter colour-ringed resident Turnstones visited the West Harbour roost less often than colour-ringed resident adult Turnstones (Mann-Whitney $z = 1.879$, $P < 0.05$ one-tailed).

As the number of times that a roost was used was partly determined by the origin of the individual, (*i.e.* its home feeding area), and thus in turn by the number of roosts available to it at high tide, individuals from different feeding areas are treated separately in subsequent analyses. In these investigations, comparisons are made between the number of times that individuals were present at the West Harbour roost or on Headland high water sites, during either autumn or winter. On occasions during both seasons, individuals disappeared from the study area, and in these cases data points are extrapolated to cover the full period in question; (provided that the individual was known to be alive and resident in the study area for a minimum of 50% of the high water searches). Analysis involving Headland residents excluded individuals known to be resident at Parton and which were seen to roost over high water at Steetley and Crimdon in preference to West Harbour.

The number of times that individual Turnstones were seen at the West Harbour roost was in part correlated to their dominance at the roost (data are from 1992/93). Figs. 5.7 and 5.8 show that in autumn 1992, individual roost attendance at West Harbour was positively correlated to individual dominance at the West Harbour roost, for both Headland residents ($r = 0.606$, d.f. = 10, $t = 2.406$, $P < 0.05$ one-tailed) and West Harbour to North Gare residents ($r = 0.755$, d.f. = 7, $t = 3.043$, $P < 0.01$ one-tailed). In winter this correlation was however not so strong, either for Headland residents (Fig. 5.9; $r = 0.449$, d.f. = 8, $t = 1.423$, $P < 0.10$), or for West Harbour to North Gare residents (Fig. 5.10; $r = 0.368$, d.f. = 6, $t = 0.969$, n.s.).

Individual feeding dominance (on home feeding areas), however, was not correlated with the number of times that individuals used the West Harbour roost in autumn, either for Headland residents (Fig. 5.11; $r = 0.333$, d.f. = 10, $t = 1.116$, n.s.) or for West Harbour to North Gare residents (Fig. 5.12; $r = 0.338$, d.f. = 6, $t = 0.879$, n.s.). This was also the case in winter, again for Headland residents (Fig. 5.13; $r = -0.237$, d.f. = 8, $t = -0.689$, n.s.) and for West Harbour to North Gare residents (Fig. 5.14; $r = 0.011$, d.f. = 6, $t = 0.026$, n.s.).

Individuals of high roost dominance were seen at the West Harbour roost on days of similar median high tide levels as more subordinate individuals (for Headland residents: $r_S = -0.027$, $n = 12$, n.s.; for West Harbour to North Gare residents: $r_S = -0.255$, $n = 9$, n.s.). There was a tendency however for Headland residents that were subordinate whilst feeding

Fig. 5.7. Turnstone roost attendance and dominance at West Harbour: Headland residents 10/8/92 - 24/10/92.

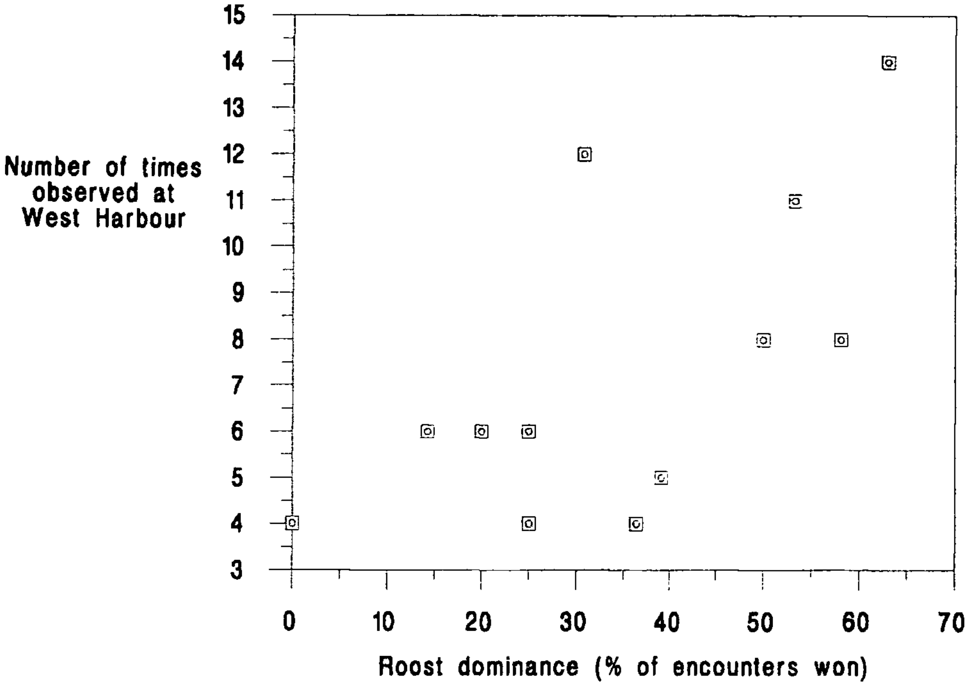


Fig. 5.8. Turnstone roost attendance and dominance at West Harbour: West Harbour to North Gare residents 8/9/92 - 24/10/92.

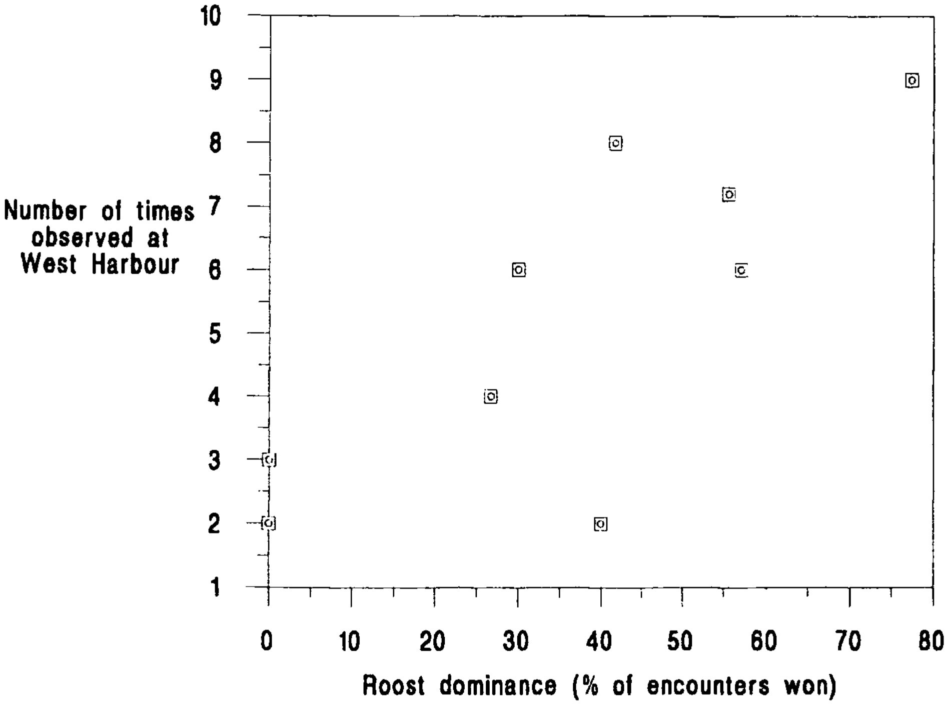


Fig. 5.9. Turnstone roost attendance and dominance at West Harbour: Headland residents 25/10/92 - 31/3/93.

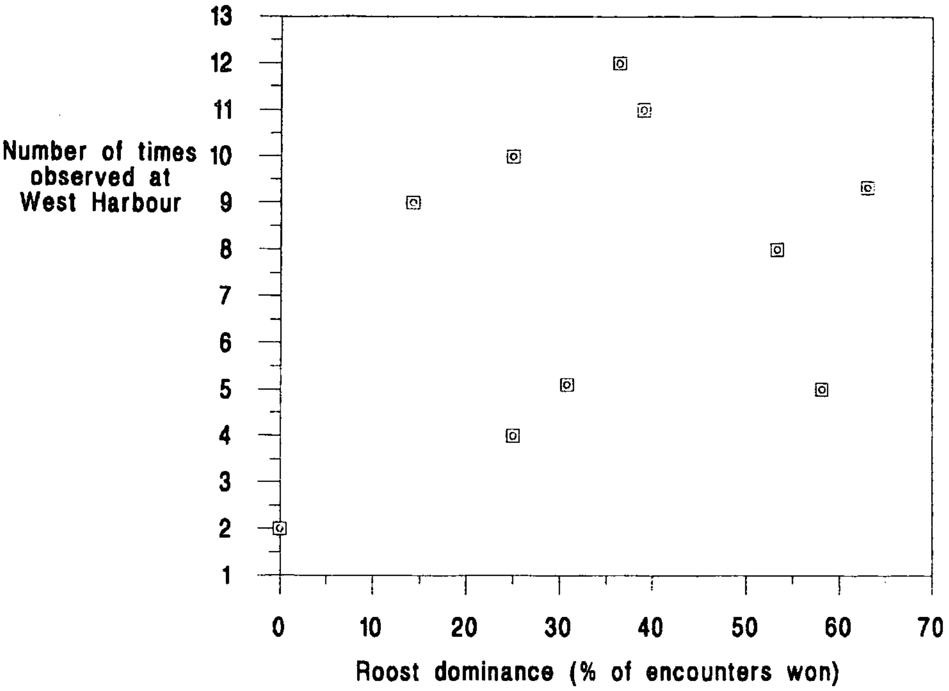


Fig. 5.10. Turnstone roost attendance and dominance at West Harbour: West Harbour to North Gare residents 25/10/92 - 31/3/93.

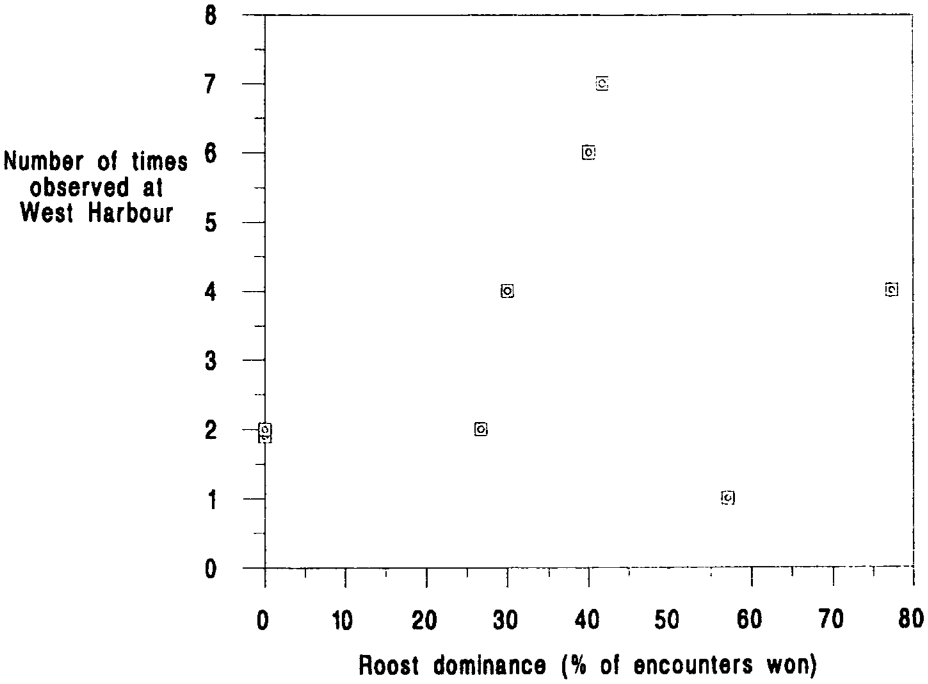


Fig. 5.11. Turnstone roost attendance at West Harbour and its relationship to dominance over low water: Headland residents 10/8/92 - 24/10/92.

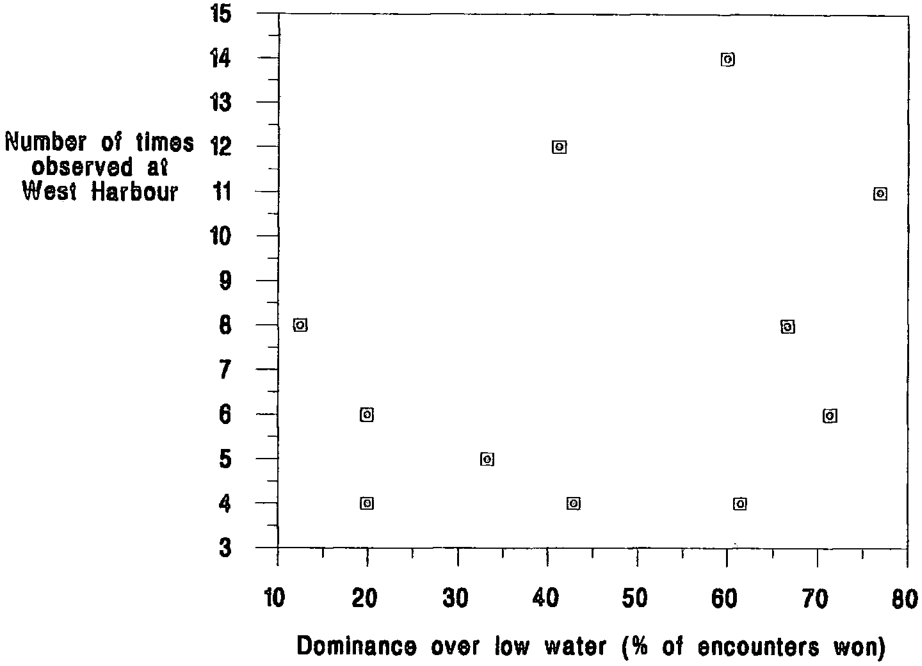


Fig. 5.12. Turnstone roost attendance at West Harbour and its relationship to dominance over low water: West Harbour to North Gare residents 8/9/92 - 24/10/92.

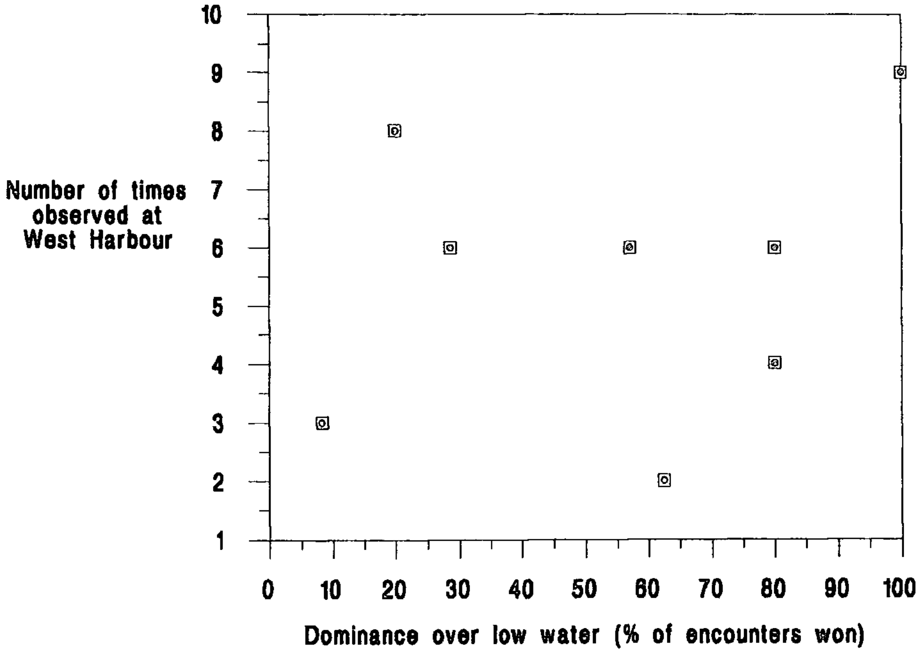


Fig. 5.13. Turnstone roost attendance at West Harbour and its relationship to dominance over low water: Headland residents 25/10/92 - 31/3/93.

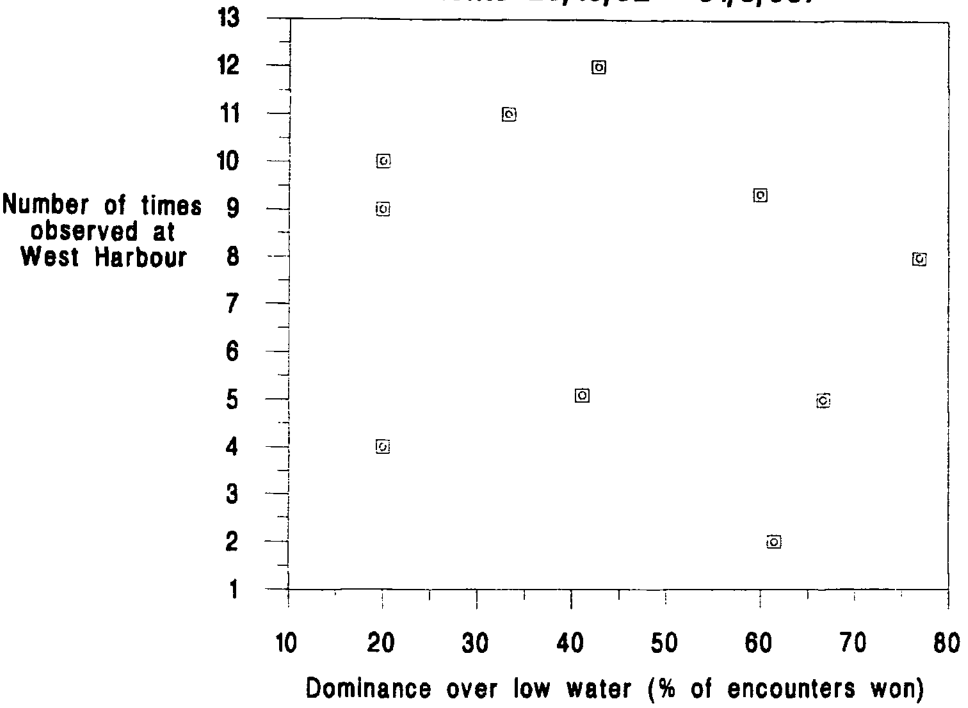
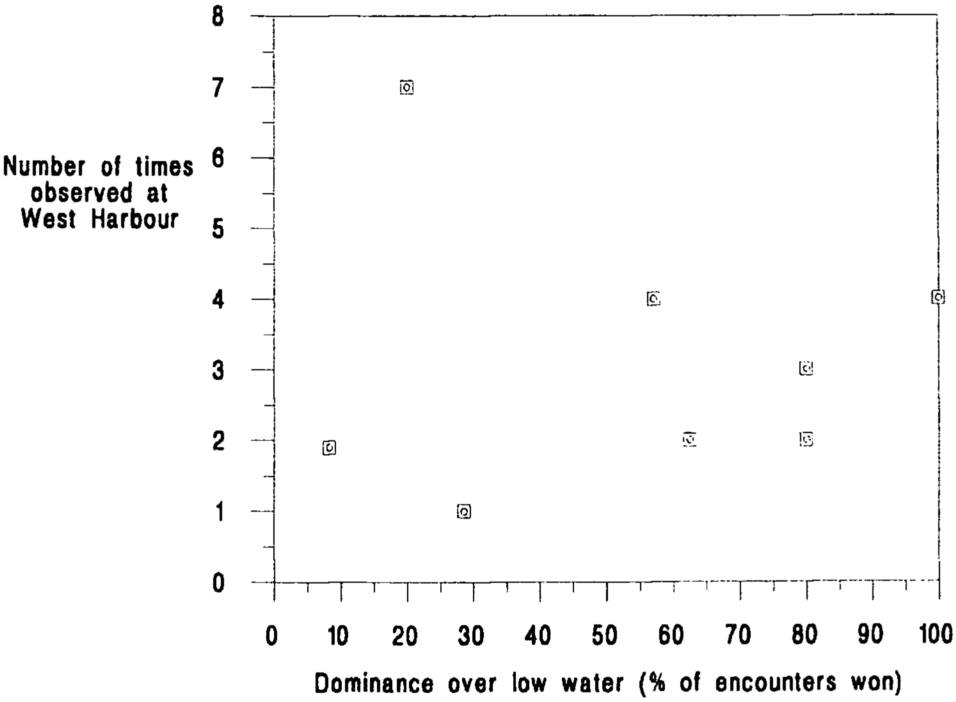


Fig. 5.14. Turnstone roost attendance at West Harbour and its relationship to dominance over low water: West Harbour to North Gare residents 25/10/92 - 31/3/93.



to visit the West Harbour roost on days of higher high tide levels than those that were more dominant (r_S = -0.484, n = 12, $P < 0.10$ one-tailed). There was no such relationship for West Harbour to North Gare residents (r_S = 0.503, n = 8, n.s.).

The number of times that individual Turnstones resident on the Headland used Headland high water sites was also related to dominance at the West Harbour roost (data are from 1992/93). Individuals that were subordinate at the West Harbour roost occurred on Headland high water sites more often than those more dominant at West Harbour, both in autumn (Fig. 5.15; r = -0.648, d.f. = 10, t = -2.692, $P < 0.05$ one-tailed) and in winter (Fig. 5.16; r = -0.659, d.f. = 8, t = -2.476, $P < 0.05$ one-tailed).

Individual feeding dominance, in contrast, was not correlated to attendance at Headland high water sites, again either in autumn (Fig. 5.17; r = -0.131, d.f. = 10, t = -0.418, n.s.) or winter (Fig. 5.18; r = -0.303, d.f. = 8, t = - 0.898, n.s.).

Individuals that were subordinate at the West Harbour roost occurred at Headland high water sites on days of higher high tide levels than those more dominant at West Harbour (r_S = 0.730, n = 10, $P < 0.05$). There was no such relationship with individual feeding dominance (r_S = 0.152, n = 10, n.s.).

5.3.2. Purple Sandpiper.

5.3.2.1. Segregation within the roost.

This section aims to establish whether Purple Sandpipers mixed freely together at the roost, or whether they segregated into groups from different feeding areas, of different sizes or different ages.

Tables 5.14 and 5.15 show the results of nearest neighbour analysis for groups of Purple Sandpipers from different feeding areas, in late winter / early spring 1993 and in winter and spring 1993/94 respectively. In the first period, individuals from the same area

Fig. 5.15. Turnstone attendance at Headland high water sites and its relationship to dominance at the West Harbour roost: 10/8/92 - 24/10/92.

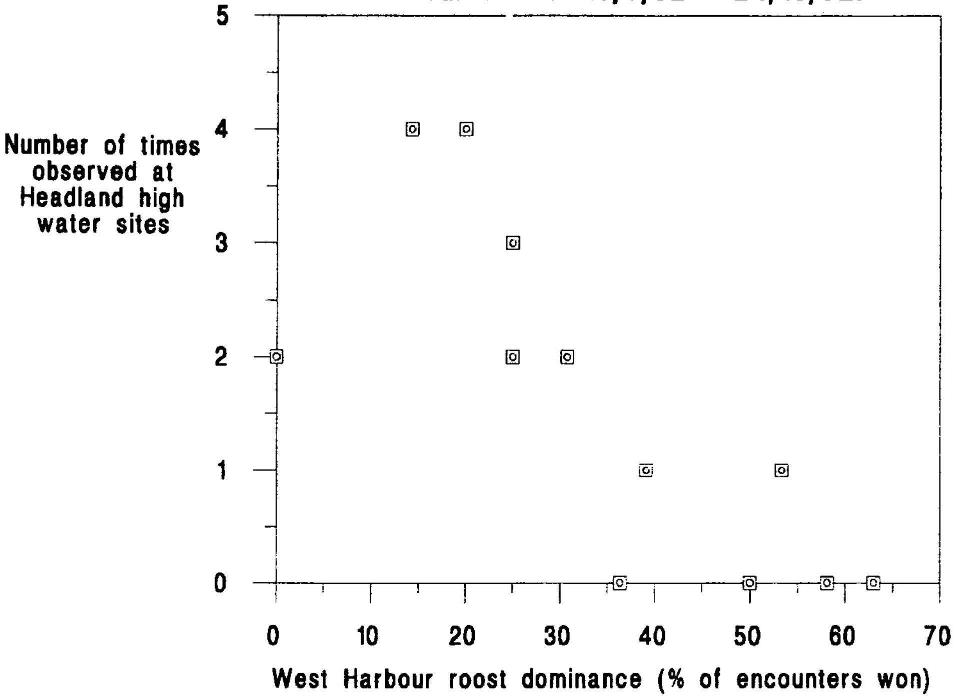


Fig. 5.16. Turnstone attendance at Headland high water sites and its relationship to dominance at the West Harbour roost: 25/10/92 - 31/3/93.

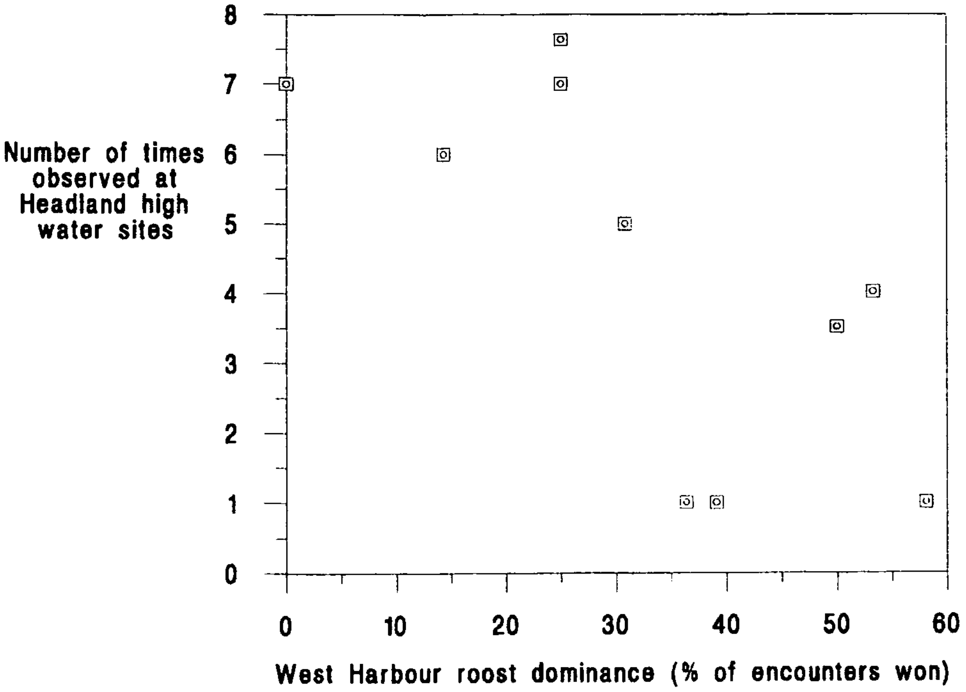


Fig. 5.17. Turnstone attendance at Headland high water sites and its relationship to dominance over low water: 10/8/92 - 24/20/92.

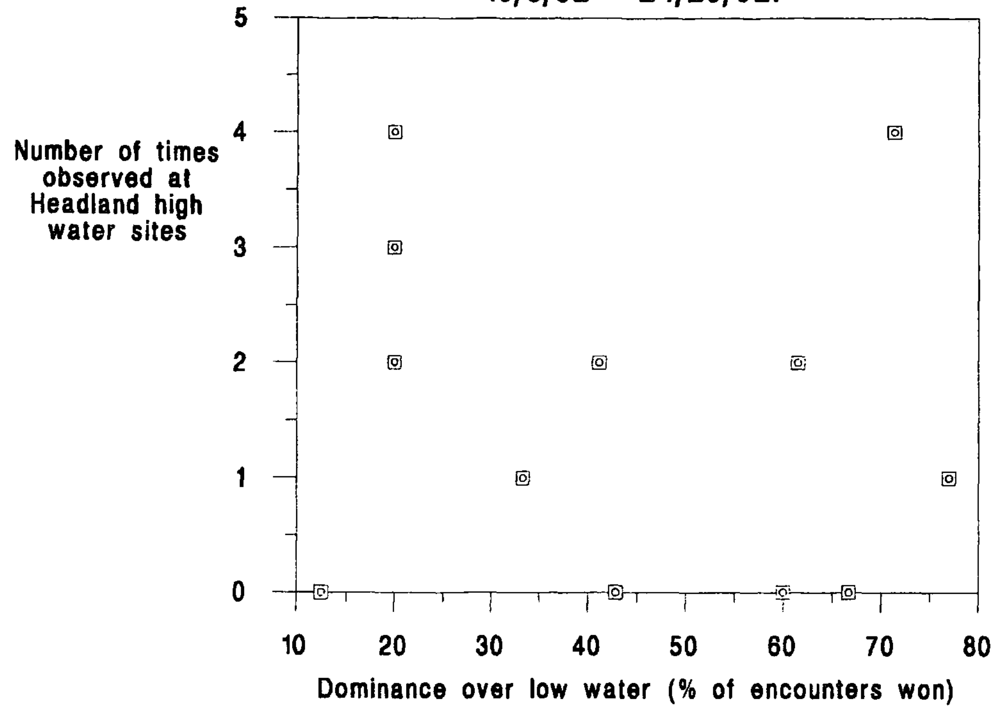
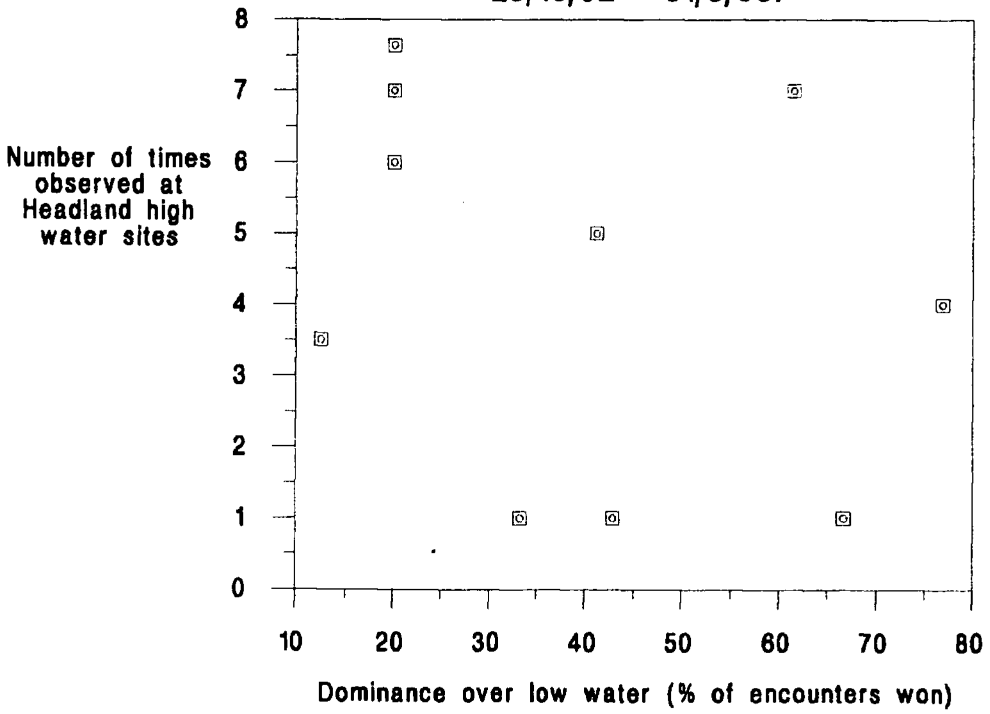


Fig. 5.18. Turnstone attendance at Headland high water sites and its relationship to dominance over low water: 25/10/92 - 31/3/93.



were each other's nearest neighbour no more or less than expected ($\chi^2 = 0.721$, d.f. = 1, n.s.). In winter and spring 1993/94 however, individuals resident in one area were the nearest neighbours of individuals from the same area significantly more often than expected (combining West Harbour to North Gare residents with North and South residents: $\chi^2 = 20.824$, d.f. = 1, $P < 0.001$). The difference may be due to inaccurate classification of individuals in the first period: most individuals were only caught in March 1993 and their classification for the period immediately after was based on only a few sightings before their departure in spring. Few individuals, however, were reclassified the following winter (see Chapter 2).

Table 5.16 shows the results of nearest neighbour analysis for groups of Purple Sandpipers of different bill-length size classes (data from late winter / early spring 1993). Individuals of the medium and large bill-length size classes were the nearest neighbours of individuals from their own size class significantly more often than expected ($\chi^2 = 11.991$, d.f. = 4, $P < 0.05$).

Table 5.17 shows the results of nearest neighbour analysis for groups of Purple Sandpipers of different ages. Individuals from the same age class were each other's nearest neighbour no more or less than expected ($\chi^2 = 2.272$, d.f. = 1, n.s.).

5.3.2.2. Intraspecific aggression at the roost.

Encounters over roosting sites comprised 60.1% ($n = 288$) of aggression recorded between Purple Sandpipers at the West Harbour roost, the remainder being caused by infringements of individual distance. The proportion of encounters attributable to roosting sites was significantly greater than it was for Turnstones ($\chi^2 = 4.677$, d.f. = 1, $P < 0.05$).

As wind speed increased, an increasing proportion of encounters were attributable to aggression over roosting sites (Table 5.18; $\chi^2 = 20.747$, d.f. = 6, $C = 0.259$, $P < 0.01$).

Table 5.14. Nearest colour-ringed neighbours of focal Purple Sandpipers from different areas; (data from 1992/93).

		Nearest Neighbour	
		H	WH
Focal Bird	H	24	18
	WH	25	29

H = Headland residents and WH = West Harbour to North Gare residents.

Table 5.15. Nearest colour-ringed neighbours of focal Purple Sandpipers from different areas; (data from 1993/94).

		Nearest Neighbour		
		H	WH	N + S
	H	29	7	1
Focal Bird	WH	11	25	3
	N + S	0	5	0

N + S = North and South residents.

Table 5.16. Nearest colour-ringed neighbours of focal Purple Sandpipers of different bill-length size classes.

		Nearest Neighbour		
		Small	Medium	Large
	Small	3	17	9
Focal Bird	Medium	12	39	6
	Large	5	11	11

Table 5.17. Nearest colour-ringed neighbours of focal Purple Sandpipers of different age classes.

		Nearest Neighbour	
		Adult	First-winter
Focal Bird	Adult	61	16
	First-winter	23	13

Most encounters involved simple threat displays with the wings held in (Table 5.19). Threat displays with the wings held out and pecking were less frequent; only one chase was recorded and there were no fights. Only 1.5% (*n* = 614) of encounters were not won by the initiator, a significantly lower proportion than for Turnstones ($\chi^2 = 14.163$, d.f. = 1, $P < 0.001$). In comparison to aggression amongst feeding Purple Sandpipers, there were fewer pecks and chases than expected in roosting aggression, but more threats with the wings held out (combining wings out to in with wings out; chases with peck-chases: $\chi^2 = 40.747$, d.f. = 4, $P < 0.001$). Encounters over roosting sites were of greater intensity than those caused by an infringement of individual distance (Table 5.20; combining wings out to in with wings out as 'threats with wings out'; pecks with chases as higher intensity displays: $\chi^2 = 13.843$, d.f. = 2, $C = 0.214$, $P < 0.001$).

The forms of aggression recorded between roosting Purple Sandpipers changed seasonally (Table 5.21; combining wings out to in with wings out as 'threats with wings out'; pecks with chases as higher intensity displays: $\chi^2 = 19.058$, d.f. = 4, $P < 0.001$). Pecks (and chases) were more frequent in autumn and less frequent in spring. Encounters involving one or both individuals holding their wings out were more frequent in spring and less frequent in winter.

The intensity of aggression also changed with wind speed (Table 5.22; combining wings out to in with wings out as 'threats with wings out'; pecks with chases as higher intensity displays: $\chi^2 = 33.059$, d.f. = 12, $C = 0.227$, $P < 0.001$). Pecks (and chases) were more frequent in higher winds and encounters with one or both individuals holding their wings out less frequent.

The rate of encounters over roosting sites, which varied between 0 and 5 per five minute period, per individual Purple Sandpiper, increased as wind speed became greater (Fig. 5.19; $t = 4.268$, d.f. = 161, $P < 0.001$ one-tailed); the rate was also greater the earlier it was relative to high water (Fig. 5.20; $t = -2.322$, d.f. = 161, $P < 0.05$ one-tailed):

Table 5.18. The cause of encounters between Purple Sandpipers at the West Harbour roost and the relationship with wind speed; (data from August 1993 to May 1994).

	Wind Speed						
	1	2	3	4	5	6	7
Roosting Site	6	32	31	23	34	35	12
Individual Distance	4	40	28	8	23	9	3

Figures represent frequencies of encounters recorded.

Table 5.19. The frequencies of different forms of aggressive interactions recorded between Purple Sandpipers roosting at West Harbour; (data from February 1992 to May 1994).

	Threat			Peck	Chase	Peck-chase / Fight
	Wings in	Wings out to in	Wings out			
Initiator Won	454	64	9	77	1	0
Initiator Lost	4	1	4	0	0	0
Total	458 (74.6)	65 (10.6)	13 (2.1)	77 (12.5)	1 (0.2)	0

Figures represent frequencies of encounters recorded; figures in parentheses are percentages of the total number of encounters recorded.

Table 5.20. The intensity and cause of encounters between Purple Sandpipers at the West Harbour roost; (data from August 1993 to May 1994).

	Wings in	Wings out to in	Wings out	Peck	Chase
Roosting Site	112	31	3	27	0
Individual Distance	97	11	1	5	1

Figures represent frequencies of encounters recorded.

Table 5.21. The intensity of encounters between Purple Sandpipers at the West Harbour roost and its relationship with season; (see 3.3.1.1.2 for definition of seasons; data from February 1992 to May 1994).

Season	Wings in	Wings out to in	Wings out	Peck	Chase
Autumn	39	7	1	11	0
Winter	386	45	10	64	1
Spring	33	13	2	2	0

Figures represent frequencies of encounters recorded.

Table 5.22. The intensity of encounters between Purple Sandpipers at the West Harbour roost and its relationship with wind speed; (data from February 1992 to May 1994).

Wind speed (Beaufort)	Wings in	Wings out to in	Wings out	Peck	Chase
1	10	4	0	3	0
2	98	22	8	10	0
3	65	15	1	7	0
4	155	10	3	31	0
5	71	8	1	10	1
6	43	5	0	14	0
7	12	1	0	2	0

Figures represent frequencies of encounters recorded.

Fig. 5.19. The relationship between the rate of intraspecific aggression over roosting sites per individual Purple Sandpiper and wind speed.

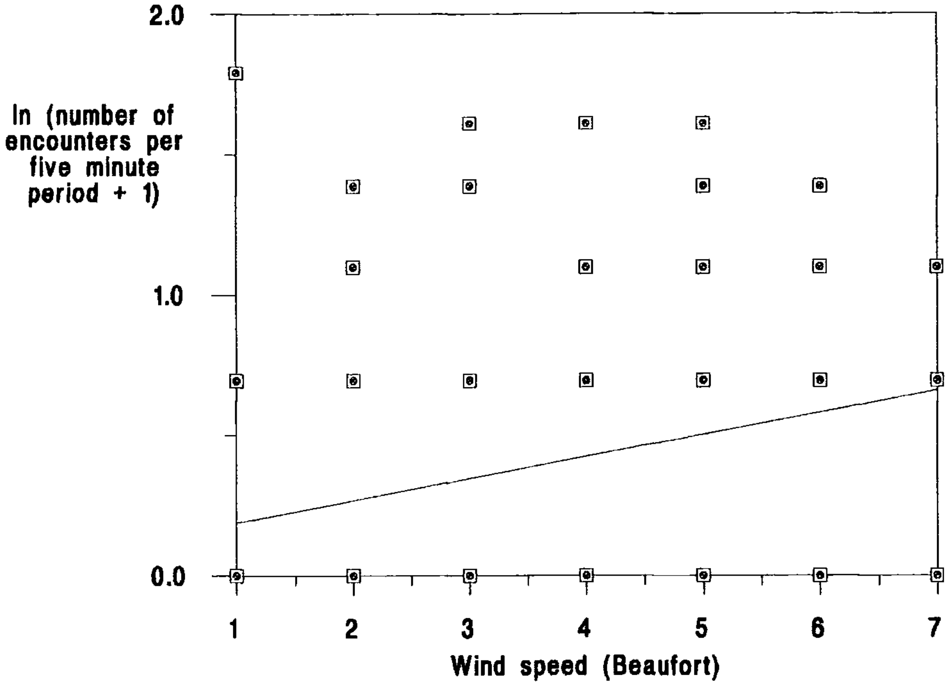
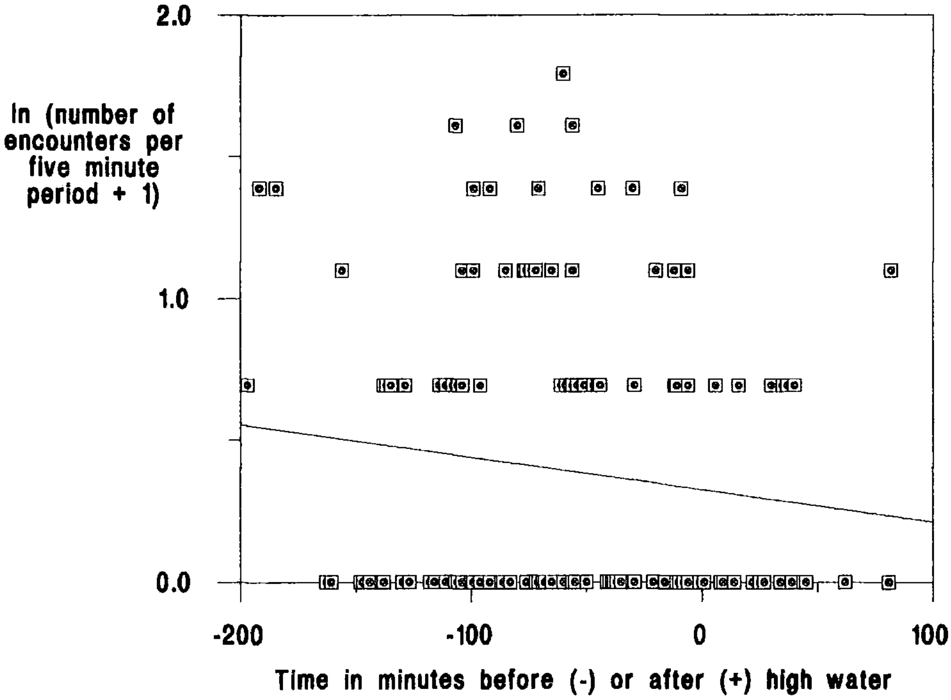


Fig. 5.20. The relationship between the rate of intraspecific aggression over roosting sites per individual Purple Sandpiper and time.



$$\ln(\text{Aggression Rate} + 1) = 0.021 + 0.088\ \text{Wind Speed (Beaufort)} - 1.5 \times 10^{-3}\ \text{T}$$

where T is the time in minutes before (-) or after (+) high water; ($r^2 = 0.120$; $F_{2,161} = 11.026$, $P < 0.001$).

No significant trends were detected in multiple regression between the rate of aggression over roosting sites and conspecific roost density ($t = 0.867$, $n = 112$, n.s.) or date relative to midwinter ($t = -0.116$, n.s.). Similarly the rate of encounters over roosting sites not related to roosting position (using residuals from the above equation: Kruskal-Wallis $\chi^2 = 1.505$, d.f. = 2, n.s.).

The rate of intraspecific encounters resulting from infringements of individual distance was not related to wind speed ($t = 0.580$, $n = 162$, n.s.), conspecific roost density ($t = 0.918$, n.s.), time relative to high water ($t = -0.874$, n.s.) or date relative to midwinter ($t = -1.023$, n.s.). Similarly the rate of encounters over infringements of individual distance was not related to roost position (Kruskal-Wallis $\chi^2 = 0.406$, d.f. = 2, n.s.).

5.3.2.3. Purple Sandpiper dominance hierarchies at the West Harbour roost.

Dominance hierarchies for Purple Sandpipers roosting at West Harbour are shown for each year in Appendix 15. Data were only collected from winter and spring each year, when the proportions of the two populations present at Hartlepool were stable. Prior to this, in autumn, the Norwegian population was more dominant in this area (see 3.3.1.1.2 for definition of seasons). In 1992/93, only one of 30 interactions between colour-ringed individuals went against rank order and in 1993/94, seven of 25 (combining years: Sign Test $n = 55$, $x = 8$, $P < 0.001$). As with Turnstones, Purple Sandpiper dominance hierarchies at the roost were thus very stable within years. There was a positive correlation between dominance of individuals at the West Harbour roost in 1992/93 and 1993/94 ($r_s = 0.783$, $n = 20$, $P < 0.001$). As, however, individuals tended to increase in dominance between their first and second winters (see below), individual dominance was calculated separately for each year.

The relationship between dominance and body size was investigated for Purple Sandpipers using bill-length size classes. In the present study, bill-length size class was highly significantly, positively correlated to body mass and wing-length (see also Summers 1988, Summers *et al.* 1992). In 1992/93, Purple Sandpiper dominance rank at the West Harbour roost was significantly related to bill-length size class (Kruskal-Wallis $\chi^2 = 6.588$, d.f. = 2, $P < 0.05$, n (small) = 7, n (medium) = 19, n (large) = 6): individuals of the large size class were of high rank and those of the small size class of low rank. Larger size classed individuals won 16 of 19 interactions with individuals of smaller size classes (Sign Test $P < 0.01$ one-tailed). Female Norwegian Purple Sandpipers tended to be of lower dominance rank than females of the probable Greenland / Canada population, though this tendency was not significant (Mann-Whitney $z = 1.604$, $P < 0.10$ one-tailed, n (Norway) = 4, n (Greenland/Canada) = 6). Male and female Norwegian Purple Sandpipers showed no significant difference in dominance rank ($z = 0.677$, n.s., n (male) = 7, n (female) = 4).

In 1993/94, dominance rank was related to bill-length size class only at the 10% probability level (Kruskal-Wallis $\chi^2 = 5.427$, d.f. = 2, $P < 0.10$, n (small) = 6, n (medium) = 14, n (large) = 2). Individuals of the small size class were of lower rank than individuals of the medium size class (Mann-Whitney $z = 2.064$, $P < 0.05$ one-tailed) and than individuals of the large size class ($z = 1.677$, $P < 0.05$ one-tailed). Individuals of the medium and large size classes were of similar rank ($z = 0.795$, n.s.). As in 1992/93, larger size classed individuals won a higher proportion of interactions with individuals of smaller size classes (Sign Test $n = 14$, $x = 3$, $P < 0.05$ one-tailed). Female Norwegian Purple Sandpipers tended, though insignificantly, to be of greater dominance rank than male Norwegian Purple Sandpipers (Mann-Whitney $z = 1.497$, $P < 0.10$ one-tailed, n (male) = 6, n (female) = 4). Female Norwegian Purple Sandpipers and females of the probable Greenland / Canada population were of similar rank (Mann-Whitney $U = 3$, n (Greenland/Canada) = 6, n (Norway) = 4, n.s.).

Within small and large bill-length size classes, dominance was not related to size, as expressed by bill-length, either in 1992/93 (small: $r_s = 0.280$, $n = 7$, n.s.; large: $r_s = 0.464$, $n = 6$, n.s.) or 1993/94 (small: $r_s = -0.406$, $n = 6$, n.s.). Within the medium bill-length size class however, dominance was related to bill-length in 1992/93 ($r_s = 0.415$, $n = 19$, $P < 0.05$ one-tailed), though not in 1993/94 ($r_s = 0.310$, $n = 14$, n.s.).

The dominance rank at the West Harbour roost, of those Purple Sandpipers classed as Headland, West Harbour to North Gare and North and South residents did not differ, either in 1992/93 (Mann-Whitney $z = 0.021$, n.s.) or in 1993/94 (Kruskal-Wallis $\chi^2 = 0.061$, d.f. = 2, n.s.). Headland residents won 13 of 19 interactions with West Harbour to North Gare residents (Sign Test, n.s.).

There was no difference in the dominance rank of adult and first-winter Purple Sandpipers at the West Harbour roost in 1992/93 (Mann-Whitney $z = 0.080$, n.s., n (adult) = 21, n (first-winter) = 11). Adults however, won 31 (67.4%) of 46 interactions with first-winter birds (Sign Test $P < 0.05$ one-tailed). The dominance rank of second-winter Purple Sandpipers at the West Harbour roost in 1993/94 did not differ from that of older adults (Mann-Whitney $z = 0.949$, n.s., n (adult) = 14, n (second-winter) = 6). Colour-ringed second-winter Purple Sandpipers won seven of nine interactions with older, colour-ringed adults (Sign Test n.s.). There was a tendency for individuals to be of higher roosting dominance in their second winter than in their first, though this tendency was insignificant (Wilcoxon $T = 7$, $n = 7$, n.s.).

Roosting dominance was positively correlated to feeding dominance (on home feeding areas) in 1992/93 (combining Headland with West Harbour to North Gare residents: $r_s = 0.538$, $n = 17$, $P < 0.05$ one-tailed), though not in 1993/94 ($r_s = 0.064$, $n = 19$, n.s.). Three 'pairs' of colour-ringed Purple Sandpipers were seen interacting both whilst roosting at West Harbour and whilst feeding. In one of these cases the outcome of the interaction was different when roosting than when feeding, and in two cases the same.

5.3.2.4. Position at the roost and conspecific roost density.

Purple Sandpiper roost density and to a lesser degree, individual roost position, were both affected by the number of conspecifics at the roost. As the number of conspecifics at the roost increased, more individuals tended to be found in the middle of flocks (Table 5.23; $\chi^2 = 9.397$, d.f. = 4, $C = 0.181$, $P < 0.10$), whilst conspecific densities became significantly greater (Table 5.24; $\chi^2 = 12.091$, d.f. = 4, $C = 0.204$, $P < 0.05$). In order to reduce the influence of roost size on calculations involving roost position and conspecific roost density, data in subsequent analyses have been taken, (as with Turnstones), solely from days on which the roost contained 100 or more conspecifics; (Purple Sandpiper numbers at West Harbour never exceeded 399, as those of Turnstone did).

There was, notably, a high correlation between roost position and conspecific roost density: middle positions were of higher density than both edge and bottom positions (data from observations in 1993/94; Kruskal-Wallis $\chi^2 = 40.644$, d.f. = 2, $P < 0.001$).

Adult Purple Sandpipers were found more often in the middle of roost flocks than first-winter individuals, less often at the edges, though in similar proportions at the bottom (Table 5.25; $\chi^2 = 9.013$, d.f. = 2, $P < 0.05$). Individuals of different bill-length size classes did not differ in the frequency with which they were seen in the middle, edge and bottom of flocks however (Table 5.26; $\chi^2 = 2.883$, d.f. = 4, n.s.).

The proportion of times that an individual Purple Sandpiper was recorded at the edge of flocks was negatively correlated with its dominance (data from 1992/93; Fig. 5.21; $r = -0.518$, d.f = 19, $P < 0.01$ one-tailed), whilst the proportion of times that an individual was seen at the bottom of flocks increased with dominance (Fig. 5.22; $r = 0.560$, d.f. = 19, $P < 0.01$). There was a positive relationship between individual dominance and the

Table 5.23. The relationship between Purple Sandpiper individual roost position and roost size; (data are from observations of colour-ringed birds in 1992/93).

	Roost Size (number of conspecifics)		
	0 - 99	100 - 169	170+
Middle	21	38	54
Edge	45	37	44
Bottom	12	13	14

Table 5.24. The relationship between Purple Sandpiper conspecific roost density and roost size; (data are from observations of colour-ringed birds in 1992/93).

	Roost Size (number of conspecifics)		
	0 - 99	100 - 169	170+
Low	22	17	29
Medium / Low	48	44	52
Medium	7	23	30
Medium / High	1	2	1
High	0	2	0

Table 5.25. Individual roost positions of adult and first-winter Purple Sandpipers; (data are from observations of colour-ringed birds in 1992/93).

	Roost Position		
	Middle	Edge	Bottom
Adult	74	49	21
First-winter	18	32	6

Table 5.26. Individual roost positions of Purple Sandpipers of different bill-length size classes; (data are from observations of colour-ringed birds in 1992/93).

	Roost Position		
	Middle	Edge	Bottom
Small	10	11	2
Medium	37	39	11
Large	26	15	6

Table 5.27. Conspecific roost densities of adult and first-winter Purple Sandpipers; (data are from observations of colour-ringed birds in 1992/93).

	Conspecific Roost Density				
	L	M / L	M	M / H	H
Adult	27	69	48	0	0
First-winter	19	27	9	1	0

L = Low, M / L = Medium / Low, M = Medium, M / H = Medium / High and H = High.

Table 5.28. Conspecific roost densities of Purple Sandpipers of different bill-length size classes; (data are from observations of colour-ringed birds in 1992/93).

	Conspecific Roost Density				
	L	M / L	M	M / H	H
Small	7	14	2	0	0
Medium	20	43	23	1	0
Large	10	21	16	0	0

Fig. 5.21. The relationship between the percentage of observations of individual Purple Sandpipers that were at the edge of roosting flocks and their dominance.

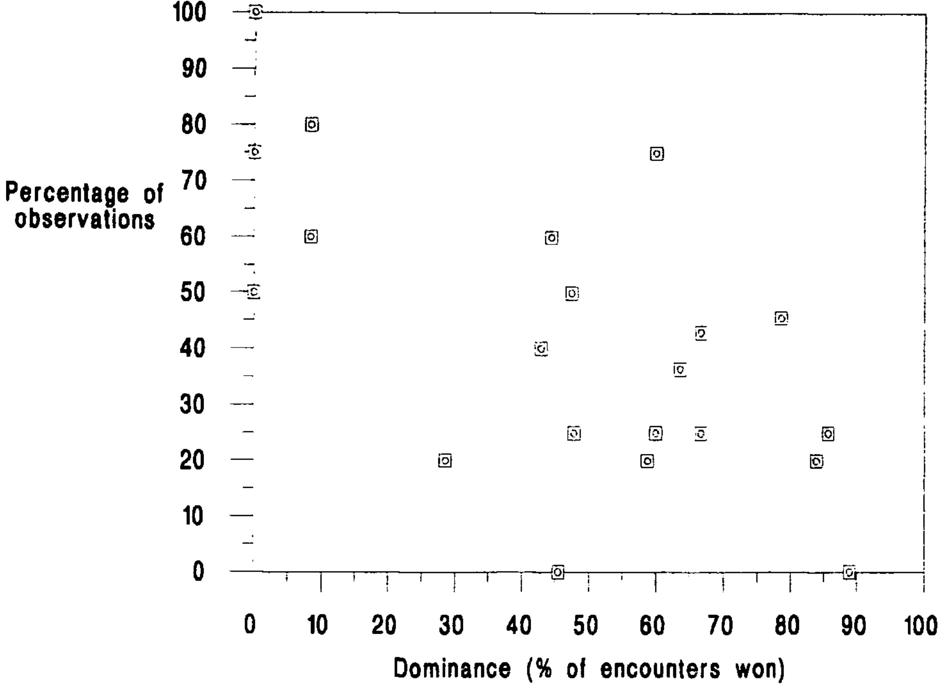


Fig. 5.22. The relationship between the percentage of observations of individual Purple Sandpipers that were at the bottom of roosting flocks and their dominance.

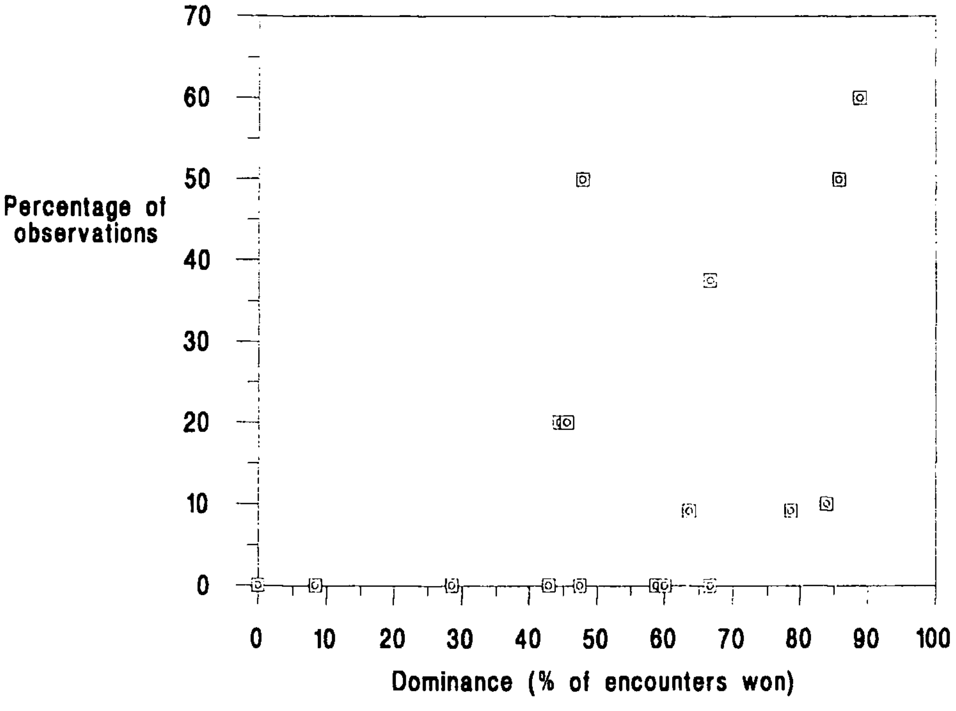


Fig. 5.23. The relationship between the percentage of observations of individual Purple Sandpipers that were in the middle of roosting flocks and their dominance.

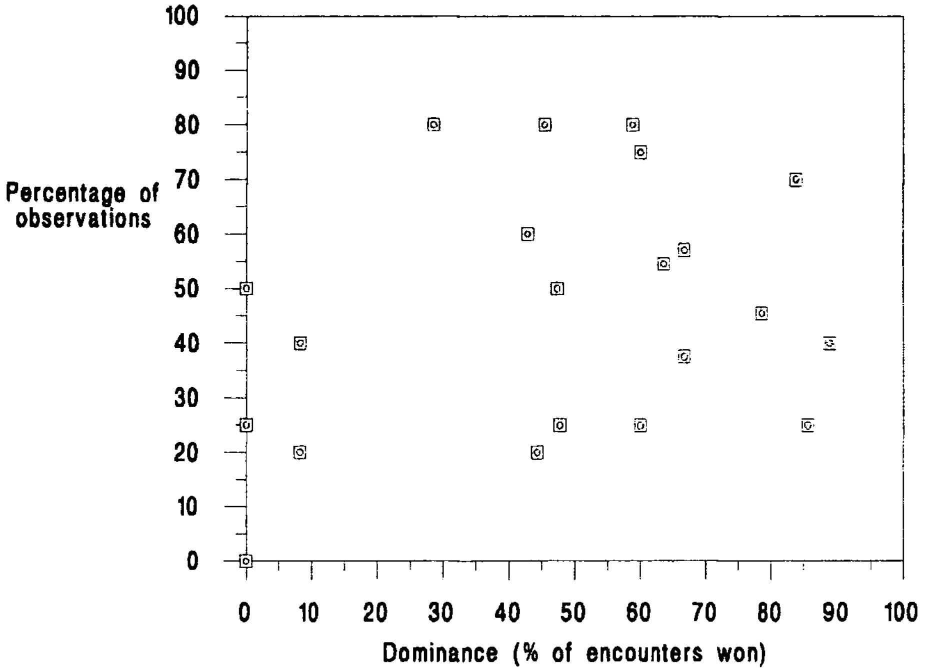
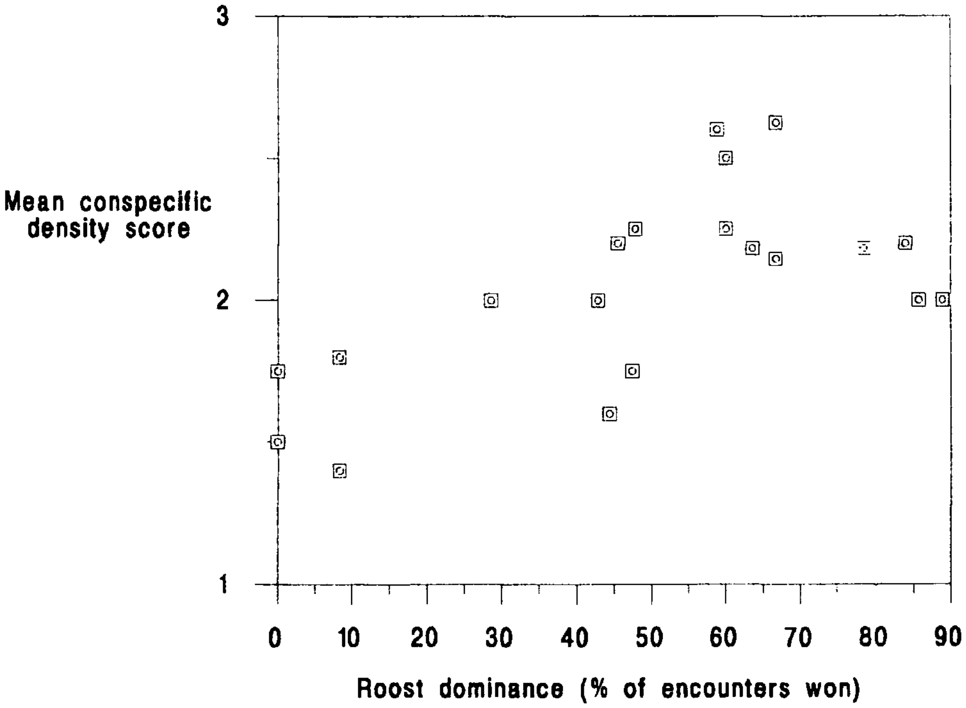


Fig. 5.24. Purple Sandpiper dominance and its relationship to individual conspecific roost density.



proportion of times that individuals were seen in the middle of flocks (Fig. 5.23; $r = 0.384$, d.f. = 19, $P < 0.05$ one-tailed).

Adult Purple Sandpipers were found at higher conspecific roost densities than first-winter Purple Sandpipers (Table 5.27; combining Medium, Medium / High and High: $\chi^2 = 7.370$, d.f. = 2, $C = 0.189$, $P < 0.05$). Individuals of different bill-length size classes were though found at similar conspecific roost densities (Table 5.28; combining Medium, Medium / High and High: $\chi^2 = 5.154$, d.f. = 4, $C = 0.178$, n.s.).

The mean conspecific density that an individual was recorded roosting at, was positively correlated to its dominance (data from 1992/93; Fig. 5.24; $r_s = 0.609$, $n = 21$, $P < 0.01$).

5.3.2.5. Attendance at the West Harbour roost and Headland high water sites.

Individual resident Purple Sandpipers were seen at the West Harbour roost proportionally less frequently in winter than in autumn (Appendix 16; Wilcoxon $T = 0$, $n = 8$, $P = 0.01$). Individuals were however seen at West Harbour as frequently in spring as in either winter ($T = 34.5$, $n = 13$, n.s.) or autumn ($T = 5$, $n = 6$, n.s.). Insufficient data were available to analyse seasonal variation in individual use of Headland high water sites.

Headland residents were seen less often at the West Harbour roost during late winter / early spring 1993 than West Harbour to North Gare residents ($t = 2.801$, d.f. = 31, $P < 0.01$). Adult Purple Sandpipers were seen at West Harbour as many times as first-winter Purple Sandpipers, whether they were Headland residents ($t = 1.308$, d.f. = 15, n.s.) or West Harbour to North Gare residents ($t = 0.869$, d.f. = 14, n.s.). There was no difference in the proportion of first-winter birds in flocks of Purple Sandpipers at West Harbour and on Headland high water sites in 1992/93 (Wilcoxon $T = 6$, $n = 6$, n.s.).

The number of times that an individual Purple Sandpiper was seen at the West Harbour roost was also in part related to the individual's dominance at the roost. Fig. 5.25 shows that in late winter / early spring 1993, Headland residents visited the West Harbour roost more frequently, if they were more dominant there ($r = 0.495$, d.f. = 13, $t = 2.052$, $P < 0.05$ one-tailed). There was no such relationship for West Harbour to North Gare residents in the same period however (Fig. 5.26; $r = -0.286$, d.f. = 13, $t = -1.074$, n.s.). The difference between individuals from the different areas can be accounted for by the lack of suitable alternative high water sites for Purple Sandpipers resident between West Harbour and North Gare. The lack of alternate sites meant that individuals from this area attended the West Harbour roost more frequently than those from the Headland and there was little variation between individuals.

In winter 1993/94, there was no relationship between roost attendance and individual roost dominance, for either Headland residents (Fig. 5.27; $r = 0.177$, d.f. = 9, $t = 0.541$, n.s.) or West Harbour to North Gare residents (Fig. 5.28; $r = 0.280$, d.f. = 5, $t = 0.651$, n.s.).

Individual feeding dominance (on home feeding areas) was slightly, though insignificantly, correlated with an individual's frequency of use of the West Harbour roost for Headland residents in late winter / early spring 1992 (Fig. 5.29; $r = 0.493$, d.f. = 9, $t = 1.702$, $P < 0.10$). There was no such relationship for West Harbour to North Gare residents in the same period (Fig. 5.30; $r = 0.098$, d.f. = 6, $t = -0.240$, n.s.).

In winter 1993/94, there was no correlation between individual feeding dominance and attendance at the West Harbour roost for either Headland residents (Fig. 5.31; $r = -0.025$, d.f. = 9, $t = -0.074$, n.s.) or West Harbour to North Gare residents (Fig. 5.32; $r = 0.219$, d.f. = 5, $t = 0.502$, n.s.).

In late winter / early spring 1993, Headland residents that were subordinate at West Harbour tended, though insignificantly, to be seen at the West Harbour roost on days of

Fig. 5.25. Purple Sandpiper roost attendance and dominance at West Harbour: Headland residents 8/3/93 - 7/4/93.

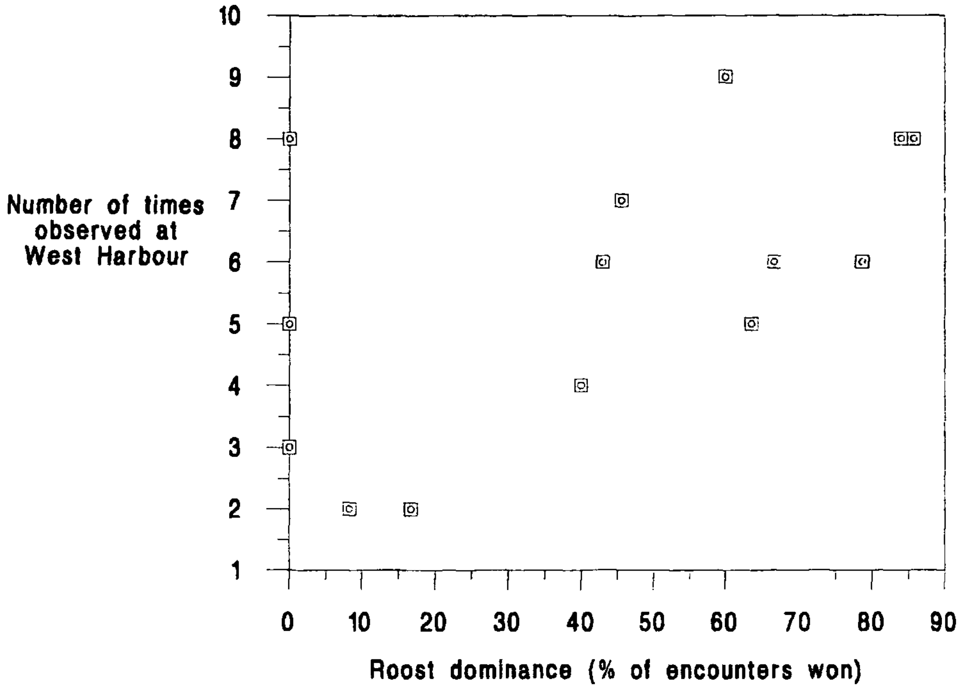


Fig. 5.26. Purple Sandpiper roost attendance and dominance at West Harbour: West Harbour to North Gare residents 8/3/93 - 7/4/93.

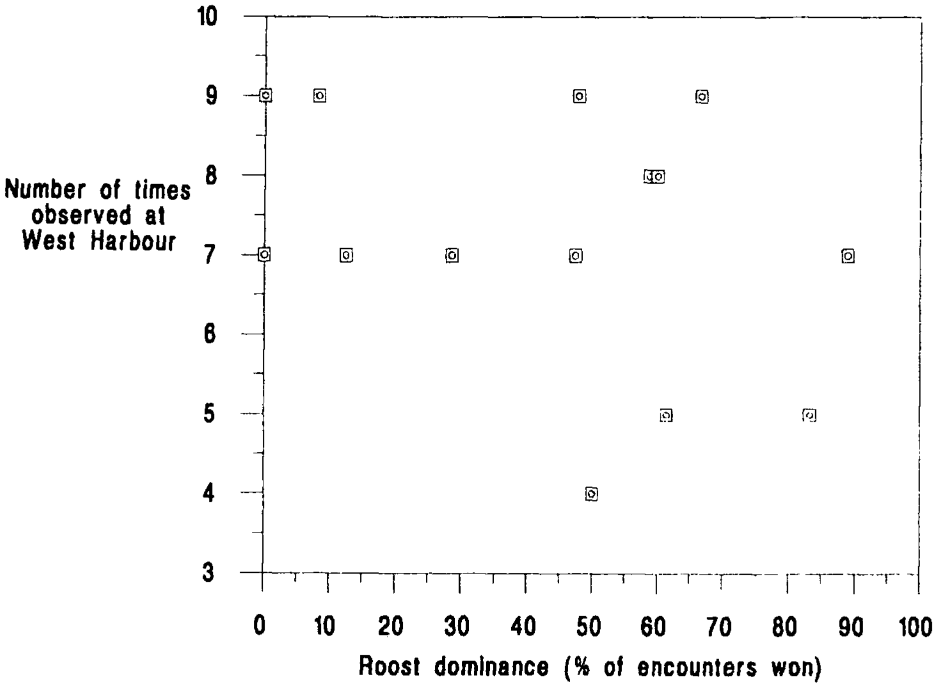


Fig. 5.27. Purple Sandpiper roost attendance and dominance at West Harbour: Headland residents 21/12/93 - 31/3/94.

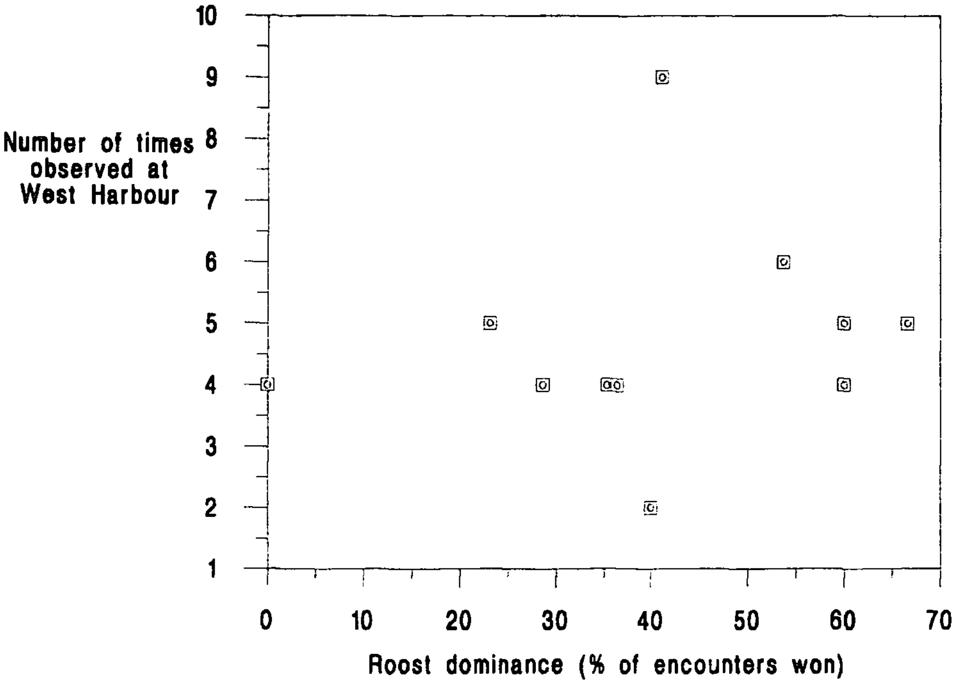


Fig. 5.28. Purple Sandpiper roost attendance and dominance at West Harbour: West Harbour to North Gare residents 15/11/93 - 31/3/94.

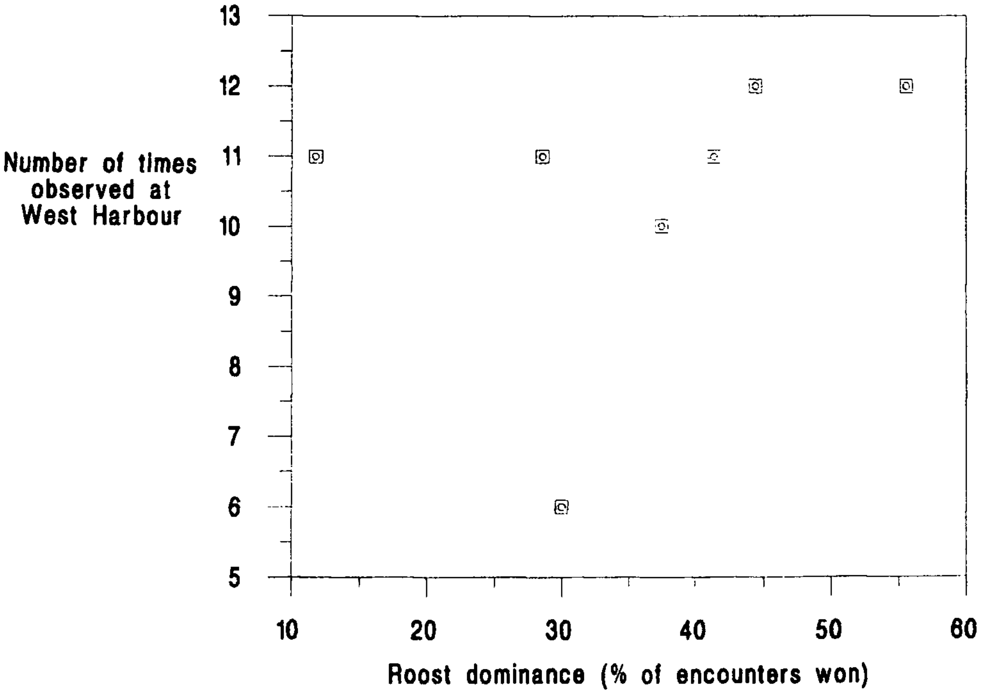


Fig. 5.29. Purple Sandpiper roost attendance at West Harbour and its relationship to dominance over low water: Headland residents 8/3/93 - 7/4/93.

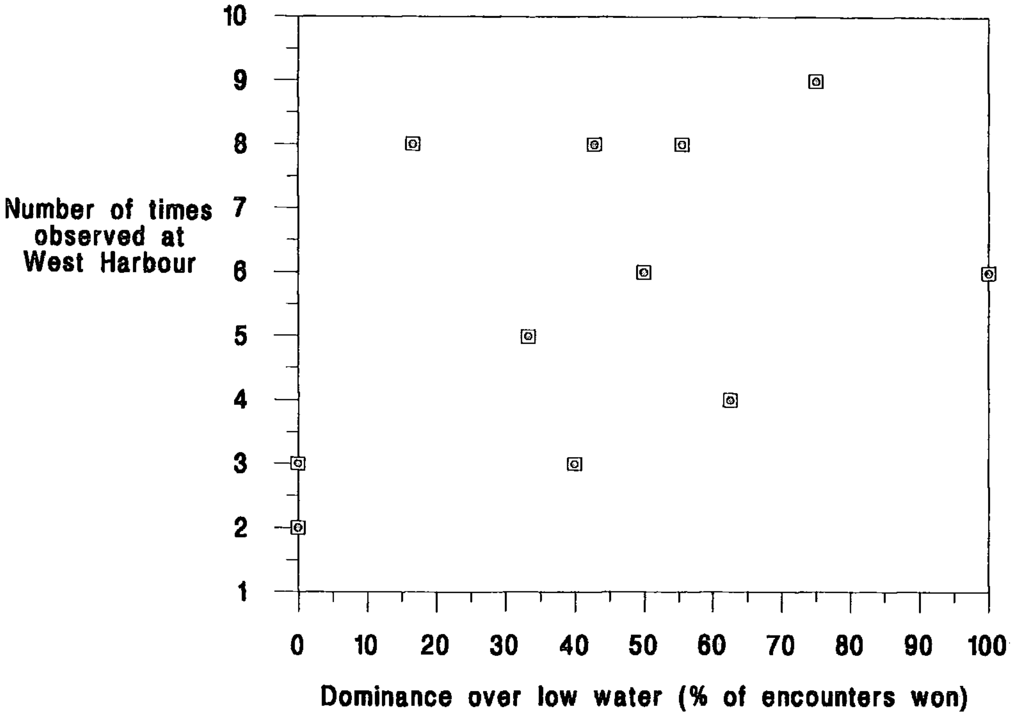


Fig. 5.30. Purple Sandpiper roost attendance at West Harbour and its relationship to dominance over low water: West Harbour to North Gare residents 8/3/93 - 7/4/93.

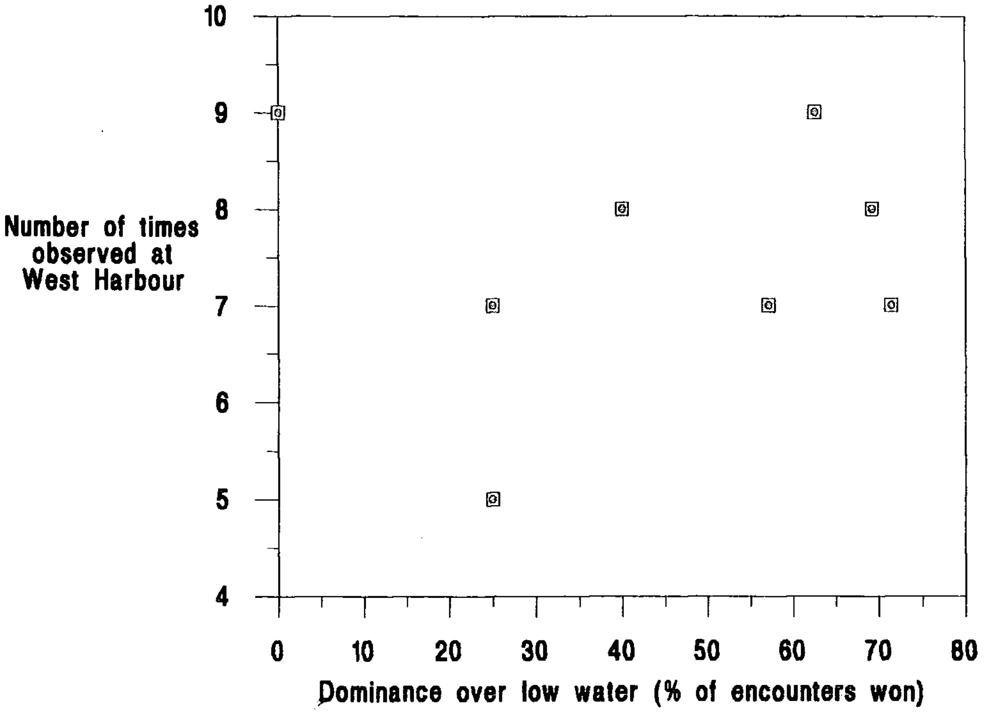


Fig. 5.31. Purple Sandpiper roost attendance at West Harbour and its relationship to dominance over low water: Headland residents 21/12/93 - 31/3/94.

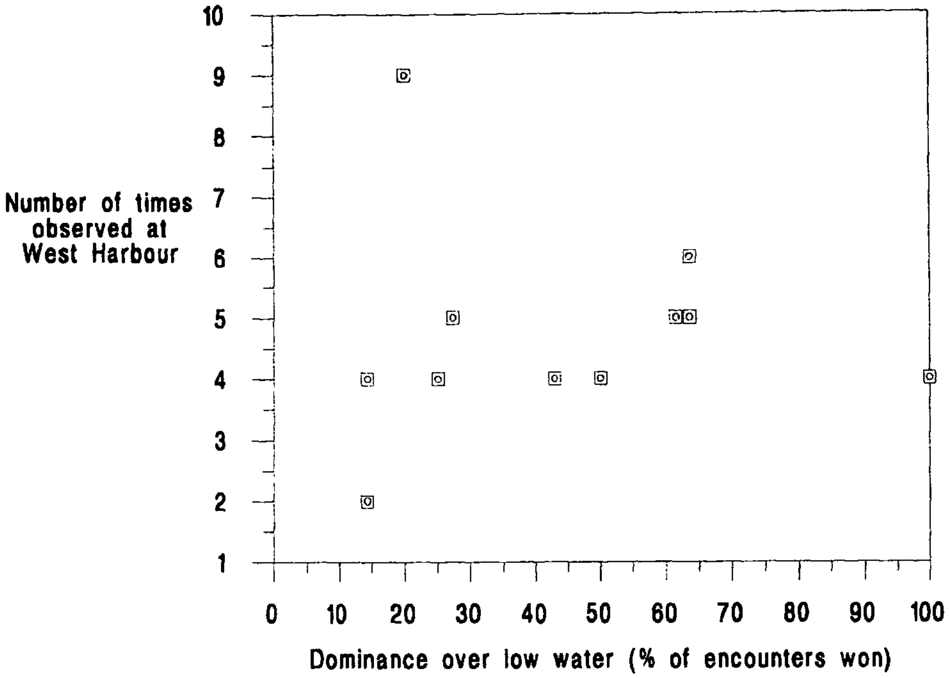
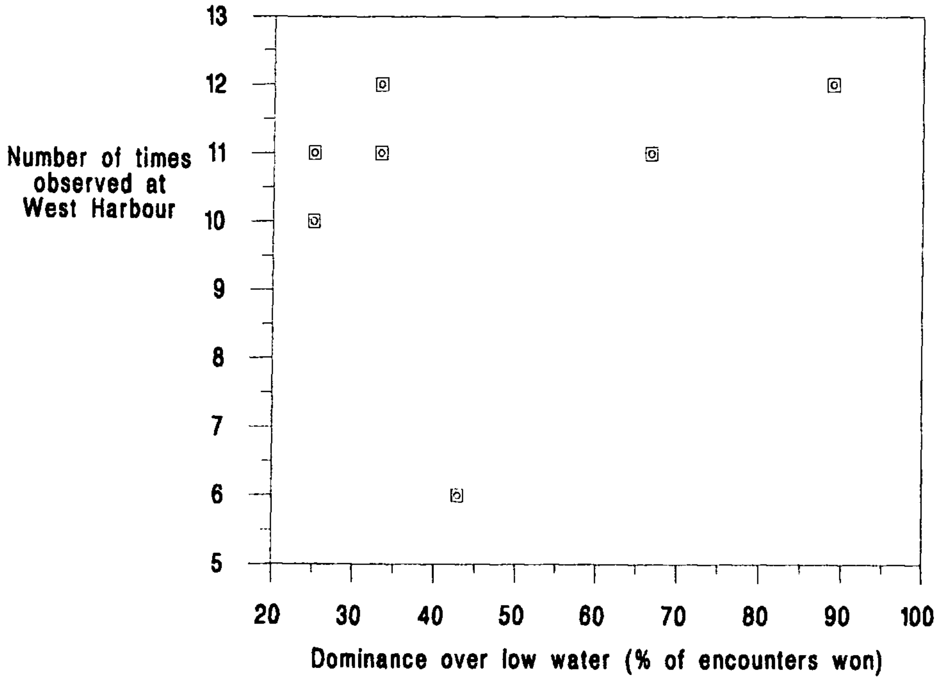


Fig. 5.32. Purple Sandpiper roost attendance at West Harbour and its relationship to dominance over low water: West Harbour to North Gare residents 15/11/93 - 31/3/94.



higher median high tide levels than more dominant individuals (r_s = -0.472, n = 15, $P <$ 0.10). Similarly, Headland residents that were subordinate whilst feeding were seen at the West Harbour roost on days of higher median high tide levels than those individuals of higher dominance (r_s = 0.573, n = 11, $P < 0.05$ one-tailed). West Harbour to North Gare residents of high roost dominance were seen at the West Harbour roost on days of similar median high tide levels as more subordinate individuals however (r_s = 0.006, n = 15, n.s.). Similarly individuals from this area of high feeding dominance were seen at the West Harbour roost on days of similar median high tide levels as individuals of lower feeding dominance (r_s = 0.083, n = 8, n.s.).

The number of times that individual Purple Sandpipers resident on the Headland used Headland high water sites during winter 1993/94 was not related to their dominance at the West Harbour roost (Fig. 5.33; r = -0.208, d.f. = 9, t = -0.639, n.s.). Attendance to Headland high water sites was also not related to feeding dominance (Fig. 5.34; r = 0.172, d.f. = 9, t = 0.525, n.s.). or dominance over high water on the Headland (Fig. 5.35; r = 0.061, d.f. = 6, t = 0.149, n.s.). Dominance on the Headland over high water was not correlated either with feeding dominance (r_s = 0.317, n = 8, n.s.) or dominance at the West Harbour roost (r_s = 0.121, n = 8, n.s.).

Individuals that were dominant at the West Harbour roost occurred on Headland high water sites on days of similar median high water levels as those individuals more subordinate at West Harbour (r_s = 0.014, n = 11, n.s.). There were similarly no relationships between the median height of high water on days that individuals used Headland high water sites and either their feeding dominance (r_s = 0.147, n = 11, n.s.) or Headland high water dominance (r_s = 0.102, n = 8, n.s.).

Individuals of different bill-length size classes varied in their attendance to the West Harbour roost. Of Headland residents in late winter / early spring 1993, individuals of the large bill-length size class were seen at the roost most often and individuals of the small

Fig. 5.33. Purple Sandpiper attendance at Headland high water sites and its relationship to dominance at the West Harbour roost: 21/12/93 - 31/3/94.

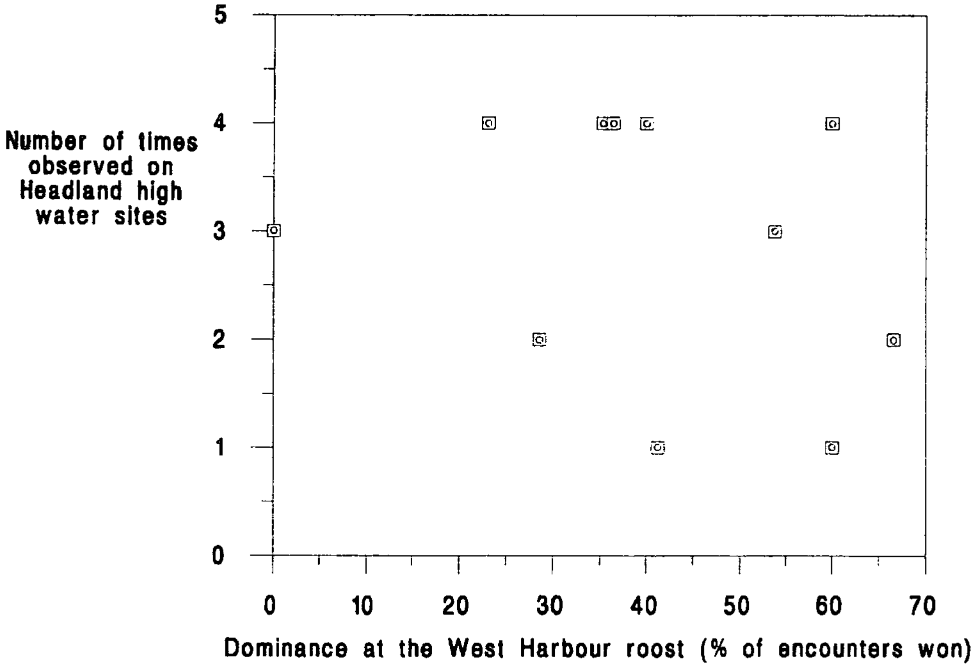


Fig. 5.34. Purple Sandpiper attendance at Headland high water sites and its relationship to dominance over low water: 21/12/93 - 31/3/94.

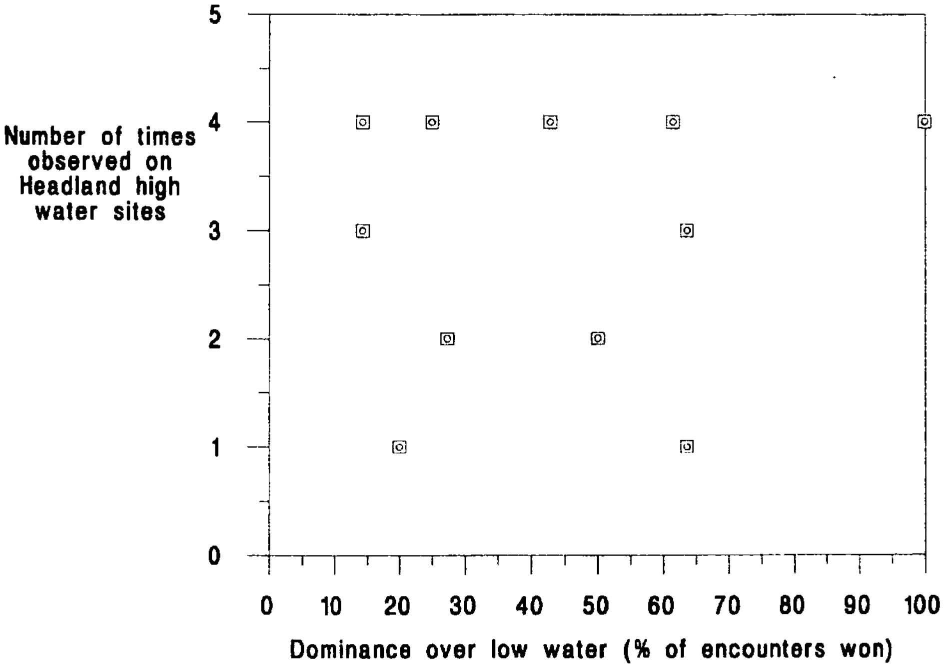
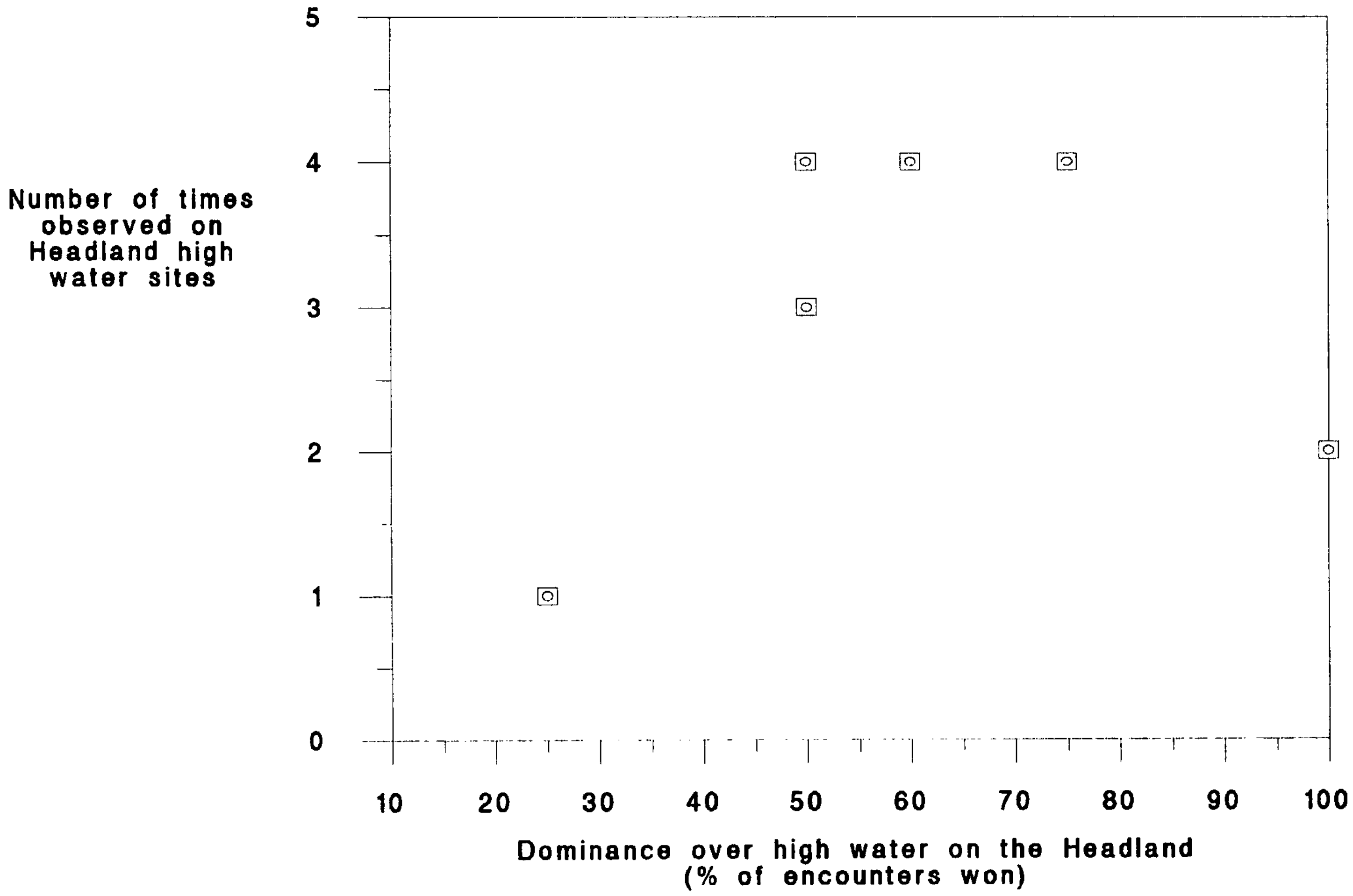


Fig. 5.35. Purple Sandpiper attendance at Headland high water sites and dominance over high water on the Headland: 21/12/93 - 31/3/94.



bill-length size class least often (one-way ANOVA $F_{2,14} = 4.312$, $P < 0.05$ one-tailed). This variation is probably related to the dominance of larger size classed individuals: dominant individuals attended the West Harbour roost more frequently in this period. There was no such relationship for West Harbour to North Gare residents in the same period (one-way ANOVA $F_{2,13} = 0.152$, n.s.). In winter 1993/94, medium bill-length size classed Headland residents tended to occur at the West Harbour roost more often than small bill-length size classed birds, though this trend was insignificant (Mann-Whitney $z = 1.298$, $P < 0.10$ one-tailed). There was no difference in the attendance of medium and small bill-length size classed individuals to Headland roosts in the same period ($t = 0.132$, d.f. = 9, n.s.).

5.3.3. Interspecific aggression at the West Harbour roost.

Table 5.29 below summarises all the interspecific aggressive interactions recorded at the West Harbour roost involving colour-ringed Turnstones and Purple Sandpipers (data from July 1993 to May 1994). Only four of 45 encounters were won by the smaller species (Sign Test $P < 0.001$). In each of these four cases, Purple Sandpipers won encounters with Turnstones - two species not dissimilar in size. All interspecific encounters at the West Harbour roost were won by the initiator.

Interspecific encounters accounted for 14.3% of all roost aggression recorded for Turnstones ($n = 286$) and 12.8% of all roost aggression recorded for Purple Sandpipers ($n = 336$); (data from 1993/94).

The proportions of encounters over roosting sites and due to infringements of individual distance were similar in inter- and intraspecific aggression for both Turnstones (Table 5.30; $\chi^2 = 0.056$, d.f. = 1, n.s.) and Purple Sandpipers (Table 5.31; $\chi^2 = 0.426$, d.f. = 1, n.s.). In aggression between Turnstones and Purple Sandpipers, however, Purple Sandpipers tended to be less likely to win encounters over roosting sites than those over infringements of individual distance (Table 5.32).

Table 5.29. Interspecific aggression at the West Harbour roost.

Winner	Loser	*n*
Redshank	Turnstone	1
Turnstone	Purple Sandpiper	35
Purple Sandpiper	Turnstone	4
Turnstone	Dunlin	1
Redshank	Purple Sandpiper	3
Knot	Purple Sandpiper	1

Figures represent numbers of encounters recorded.

Table 5.30. Causes of intra- and interspecific aggression involving Turnstones at the West Harbour roost; (data from July 1993 to May 1994).

	Intraspecific aggression	Interspecific aggression
Roosting site	117	22
Individual distance	116	19

Figures represent numbers of encounters recorded.

Table 5.31. Causes of intra- and interspecific aggression involving Purple Sandpipers at the West Harbour roost; (data from July 1993 to May 1994).

	Intraspecific aggression	Interspecific aggression
Roosting site	173	23
Individual distance	115	20

Figures represent numbers of encounters recorded.

Table 5.32. Causes of aggression between Turnstones and Purple Sandpipers at the West Harbour roost; (data from July 1993 to May 1994).

	Turnstone won	Purple Sandpiper won
Roosting site	20	1
Individual distance	15	3

Figures represent numbers of encounters recorded.

Table 5.33. The intensity of intra- and interspecific aggression involving Turnstones at the West Harbour roost.

	Threat	Peck	Chase	Peck-chase	Fight
Intraspecific aggression	623	148	15	1	5
Interspecific aggression	23	18	0	0	0

Figures represent numbers of encounters recorded.

Table 5.34. The intensity of intra- and interspecific aggression involving Purple Sandpipers at the West Harbour roost.

	Threat	Peck	Chase
Intraspecific aggression	536	77	1
Interspecific aggression	25	18	0

Figures represent numbers of encounters recorded.

Interspecific encounters were of a greater intensity than intraspecific encounters for both Turnstones (Table 5.33; combining pecks, chases, peck-chases and fights: χ^2 = 10.141, d.f. = 1, $P < 0.01$) and Purple Sandpipers (Table 5.34; combining pecks and chases: χ^2 = 25.094, d.f. = 1, $P < 0.001$).

5.4. Discussion.

5.4.1. Causes, rates and intensity of aggression at the West Harbour roost.

Aggression at avian roosts normally results either from individuals seeking favourable roosting positions (*e.g.* Swingland 1977, King 1981, Weatherhead and Hoysak 1984, Still *et al.* 1987, Summers *et al.* 1987, Jenni 1993) or from an infringement of individual distance (*e.g.* Johnson and Nakamura 1981). The latter may be caused either by individuals passing or landing too close to others (*e.g.* Brooke 1972), or by an increase in roost density (*e.g.* Burger *et al.* 1977). In the present study, aggression involving roosting Turnstones was attributed equally to individuals seeking better roosting positions and to infringements of individual distance, though for Purple Sandpipers a larger proportion of aggression was a result of encounters over roosting sites.

For Turnstones, the rate of intraspecific aggression over infringements of individual distance increased as conspecific density increased. Previous studies of both waders (Recher and Recher 1969, Goss-Custard 1977, Burger *et al.* 1979, Fleischer 1983, Metcalfe and Furness 1987) and other species (Burger *et al.* 1977) have also recorded such an increase in aggression rate with flock density. As Burger *et al.* (1977) noted however, some studies have found that aggression rates are affected not by flock density, but rather by total flock size (*e.g.* Marler 1956). For Purple Sandpipers, the rate of intraspecific aggression over individual distance was independent of conspecific roost density, (and of all other factors considered). This result contrasts with the findings of Metcalfe and Furness (1987), that individual aggression rates amongst foraging Purple Sandpipers increased with conspecific density. Variation in the rate of encounters over individual distance for Purple

Sandpipers could result either from variation in total flock size or from variation in the numbers of birds moving through the flock. As Purple Sandpipers spent little time running, walking or flying at the roost in comparison to Turnstones (see Chapter 3), the latter explanation is perhaps unlikely.

For both species, the individual rate of aggression over roosting sites, and to some extent the associated intensity of aggression (Tables 5.6 and 5.23), increased with wind speed, implying that some sites were preferable for microclimatic reasons. Swingland (1977) similarly found that as wind speed increased, adult Rooks *Corvus frugilegus* increasingly displaced young Rooks from more sheltered sites further down trees, (though these sites were more vulnerable to predators). Roosting adult Redshank have also been noted to force juveniles from the sheltered sides of flocks in increased wind speeds (Whitlock 1979), implying that leeward edges may be as favourable as the middle of flocks in some circumstances. In contrast to this however, Johnson and Nakamura (1981) found that the aggressive behaviour of roosting Pacific Golden Plovers *Pluvialis fulva* was depressed in extreme winds, though interactions were noted even 'when the birds could scarcely maintain their footing'. For Purple Sandpipers, gaining a favourable roosting site was perhaps the most important reason for aggression at the roost, encounters caused by an infringement of individual distance being significantly less intense (Table 5.21). Purple Sandpipers were most aggressive over roosting sites before high water, when birds were still arriving at the roost, or had recently arrived. Thereafter the rates of aggression over roosting sites declined and, except when disturbed, individual Purple Sandpipers spent most of their time sleeping (see Chapter 3).

Although both Turnstones and Purple Sandpipers were commonly found in mixed-species flocks at the West Harbour roost (see Chapter 6), interspecific encounters involving either species were comparatively infrequent. Studies of aggression in flocks of foraging waders have also found that, in comparison to intraspecific aggression, interspecific aggression is relatively infrequent (Recher and Recher 1969, Metcalfe and Furness 1987, the present study). It is unlikely that interspecific competition for roosting sites is as infrequent as the present results suggest, however, especially between species not too dissimilar in size, which could gain shelter from each other (Whitlock 1979). The outcome of most interspecific encounters recorded in the present study was determined simply by the relative size of the two species involved, so that larger species might normally be able to displace individuals of smaller species without any aggression at all. If such a simple displacement does not occur, subsequent aggression may, as found for both Turnstones and Purple Sandpipers, be more intense than that seen in intraspecific encounters (Tables 5.34 and 5.35) - perhaps because more than a simple threat display is needed to relay intent to a different species. It is worth noting however, that whilst in the present study intraspecific aggression was found to be less intense than interspecific, Recher and Recher (1969) and Metcalfe and Furness (1987) both found the opposite to hold.

5.4.2. Individual dominance at the West Harbour roost.

Dominance hierarchies of both Turnstones and Purple Sandpipers roosting at West Harbour were particularly stable: only a few encounters went against rank order and most encounters were won by the initiator. As in foraging birds, age was found to be an important determinant of the outcome of encounters at the West Harbour roost, for both Turnstones and Purple Sandpipers. Although adults did not differ in rank from first-winter individuals, they won a significantly greater proportion of encounters with first-winter individuals. Adult Turnstones were also dominant over individuals in their second-winter. Previous studies, primarily of feeding behaviour, have also found that adult Turnstones dominated first-winter individuals (Groves 1978, Whitfield 1985a). As on feeding grounds, the dominance of adults over first-winter birds may be a result of two factors: the inexperience of first-winter individuals in aggressive interactions (Groves 1978, Whitfield 1985a) or the greater body-size or mass of adults (*e.g.* for Turnstones: Summers *et al.* 1976, the present study). The subordination of second-winter Turnstones to older adults at the

West Harbour roost suggests that experience in aggression is important in determining dominance status.

Purple Sandpiper dominance at the West Harbour roost, as on feeding grounds, was found to be positively correlated to size, (as expressed by bill-length size class). As discussed earlier, Purple Sandpipers are sexually dimorphic in body-size, with females being larger than males (Tatarinkova 1977, Summers *et al.* 1992) and it is not clear whether females dominate males due to their sex or simply due to the size difference. As on feeding grounds however, the dominance at the West Harbour roost of individuals of the medium bill-length size class, (*i.e.* Norwegian females and males from the probable Greenland / Canada population), was positively correlated to their size, (as expressed by bill-length), thus suggesting that it is size alone that is important.

The stability of the dominance hierarchies at the West Harbour roost suggests that, as on feeding grounds, individuals are able to recognise other birds of different rank. Such recognition may occur either by individual recognition (Collias 1943) or by status signalling (Rohwer 1975) and in support of the former theory, Whitfield (1986, 1987) has found that individual Turnstones are able to recognise neighbours during the breeding season. During winter, the stability and small size of groups of both Turnstones and Purple Sandpipers on feeding grounds (Whitfield 1985a, Metcalfe 1986) may facilitate individual recognition, even though plumage at this time is less distinct. As groups from different feeding areas tend to remain segregated at the West Harbour roost, despite the size of flocks, individual recognition may also be possible in roosting flocks and this would aid the stability of dominance hierarchies.

5.4.3. Structuring within flocks: roost position and conspecific roost density.

Nearest neighbour analysis revealed that segregation occurred at the West Harbour roost, between groups of Turnstones and Purple Sandpipers from different feeding areas and between Purple Sandpipers of different bill-length size classes. Furness and Galbraith

(1980b) have also reported a tendency for the same individuals to occur together on different days within a roosting flock of Redshank, whilst Orians (1961) reported that some thrushes were segregated by sex within or even between roosts. As well as roosting in different groups however, individuals may also be variably distributed into the middle, edge (and bottom) of flocks through competition for roost sites.

Roosting in the middle of flocks has two advantages: increased protection from predation and shelter from adverse weather. Kus *et al.* (1984) found that first-winter Dunlins suffered greater predation from a Merlin than adults and suggested that this was a result of the predominance of first-winter birds at the edge of Dunlin flocks; Bijlsma (1990) obtained similar results when studying the predation of Dunlins by large raptors in Mauritania. At West Harbour, roosting at the bottom of flocks on the island may also provide anti-predator advantages, as a raptor is unlikely to dive on a bird that will take off from the roost close to the water. Whitlock (1979) modelled roosting flocks of waders and found that wind speeds were reduced in central positions. He also found, however, that birds moved to the sheltered sides of flocks in strong winds, suggesting that in such circumstances, leeward edges may have been preferable to the middle of flocks. Densities of birds are often greater in the middle of flocks (Still *et al.* 1987, Jenni 1993, the present study) and this will reduce wind speeds, whilst also providing additional warmth: Good (1979) found that in Brown-headed Cowbird *Molothrus ater* roosts, mortality in cold weather was greater in low density areas.

Much of the observed aggression at the West Harbour roost was a result of individuals searching for favourable roosting sites. Shelter was clearly important for individuals of both species, as aggression rates increased with wind speed, and competition was therefore likely to be greatest for positions in the middle and perhaps the leeward edge of flocks. The resulting positions of individuals within the roost should as a consequence reflect observed dominance hierarchies.

For both Turnstones and Purple Sandpipers, adults were seen, as expected, more often in the middle of flocks, and first-winter individuals more often at the edge. Similar results have been reported in studies of roosts of Rooks (Swingland 1977), Red-winged Blackbirds *Agelaius phoeniceus* (Weatherhead and Hoysak 1984), Starlings *Sturnus vulgaris* (Summers *et al.* 1987), Choughs *Pyrrhocorax pyrrhocorax* (Still *et al.* 1987), Dunlins (Ruiz *et al.* 1989) and Bramblings *Fringilla montifringilla* (Jenni 1993). The differences seen in roosting position are ascribed to the dominance of adults over juveniles. Aggression of adults towards juveniles over roosting sites has been recorded in a number of these and other studies (Swingland 1977, Weatherhead and Hoysak 1984, Rabenold 1987, Still *et al.* 1987, Kelly and Thorpe 1993).

Previous studies have also found that social structuring within roosts occurred according to sex and / or body-size. Jenni (1993) found that male Bramblings were found in the centre of a roost proportionally more often than females, and that birds at the centre were heavier than those at the edge. Summers *et al.* (1987) similarly found that in a Starling roost there were proportionally more adult males in the centre and more first-year females at the periphery and that, regardless of body-size, birds in the centre were heavier than those at the edge. For Purple Sandpipers, there was no such structuring at the West Harbour roost according to size (or thus sex or population), even though larger size classed individuals were dominant over smaller ones. As the nearest neighbour analysis showed, however, some segregation occurred between these groups (possibly by sex or population rather than by size), and dominance within these groups (which may be related to size) may have then determined roost position.

Individual dominance in both Turnstones and Purple Sandpipers was itself directly correlated to roost position and density. Subordinate Turnstones and Purple Sandpipers were found more often in peripheral, less dense positions, dominants of both species more often in the middle and dominant Purple Sandpipers more often at the bottom of flocks. Only Swingland (1977) has previously made such correlations with individual dominance (rather than with age, sex or size), finding that dominant Rooks roosted in higher, safer positions than subordinates. The findings in the present study would be in accord with Weatherhead's (1983) hypothesis of communal roosting, whereby subordinates used roosts in order to acquire information concerning food resources, whilst dominants were able to roost in the middle of flocks buffered from adverse weather and predation by the subordinates.

5.4.4. Individual roost site fidelity, roost attendance and high water feeding.

Amongst non-breeding waders, fidelity of particular individuals to roost sites has been found to be high in a number of previous studies, for example amongst Redshanks (Furness and Galbraith 1980a), Oystercatchers (Goss-Custard and Durell 1983, Swennen 1984) and African Black Oystercatchers (Hockey 1985) and is no doubt related to the high within winter fidelity of many species to their wintering quarters (*e.g.* Symonds *et al.* 1984, Metcalfe and Furness 1985). In the present study, individual resident Turnstones and Purple Sandpipers were faithful to a group of roost and high water sites during autumn, winter and spring. The West Harbour roost was attended frequently by all individuals from within the study site and some individuals were also faithful to a number of smaller roosts and high water sites, which were most often used on neap tides. Even amongst individuals from the same low water feeding area however, there was much variation in the frequency with which these roosts and high water sites were used, on a day to day basis and also seasonally.

Both individual Turnstones and Purple Sandpipers attended the West Harbour roost less often in winter than autumn, though as frequently in spring as in either period. Both species increase in body-mass by between 2 and 8% during early winter (Summers *et al.* 1976, Johnson 1985, Summers *et al.* 1992, Norman and Coffey 1994, the present study), and may have needed to use other high water sites at this time in order to feed. Later in winter, high water foraging may be important to an individual's survival: Heppleston (1971) found that Oystercatcher mortality levels increased during a period when fields that were normally used for feeding over the high water period became unavailable because of snow cover. Baker (1981), in a study in Lothian, Scotland, found that during winter, Turnstones spent all the daylight hours foraging, inclusive of periods of high tide. Marshall (1981), working in the same area, similarly found large flocks of Turnstones foraging over high water during winter. Turnstones are not known to feed at night (Evans 1976a, Marshall 1981) and due to short day-length, high water feeding is likely to be important at this time. Although, in relation to other waders wintering in northern latitudes, Purple Sandpipers put on less mass in early winter (Summers *et al.* 1992) and may spend only 50% of their time in midwinter foraging (Dierschke 1993), high water foraging does occur (Waters 1966). Despite having the ability to feed at night (Blair 1961, Atkinson *et al.* 1981, Summers 1994), high water feeding may be important to Purple Sandpipers in winter, during periods of bad weather (Moore 1992) or when high tide occurs in the middle of the day.

Foraging requirements are also high in spring, as adult and some first-winter Turnstones (Thompson 1974, Cramp and Simmons 1983) and both adult and first-winter Purple Sandpipers (Atkinson *et al.* 1981) prepare to migrate to breeding grounds. During this season in my study, it is probably that both species used high water sites other than West Harbour largely in order to feed. Large numbers of Turnstones were seen feeding on grass areas at Seaton Carew over high water during spring.

Brearey (1982) found that first-winter Turnstones used the main roost in his study site, (on the south side of the Tees estuary), less often than adults. This, he suggested, arose because either the subordinate first-winter birds' inexperience at foraging (Groves 1978) forced them to use other sites over high water for feeding (Theory 1) or adults did not tolerate subordinate first-winter birds at the roost (Theory 2). Goss-Custard and Durell (1983) found that first-winter Oystercatchers were found more often in fields at high water, where feeding was possible, and that adults were found more frequently at the main roost in their study area; as individuals matured, they made increasing use of the main roost. Swennen (1984), in contrast, found that larger Oystercatcher roosts, where feeding was possible sooner after high water, contained larger sized Oystercatchers, more adults, more females (which have longer bills) and fewer birds with anatomical defects than in smaller roosts. Swennen suggested that this may have been due to the exclusion of subordinates to smaller roosts, where feeding was not possible soon after high water (Theory 2). According to Weatherhead's (1983) hypothesis of communal roosting however, such intolerance is unlikely, as subordinate first- or second-winter birds would provide dominant adults with protection from predators and microclimatically favourable roosting sites by roosting around them at the edge of flocks. This suggests a third theory, that first-winter or subordinate birds use large roosts less frequently because they seldom attain good roosting positions there (Theory 3).

In the present study, as in Brearey's (1982), first-winter Turnstones attended the main roost in the study area, *i.e.* West Harbour, less frequently than adults. No difference, however, was found between the attendance there of adult and first-winter Purple Sandpipers in late winter / early spring; at this time both age classes had to put on weight for their spring migrations and therefore probably used other high water sites for foraging to an equal extent. First-winter Purple Sandpipers by this time, had also gained experience in aggressive encounters (see Whitfield 1985a) and were less likely to have been excluded altogether from the roost due to their subordinance.

For both individual Turnstones and Purple Sandpipers, dominance was an important determinant of their frequency of use of the West Harbour roost. In autumn, and to a lesser extent in winter, those Turnstone which were dominant at the West Harbour roost occurred there more often than those that were subordinate. Purple Sandpipers that were dominant at West Harbour used the roost more frequently in spring than those that were subordinate. For Turnstones that were resident on Headland feeding areas, dominance at the West Harbour roost was inversely correlated with the frequency of use of Headland high water sites. Despite the correlation however, for both species, between roosting and feeding dominance, individual feeding dominance was not correlated with individual roost attendance at either West Harbour or the Headland high water sites. The implication of this is that the individuals that attended the West Harbour roost most infrequently, did so not because of their need to use other sites to feed over high water (Theory 1), but rather due to their subordinance at West Harbour. It is unlikely that this occurred because dominant individuals excluded subordinates from the West Harbour roost (Theory 2), despite its favourability in terms of shelter and lack of predators (Chapter 3). The roost site was not limited in size: almost all locally resident Turnstones and Purple Sandpipers often occurred there simultaneously on spring high tides, together with many other waders. If subordinates could occur at West Harbour at these times, it is improbable that they could be excluded when the number of birds present was lower. It is probable, therefore, that subordinates used the West Harbour roost less frequently, (at least in autumn for Turnstones and spring for Purple Sandpipers), because of their inability to gain good roosting positions there (Theory 3). Dominants, it would seem, used the West Harbour roost more frequently as they were able to gain favourable roosting positions there, (whilst also perhaps increasing their dominance at the site through their increased attendance). Those Turnstones that were resident on Headland feeding areas and that were dominant at the West Harbour roost, used Headland high water sites only on the lowest neap tides, when a large number of these sites, close to their feeding areas, were available. On these tides, few birds roosted at West Harbour and dominant individuals would not have been able to benefit from gaining the good roosting positions there that they would have been able to if numbers were higher.

The choice of high water site needs to be considered in terms of how individuals may best maintain their energy balance, (though at the same time, taking into account the need for a safe, undisturbed site). Energy may be saved over high water by roosting communally in microclimatically favourable sites or it may be gained by continuing feeding. Individuals that are dominant whilst roosting are able to save considerable energy over high water by roosting in preferred, sheltered positions (see 3.3.3 and Whitlock 1979) and as a result, only occasionally need to feed during this period. Individuals that are subordinate at large roosts are excluded from sheltered positions and in order not to lose too much energy, use alternate sites to feed over high water and thus gain energy. Often, individuals that are subordinate whilst roosting are also subordinate whilst feeding over low water (*e.g.* Whitfield 1985a) and, in consequence of their poor intake rates over low water (*e.g.* Ens and Goss-Custard 1984), may need to forage over high water anyway. As the present study shows, however, this is not always the case.

For both species, though particularly for Purple Sandpipers, the relationships between dominance and roost attendance did not hold in winter. The reasons for this are not clear, though the difference does perhaps relate to varying individual needs for high water feeding. In autumn, when daylight hours are relatively long, the only individuals that would regularly need to supplement their intake by foraging at high water would be those that were subordinate whilst foraging over low water. In winter, as Baker (1981) found for Turnstones, many individuals have to spend all the daylight hours foraging, regardless of their dominance rank.

Summary.

1). Within roosting flocks, both Turnstones and Purple Sandpipers were segregated into groups from different low water feeding areas. Purple Sandpiper flocks were also partially segregated into groups according to (bill-length) size class, but not according to age.

2). For both Turnstones and Purple Sandpipers, intraspecific aggression at the West Harbour roost was caused almost equally by encounters over roosting sites and encounters over infringements of individual distance. As wind speed increased, a greater proportion of observed intraspecific aggression for both species was a result of encounters over roosting sites and aggression also became more intense, *i.e.* there were more pecks and chases (and fights). Rates of intraspecific aggression over roosting sites increased with wind speed for both species and for Turnstones, the rate of aggression over infringements of individual distance increased with conspecific roost density.

3). Dominance hierarchies at the West Harbour roost were stable for both Turnstones and Purple Sandpipers within years. Dominance at the roost was correlated with dominance on 'home' feeding areas in two of three years for Turnstones and one of two years for Purple Sandpipers. There was no difference in the dominance of resident and visitant Turnstones at the West Harbour roost. Adult resident Turnstones, however, were dominant over first-winter resident Turnstones; there was not such a clear finding for Purple Sandpipers. For Purple Sandpipers, dominance was positively correlated with bill-length size class; within the medium size class, dominance was also positively correlated with bill-length.

4). Roosting flocks of both species at West Harbour were structured according to age and dominance. Adult Turnstones and Purple Sandpipers were found more often in the safe and sheltered middle of flocks and less often at the edge than first-winter birds. Adults of both species roosted at higher conspecific roost densities. Purple Sandpipers of different bill-length size classes, however, roosted in similar positions and at similar conspecific densities in roosting flocks. Dominant Turnstones and Purple Sandpipers were found more often in the middle of flocks, subordinates more often at the edge of flocks and dominant Purple Sandpipers more often at the bottom of flocks on the roost island. Dominant individuals of both species roosted at higher conspecific roost densities.

5). Individual resident Turnstones and Purple Sandpipers roosted at West Harbour less frequently in winter than in autumn; individual Turnstones resident on Hartlepool Headland were seen at Headland high water sites more frequently in winter than in autumn. First-winter resident Turnstones roosted at West Harbour less often than adult resident Turnstones. Dominance at the West Harbour roost was important in determining how often an individual used the site. Turnstones dominant at the West Harbour roost were seen there more often than subordinates; Headland high water sites were used more often by those Headland residents that were subordinate at West Harbour. Feeding dominance was not related to roost attendance. Purple Sandpipers dominant at West Harbour used the roost more often than subordinates in late winter / early spring 1993, but equally so in the subsequent winter. Again, feeding dominance was not related to roost attendance. It is concluded that subordinate individuals of both species used the West Harbour roost less frequently because of their inability to gain safe and sheltered roost positions there; other sites although not any less exposed to predators or poor weather, were closer to low water feeding grounds and offered high water feeding opportunities.

Chapter 6.

Mixed-species Roosting.

6.1. Introduction.

The phenomenon of mixed-species roosting is one that has frequently been commented upon but seldom investigated, (unlike mixed-species breeding colonies). Associations typically occur between related, often similar sized species, and the phenomenon has been noted, for example, amongst shorebirds (Swinebroad 1964, Furness 1973a, Robertson and Dennison 1979, Hale 1980), herons (Burger *et al.* 1977), hirundines (Cramp 1988) and thrushes (Orians 1961, Meanley 1965, Simms 1978). Totally unrelated species however have also been observed to roost together, *e.g.* the House Crow *Corvus splendens* and the Jungle Crow *Corvus macrorhynchos* with the Common Myna *Acridotheres tristis*, Rose-ringed Parakeet *Psittacula krameri* and Cattle Egret *Ardeola ibis* (Gadgil 1972).

Individuals may roost with other species for the same reasons that they roost with their own. Roosts might allow the interchange of information concerning the location of food resources - *i.e.* the 'information-centre' theory (Ward and Zahavi 1973). Such an interchange of information is probable, however, only between closely related species, which have similar feeding habits and which are omnivores or generalists (Gadgil 1972). Additionally individuals may roost together to conserve energy through tight flocking and by sharing favourable roost sites - *i.e.* through the roost's microclimate (*e.g.* Tast and Rassi 1973). Roosting may also reduce the risk to an individual of being taken by a predator (Lack 1966, 1968), through increased vigilance (*e.g.* Powell 1974, Siegfried and Underhill 1975), decreased individual risk (Hamilton 1971) and increased predator confusion (Neill and Cullen 1974). Gadgil (1972) proposed that this was the main reason why House Crows, Jungle Crows and Common Mynas roosted together in his study. Gadgil (1972) and Stinson

(1988) have both noted however, that whilst a mixed-species association may be of benefit to one species, it may be disadvantageous to another.

In my study, the West Harbour roost was used regularly by six wader species: Turnstone, Purple Sandpiper, Oystercatcher, Redshank, Knot and Dunlin, as well as a variety of gulls. A choice of roost sites was available within the harbour (Chapter 3), and this allowed species to associate preferentially with others. This chapter examines these associations and investigates, in particular, the possible reasons for the Turnstone / Purple Sandpiper association.

6.2. Methods.

6.2.1. Association indices.

The compositions of flocks of waders were recorded on each visit to West Harbour at high water. Two species were classed as roosting together when at least 25% of the total number present in the harbour of one species roosted together with at least 25% of the total number of the other. An index of association between two roosting species was calculated as the number of days on which one species roosted together with the other, divided by the total number of times that they were seen together and seen apart within the harbour. A minimum of 10 birds of a species was required to be present at the roost for data to be included. Data were taken from July 1991 to May 1994.

It is predicted that species of a similar size would roost together more frequently than those dissimilar in size. Similar sized species are more likely to have similar diets and thus need to exchange information concerning food resources; they are also likely to gain shelter from each other without being at a disadvantage in competition for roosting sites and as they may be taken by the same predators, they may also roost together to reduce their individual risk of predation.

6.2.2. The Turnstone / Purple Sandpiper roosting association.

The following investigations aim to reveal reasons for the Turnstone / Purple Sandpiper roost association.

6.2.2.1. Information transfer.

In order to investigate whether either Turnstones or Purple Sandpipers followed the other to food resources following an exchange of information at the roost, counts were made of the number of Turnstones and Purple Sandpipers in flocks departing from mixed roosts of the two species at West Harbour. If information transfer had taken place between Turnstones and Purple Sandpipers whilst they were at the roost, one would expect that a high proportion of flocks departing the roost would have contained a mix of the two species (see Mock *et al.* 1988).

It is possible that individuals of one species may leave with individuals of another, not to follow them to food resources, but because few conspecifics remain at the roost and it is preferable to remain in flocks rather than to be alone and at a greater risk of predation. To test whether this was the case, the numbers of each of the two species remaining at the roost when each flock departed was also recorded.

In order to investigate whether Turnstones and Purple Sandpipers shared food resources and thus whether exchange of information concerning its whereabouts was probable, both species were also observed whilst on their low water feeding grounds. Individually colour-ringed Turnstones and Purple Sandpipers were observed for periods of between one and five minutes and the number of intraspecific and interspecific interactions recorded (see Chapter 4). If the two species shared food resources, one would expect that encounters between them would be frequent and that a high proportion of the encounters between them would involve feeding opportunities. Data concerning interspecific encounters on feeding grounds were recorded between July 1993 and May 1994 (see Chapter 4).

During the winter of 1993/94 (*i.e.* 15 November 1993 to 31 March 1994), 23 colour-ringed Turnstones (excluding those that died during winter) and 20 colour-ringed Purple Sandpipers were resident at Hartlepool. If p represents the proportion of Purple Sandpipers amongst those colour-ringed and resident (*i.e.* 20/43), and q the proportion of Turnstones (*i.e.* 23/43), then the following represent the expected frequencies of particular interactions:

np^2 = the number of interactions between colour-ringed Purple Sandpipers
nq^2 = the number of interactions between colour-ringed Turnstones
$2npq$ = the number of interactions between a colour-ringed Purple Sandpiper and a colour-ringed Turnstone

where n = the total number of observations.

These frequencies are compared to observed frequencies of interactions recorded between colour-ringed foraging birds. Observations have shown that the two species do share feeding grounds (Chapter 4) and thus if the number of interactions observed between the two species whilst feeding is less than expected, then it would be because of the lack of competition between them on feeding grounds.

6.2.2.2. Roost microclimate.

If two species roosted together for any energetic benefits that flocking confers, one would expect that as wind speed increases, the two would roost together no less or possibly even more frequently. If the two species roost together less frequently as wind speed increases it would be because one species is more able to gain sheltered roosting positions by being away from the other. The two species would similarly be expected to roost together no less or possibly more frequently on cloudy as opposed to sunny days. To determine if species did roost together for energetic benefits, wind speed was estimated, (on the Beaufort scale), and the day classed as sunny or cloudy on each high water visit to West Harbour (see Chapter 3).

Roosting at the centre of flocks is usually microclimatically favourable to being at the periphery (Whitlock 1979, Weatherhead and Hoysak 1984) and a species would be unlikely to roost together with another for microclimatic reasons if it were excluded from such central positions. If Turnstones and Purple Sandpipers do roost together for such energetic benefits, one would thus expect that equal percentages of each species would be found in the middle, edge and bottom of mixed flocks of the two species, *i.e.* that neither species would be in a relatively poorer microclimatical position within the flock. The position of Turnstones and Purple Sandpipers in such mixed flocks on the West Harbour island was recorded in the winter of 1993/94. The definitions of middle, edge and bottom are given in Chapter 5.

6.2.2.3. Decreased risk of being taken by a predator.

The risk of predation to an individual may be reduced by associating with others in order to share vigilance (Pulliam 1973; see also Elgar 1989, Lima 1995). The increased chance of predator detection allows individuals to reduce their own vigilance levels and thus devote more time to other activities (Powell 1974, Lazarus 1978, Abramson 1979). Although vigilance is normally only shared with conspecifics, mixed species associations may allow the sharing of vigilance between species (*e.g.* Thompson and Barnard 1983, Metcalfe 1984c, Jacobsen and Ugelvik 1994). In order to determine with which species Turnstones and Purple Sandpipers shared vigilance and thus which species helped to reduce their individual risk of predation, the vigilance of individuals of both species was observed in mixed species roosting flocks at West Harbour.

Observations on individual vigilance were made at West Harbour between 8 October 1993 and 19 August 1994. Individuals in roosting flocks were watched for periods of one minute and the number of scans and total time spent scanning, (recorded to a half-second on a stopwatch), were recorded. Individuals were defined as scanning when they were standing with the head in a horizontal or higher position (and thus were not running, flying, preening, bathing, in an aggressive encounter or sleeping - see Chapter 3). Individuals may also scan for predators by peeking from sleeping positions (Amlaner and McFarland 1981, Lendrem 1983, 1984, Gauthier-Clerc *et al.* 1994). It was not, however, always possible to see this behaviour from the distances involved in the present study and so such behaviour was not included in the scans recorded. Vigilance time was defined as the time (in seconds) spent scanning per minute. Only adult birds were considered, as vigilance time may vary with age (Robinson 1992). Observations were terminated if all or part of the flock was disturbed during the one minute focal period. The number of birds of each species within the flock was also recorded. Only birds within distinct flocks were observed, flocks being no greater than 10m in length. The number of birds recorded was thus similar to the 'overall bird density', (*i.e.* the number of birds within 10m of the focal bird), measured by Metcalfe (1984b,c).

There were few obstacles to visibility for roosting waders at West Harbour and so this factor was not taken into account in vigilance calculations. Previous studies have shown, however, that vigilance may increase if visibility is limited (Barnard and Stephens 1983, Metcalfe 1984b, Lima 1987, Pöysä 1994).

6.3. Results.

6.3.1. Association Indices.

Association indices between the six main shorebird species seen at West Harbour are shown in Table 6.1. In general birds associated with species of a similar size, smaller species notably often roosting together. Turnstones, for example, commonly roosted with Purple Sandpipers and Dunlins. There was a significant negative correlation between the association indices recorded between Turnstone and other species and the mass of those

Table 6.1. Association indices between roosting shorebird species at West Harbour.

	Redshank	Knot	Turnstone	Purple Sandpiper	Dunlin
Oystercatcher	0.400 (5)	0.133 (15)	0.342 (73)	0.197 (71)	0 (12)
Redshank		-	0.409 (22)	0.591 (22)	-
Knot			0.381 (21)	0.182 (22)	0.333 (9)
Turnstone				0.588 (119)	0.875 (16)
Purple Sandpiper					0.625 (16)

Figures in parentheses are the sample sizes in days. Species are ranked in order of decreasing body mass (Cramp and Simmons 1983).

species (r_S = -0.9, n = 5, P = 0.05 one-tailed). Indices between Purple Sandpiper and other species showed less correlation with those species' masses (r_S = -0.5, n = 5, P = 0.250 one-tailed). Indices involving Oystercatcher tended to be positively correlated to species' mass (r_S = 0.7, n = 5, P < 0.20 one-tailed), though not significantly.

Typically, indices were not correlated with the absolute numbers of either species involved, nor were they affected by which species was more numerous. However, Turnstones and Purple Sandpipers were seen together more frequently when Purple Sandpiper numbers were high (Mann-Whitney z = 3.264, P < 0.01), Purple Sandpipers and Knots when Knot numbers were small (z = 2.896, P < 0.01), Purple Sandpipers and Oystercatchers when Oystercatcher numbers were small (z = 2.616, P < 0.01), and Turnstones and Oystercatchers when Turnstone numbers were small (z = 2.209, P < 0.05) and when Oystercatcher numbers were small (z = 2.517, P < 0.05). Caution must therefore be exercised when interpreting these indices. (Other non-significant relationships between associations and the numbers of the species involved are shown in Appendix 17).

6.3.2. The Turnstone / Purple Sandpiper roosting association.

As indicated above, the association index recorded between roosting Turnstones and Purple Sandpipers was high (58.8%), matched only by those seen between Dunlin and these two species and that between Purple Sandpiper and Redshank. The following section investigates possible reasons for the high Turnstone / Purple Sandpiper association.

6.3.2.1. Information transfer.

Data on the departures of Turnstones and Purple Sandpipers from mixed roosts at West Harbour are shown in Appendix 18. Of 68 flocks recorded departing from West Harbour, only three (4.4%) contained both Turnstones and Purple Sandpipers; 40 contained Turnstones only and 25 Purple Sandpipers only. There is little indication therefore that either species follows the other to feeding sites.

Purple Sandpipers tended to leave the roost with Turnstones only when few other Purple Sandpipers remained (Mann-Whitney $z = 1.680$, $P < 0.05$ one-tailed), and may have done so in preference to remaining in a small flock and being at greater risk to predation, rather than because they were following Turnstones to food resources. The number of conspecifics remaining at the roost did not however relate to whether Turnstones departed with Purple Sandpipers or not ($z = 1.110$, n.s.).

There was little evidence that Turnstones and Purple Sandpipers competed for and thus shared food resources. Of 301 interactions recorded involving individually colour-ringed foraging Turnstones during 1993/94, 273 (90.7%) were intraspecific, whilst only 2 (0.7%) involved Purple Sandpipers. Only 5 (2.4%) of 206 interactions involving individually colour-ringed foraging Purple Sandpipers were with Turnstones, 194 (94.2%) being intraspecific. Of the 7 interactions recorded between foraging Turnstones and Purple Sandpipers, 6 (85.7%) were over feeding sites or food items and 1 (14.3%) due to an encroachment of individual distance.

During winter 1993/94, 29 interactions were recorded between foraging colour-ringed resident birds. Of these 10 were between Turnstones and 19 were between Purple Sandpipers; no interactions were recorded between a colour-ringed Turnstone and a colour-ringed Purple Sandpiper ($\chi^2 = 26.763$, d.f. = 1, $P < 0.001$). Turnstones and Purple Sandpipers are, it would appear, unlikely to exchange information concerning the location of food, as they do not often compete for the same food or feeding sites.

6.3.2.2. Roost microclimate.

Turnstones and Purple Sandpipers roosted together less often at West Harbour when wind speeds were high, though only when Turnstones outnumbered Purple Sandpipers (Table 6.2; $z = 2.774$, $P < 0.01$). On occasions when Purple Sandpipers outnumbered Turnstones, wind speed was not related to their association (Table 6.3; $t = 0.352$, d.f. = 38).

Table 6.2. The frequencies (in numbers of days) with which Turnstones and Purple Sandpipers were together and apart at the West Harbour roost, in relation to wind speed; on occasions when Turnstones outnumber Purple Sandpipers.

	Wind Speed (Beaufort)						
	1	2	3	4	5	6	7
Together	14	18	4	3	2	3	0
Apart	5	7	8	8	3	3	1

Table 6.3. The frequencies (in numbers of days) with which Turnstones and Purple Sandpipers were together and apart at the West Harbour roost, in relation to wind speed; on occasions when Purple Sandpipers outnumber Turnstones.

	Wind Speed (Beaufort)						
	1	2	3	4	5	6	7
Together	2	11	2	8	3	0	0
Apart	4	1	4	2	1	1	1

Table 6.4. Turnstone and Purple Sandpiper shelter indices when roosting apart on the West Harbour island.

	Shelter Index				
	Turnstone (T)	Purple Sandpiper (P)	Wind speed (Beaufort)	Number of Turnstones	Number of Purple Sandpipers
6/9/91	+3	-4	2	686	22
12/9/91	+1	-1	3	655	36
27/9/91	-1	0	1	620	42
21/10/91	+3	-3	1	454	94
19/2/92	-2	0	1	400	232
5/5/92	0	-1	2	250	206
13/8/92[a]	+4	+2	5	232	23
28/8/92[a]	+4	+3	4	234	35
1/9/92[a]	+4	+2	3	285	35
8/9/92[a]	+4	+4	4	114	16
10/9/92[a]	+3	+2	4	145	18
15/9/92[a]	+3	+4	6	212	16
9/10/92[a]	+3	+2	6	128	30
20/3/93	-3	+1	4	64	88
24/3/93	0	-2	4	96	76
11/1/94	-1	+4	5	41	210
9/3/94	-3	+1	5	23	54

[a] -Turnstone using shelter on top of the island.

Table 6.5. The frequencies (in numbers of days) with which Turnstones and Purple Sandpipers were together and apart at the West Harbour roost on sunny and on cloudy days.

	Sunny Days	Cloudy Days
Together	35	35
Apart	29	20

When Turnstones and Purple Sandpipers did roost apart on the West Harbour island, neither species roosted in a site of greater shelter than the other (Table 6.4; Sign Test $x = 6$, $n = 16$, $P = 0.455$). The more numerous species was, however, more likely to roost in a more sheltered position (Sign Test $x = 3$, $n = 16$, $P < 0.05$). The Turnstone / Purple Sandpiper roost association was unaffected by whether the day was sunny or cloudy (Table 6.5; $\chi^2 = 0.643$, d.f. = 1).

Turnstones and Knots were found to roost together more often when wind speeds were high ($t = 2.579$, d.f. = 19, $P < 0.05$). Purple Sandpipers and Dunlins also tended to roost together more often in high winds, though this tendency was insignificant ($t = 1.266$, d.f. = 14, $P < 0.30$). Other, non-significant relationships between roost associations and wind speed are shown in Appendix 17.

In mixed flocks of Turnstones and Purple Sandpipers, the percentages of Turnstones that were found in the middle of flocks were greater than those of Purple Sandpipers (Wilcoxon $T = 0$, $n = 8$, $P < 0.01$ one-tailed). Purple Sandpipers were found at the edge of flocks in greater percentages than Turnstones ($T = 3$, $n = 8$, $P < 0.05$), though at the bottom in similar percentages ($T = 10$, $n = 8$, n.s.).

The percentage of Turnstones in each part of the flock was independent of total flock size (Middle $r = -0.244$, d.f. = 6; Edge $r = -0.060$, d.f. = 6; Bottom $r = 0.419$, d.f. = 6). Similarly total flock size had no effect on the percentage of Purple Sandpipers in each part of the flock (Middle $r = -0.046$, d.f. = 6; Edge $r = 0.121$, d.f. = 6; Bottom $r = -0.094$, d.f. = 6).

A greater proportion of Purple Sandpipers were found at the bottom of flocks if the proportion at the edge decreased ($r = -0.917$, d.f. = 6, $P < 0.01$). Similarly an increased proportion of Turnstones were found at the bottom ($r = -0.846$, d.f. = 6, $P < 0.01$) and the middle of flocks ($r = -0.861$, d.f. = 6, $P < 0.01$) if the proportion at the edge decreased.

Purple Sandpipers occurred in the middle of flocks more often as the ratio of Purple Sandpipers to Turnstones increased, though only if total flock size was taken into account ($t = 2.327$, d.f. = 5, $P < 0.05$ one-tailed). Most Purple Sandpipers thus only gained central, microclimatically favourable positions when the proportion of Turnstones in the flock was low.

Wind speed did not affect the proportion of Turnstones found in each part of the flock (Middle $r = -0.084$, d.f. = 6; Edge $r = 0.243$, d.f. = 6; Bottom $r = -0.321$, d.f. = 6). Similarly the proportion of Purple Sandpipers found in each part of the flock was independent of wind speed (Middle $r = 0.450$, d.f. =6; Edge $r = -0.482$, d.f. = 6; Bottom $r = 0.437$, d.f. =6).

6.3.2.3. Vigilance.

Regression analysis showed that, for both Turnstones and Purple Sandpipers, vigilance time, (measured as the time spent scanning per minute), decreased as the number of conspecifics in the flock increased (Figs. 6.1 and 6.2). Individual Turnstones shared vigilance with other Turnstones ($t = -5.237$, d.f. = 152, $P < 0.001$) and to a lesser degree with Purple Sandpipers ($t = -3.200$, d.f. = 152, $P < 0.01$). Turnstone vigilance time, however, became greater with an increased presence of gulls ($t = 2.475$, d.f. = 152, $P < 0.05$):

$$\ln(\text{Vigilance Time} + 1) = 2.285 - 0.394 \ln(\text{T} + 1) - 0.142 \ln(\text{P} + 1) + 0.470 \ln(\text{G} + 1)$$

$$(r^2 = 0.249;\ F_{3,152} = 16.798,\ P < 0.001)$$

where ln is the natural logarithm and T, P and G represent the number of Turnstones, Purple Sandpipers and gulls respectively within the flock.

Turnstone vigilance time was positively correlated with the number of scans recorded per minute ($r = 0.323$, d.f. = 154, $P < 0.001$).

Fig. 6.1. The relationship between Turnstone vigilance time and the number of conspecifics in the flock.

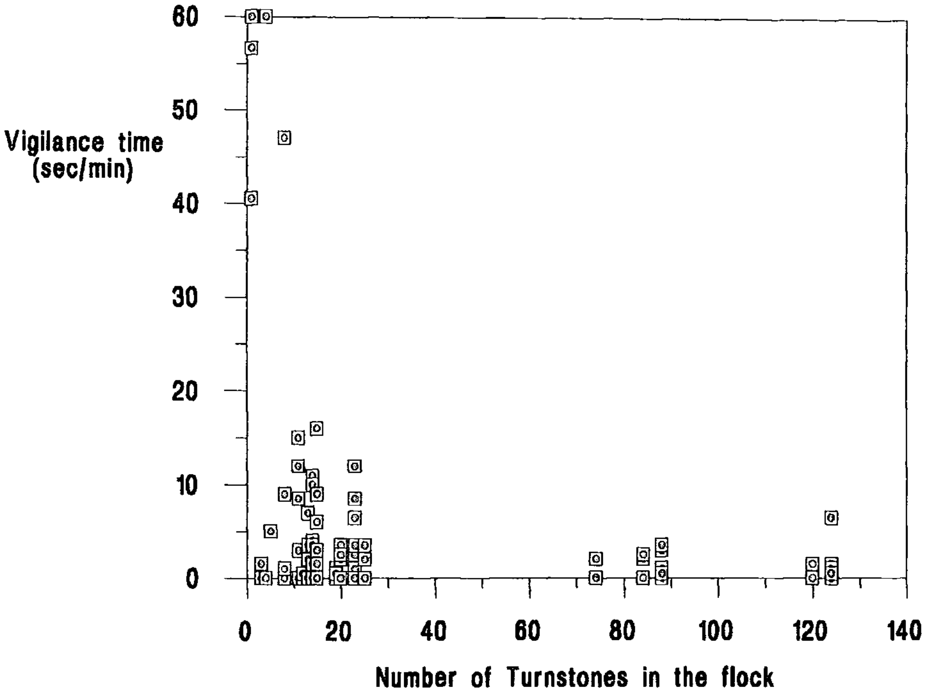
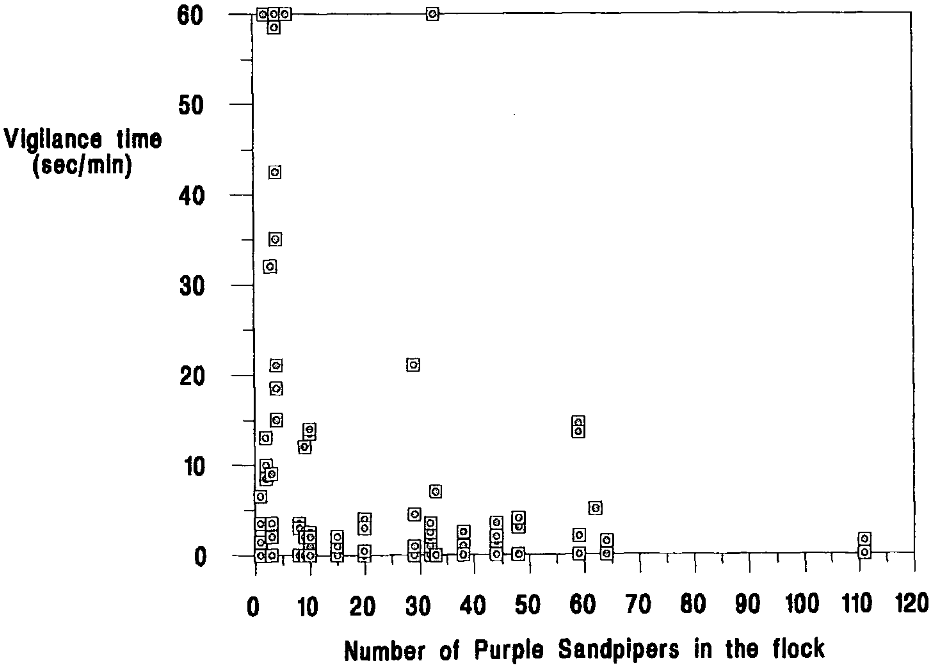


Fig. 6.2. The relationship between Purple Sandpiper vigilance time and the number of conspecifics in the flock.



Individual Purple Sandpipers shared vigilance with conspecifics ($t = -3.538$, d.f. = 153, $P < 0.001$) and with Turnstones ($t = -4.721$, d.f. = 153, $P < 0.001$), though spent more time vigilant if the number of Redshanks in the flock increased ($t = 2.041$, d.f. = 153, $P < 0.05$):

$$\ln(\text{Vigilance Time} + 1) = 2.088 - 0.301 \ln(P + 1) - 0.241 \ln(T + 1) + 0.095 \ln(R + 1)$$

$$(r^2 = 0.308;\ F_{3,153} = 22.738,\ P < 0.001)$$

where the number of Redshanks in the flock is represented by R.

Purple Sandpiper vigilance time was positively correlated with the number of scans per minute recorded ($r = 0.399$, d.f. = 155, $P < 0.001$).

Although neither species was found to share vigilance with Dunlins, this may simply have been a result of the absence of Dunlins in roosting flocks on the days when the observations were taken.

6.3.3. Seasonal changes in association.

Sufficient data were obtained to investigate if and how the Turnstone / Purple Sandpiper roost association changed seasonally. Table 6.6 below shows that in each of the three years of study, the association was strongest in the winter and spring. Combining the three years of data, this effect was significant ($\chi^2 = 9.544$, d.f. = 3, $P < 0.05$).

The associations between Turnstone and Oystercatcher and between Purple Sandpiper and Oystercatcher also changed seasonally, though not consistently from year to year (Tables 6.7 and 6.8 respectively).

The seasonal changes in the Turnstone / Purple Sandpiper association are matched by changes in the relative time of arrival of the two species at the West Harbour roost

Table 6.6. The Turnstone / Purple Sandpiper roost association and its relationship to season

	1991/92			1992/93			1993/94	
'Season'	Together	Apart		Together	Apart		Together	Apart
21/6 - 22/9	4	4		6	6		1	8
23/9 - 21/12	4	4		7	6		7	5
22/12 - 19/3	10	4		7	1		5	4
20/3 - 20/6	8	2		8	2		3	3

(The year is divided into 'seasons' according to daylength).

Table 6.7. The Turnstone / Oystercatcher roost association and its relationship to season.

	1991/92			1992/93			1993/94	
'Season'	Together	Apart		Together	Apart		Together	Apart
21/6 - 22/9	3	7		2	8		1	2
23/9 - 21/12	3	4		1	5		1	0
22/12 - 19/3	1	10		2	2		1	4
20/3 - 20/6	4	5		6	1		0	0

Table 6.8. The Purple Sandpiper / Oystercatcher roost association and its relationship to season.

	1991/92			1992/93			1993/94	
'Season'	Together	Apart		Together	Apart		Together	Apart
21/6 - 22/9	0	8		2	6		0	3
23/9 - 21/12	2	5		1	5		1	0
22/12 - 19/3	0	13		3	2		1	4
20/3 - 20/6	0	8		4	3		0	0

Table 6.9. The relative time of arrival of Turnstones and Purple Sandpipers at the West Harbour roost.

	Median Time of Arrival (minutes before High Water)		
Date	Turnstone (T)	Purple Sandpiper (P)	T - P
22/8/91	155	140	+15
17/9/93	152	143	+9
29/9/93	117	95	+22
21/10/91	139	124	+15
26/10/93	45	74	-29
1/11/93	99	100	-1
5/12/91	96	122	-26
10/2/94	132	168	-36
17/2/92	135	173	-38
5/3/92	77	149	-72
9/3/94	32	92	-60
11/4/94	145	118	+27

Correlation between date (in days after 1 July) and (T - P): $r_s = -0.466$, $n = 12$, $P < 0.20$.

(Table 6.9). Purple Sandpipers arrived, on average, earlier than Turnstones in summer, at a similar time in autumn, and progressively later through winter. Only perhaps in spring did they tend to arrive earlier again. Possible reasons as to why the association may change as a result of changes in the relative time of arrival of the two species are discussed later.

6.4. Discussion.

Associations between wader species at roosts have been noted before (*e.g.* Furness 1973a,b, Robertson and Dennison 1979). Turnstones and Purple Sandpipers commonly roost together (Brearey 1982, Cramp and Simmons 1983), whilst Turnstones have also been seen to associate with roosting Oystercatchers, Knots and Dunlins (Brearey 1982). Variation in the degree of association between roosting species has been noted in New Zealand, where Turnstones associate often with Pacific Golden Plovers and Sharp-tailed Sandpipers *Calidris acuminata*, occasionally with Knots, though seldom with Banded Dotterels *Charadrius bicinctus* (Robertson and Dennison 1979). The present study indicates that associations at West Harbour are related to species' mass. Small species such as Turnstone, and to some degree Purple Sandpiper and Dunlin associate most closely with other small species, whilst Oystercatcher tend to associate with larger species. Metcalfe (1984c) similarly noted that Turnstones in feeding flocks associate most closely with species that are closest to them in size, *e.g.* Purple Sandpiper and Redshank. In contrast to the present study however, Metcalfe suggests that Turnstone and Dunlin do not associate closely, at least whilst foraging.

The high association index recorded between roosting Turnstones and Purple Sandpipers cannot be satisfactorily explained by the information-centre theory of Ward and Zahavi (1973). The two species seldom departed from the West Harbour roost together and when they did, it was perhaps because few birds of one species remained. Both this study and that of Metcalfe and Furness (1987) additionally found that there was little competition for food between foraging Turnstones and Purple Sandpipers, this suggesting that there is only a small overlap in diet between the two. There seems little possibility therefore that the two species roost together to exchange information about food locations. Purple Sandpipers are specialist feeders on rocky shores, often finding prey by tactile contact with their bills (Feare 1966, McKee 1982, Dierschke 1993, Summers 1994). In contrast, the Turnstone is more of a generalist and detects food visually (Harris 1979, McKee 1982). The difference in foraging method between the species may in particular, reduce competition between them. Although feeding associations between Turnstones and Purple Sandpipers have often been noted (Waters 1966, Rees 1969, Metcalfe 1984b,c), Metcalfe (1989) has suggested that foraging Turnstones associate with Purple Sandpipers and other species partly to reduce aggression costs. Turnstones experience less aggression and competition for food when flocking with Purple Sandpipers, Oystercatchers and Redshanks than when with conspecifics (Metcalfe and Furness 1987, Metcalfe 1989). The foraging locations of both species also seldom change - Turnstones alone occasionally exploiting wrack beds over low water (Chapter 4) - whilst food sources, at least for Purple Sandpipers, are relatively abundant on rocky shores (Summers *et al.* 1992, Dierschke 1993). Both species are therefore likely to be highly familiar with the location of their food resources and will not need to exchange information about them at roosts.

Turnstones and Purple Sandpipers do not, it would seem, roost together to reduce energy losses. As wind speed increases and thus as the need to conserve energy becomes greater, the two species were increasingly found apart - though only if Turnstones were more numerous. The two species were also found together as frequently on sunny as on cloudy days.

Most Purple Sandpipers would not gain any energetic benefit from roosting with Turnstones, as they are more likely to be found at the edge of such mixed flocks. This, no doubt, is due to the Turnstone's dominance over the Purple Sandpiper, the former winning 89.7% (n = 39) of all encounters between the two at the West Harbour roost and 95.2% (n = 21) of encounters over roosting sites (Chapter 5). The two species were found together more often when Purple Sandpiper numbers were high and thus perhaps when individual Purple Sandpipers were less likely to be dominated by Turnstones. The proportion of Purple Sandpipers found in the middle of mixed flocks was high only when the proportion of Turnstones in them was relatively low. In these situations, with individual Purple Sandpipers able to obtain favourable roosting positions, the two species were just as likely to be found together in high as opposed to low winds. Previous studies have also noted that segregation occurs between species in mixed flocks (Hale 1980, Gadgil 1972). Robertson and Dennison (1979) found that Pacific Golden Plovers and Sharp-tailed Sandpipers also roosted at the edge of Turnstone flocks.

Whilst the Turnstone / Purple Sandpiper association is unlikely to be connected to energy conservation, the associations between other species may be. Turnstones and Knots roosted together more frequently in high winds and Purple Sandpipers and Dunlins tended to do likewise. Increasing flock sizes by mixing with other species would help individuals to conserve energy, through a reduction of wind speed within the flock. Whitlock (1979) similarly found that Knot and Dunlin increasingly sought more mutual shelter through mixed roosting as environmental conditions worsened. It is notable that in my study, the species that did roost together more often in high winds were of a similar size to each other and thus neither species was likely to be dominant over the other in encounters over roosting positions.

The time that roosting Turnstones and Purple Sandpipers spent being vigilant decreased as the number of conspecifics in the roosting flock increased. By roosting in large flocks and sharing vigilance with others, individuals are thus able to devote more time to sleeping and also to preening and bathing (see Ydenburg and Prins 1984). Lendrem (1984) similarly found that Barbary Doves *Streptopelia risoria* were able to sleep more in groups than when alone, as individuals scanned at lower rates when in groups.

Both Turnstones and Purple Sandpipers also shared vigilance with each other, though for Turnstones the presence of conspecifics was more important than that of Purple Sandpipers in reducing an individual's vigilance. Neither species was found to share vigilance with any other. Metcalfe (1984c) also found that Turnstones and Purple Sandpipers shared vigilance with each other whilst foraging and that foraging Turnstones also shared vigilance with Redshanks and Oystercatchers. Purple Sandpipers have also been seen to associate with Golden Plovers *Pluvialis apricaria* on their breeding grounds (Byrkjedal and Kålås 1983, Cresswell and Summers 1988), and it is thought that, as with Dunlins, they benefit from sharing vigilance and thus being able to feed more efficiently (Byrkjedal and Kålås 1983, Thompson and Thompson 1985). It is probable that the sharing of vigilance between Turnstones and Purple Sandpipers is the main cause of their close association whilst roosting at West Harbour.

Turnstones were more vigilant in the presence of gulls, whilst Purple Sandpipers were more vigilant as the number of Redshanks in the flock increased. Gulls frequently caused disturbance to roosting flocks and were perhaps seen as a predatory threat by Turnstones and other small waders (Chapter 3). The presence of gulls may additionally increase the vigilance of small waders by forming obstacles to visibility (Metcalfe 1984b,c) and because small waders would need to prevent the gulls from treading upon them (Metcalfe 1984c). Redshanks are much taller than Purple Sandpipers and may act similarly as obstacles to visibility and thus increase individual vigilance.

Purple Sandpipers may receive less benefit from sharing vigilance with Turnstones, than Turnstones do from sharing vigilance with the sandpipers. Purple Sandpipers are found at the edge of mixed flocks of the two species in greater percentages and are thus more at risk from predation (Hamilton 1971, Kus *et al.* 1984). Individuals at the edge of flocks also spend more time vigilant than those at the centre and so have less time to devote to other activities (Jennings and Evans 1980, Inglis and Lazarus 1981, Petit and Bildstein 1987). Purple Sandpipers do still benefit from shared vigilance whilst at the edge of mixed flocks however and roost with Turnstones for this reason except perhaps when windy conditions force them to seek greater shelter.

Though the sharing of vigilance helps to explain the association between roosting Turnstones and Purple Sandpipers, the reasons for some other high levels of association are less clear. Purple Sandpipers and Redshanks roost together particularly frequently at West Harbour, (when both species are present), despite the fact that individual Purple Sandpipers actually increase their vigilance in the presence of Redshanks. It seems improbable that the two species would roost together to exchange information about food locations as they were seen interacting whilst foraging only once (Chapter 4). Also, as the two species did not roost together more frequently in high as opposed to low winds (see Appendix 17), it seems unlikely that they associated for energetic benefits.

Turnstones similarly roosted frequently together with Dunlins, though they did not share vigilance with them. Metcalfe (1984c) likewise found that Turnstones did not share vigilance with Dunlins whilst feeding. It is again unlikely that the two species associated together at the roost to exchange information about food locations as they were seen interacting whilst foraging only once (Chapter 4). Insufficient data were obtained to investigate whether the two species roosted together to reduce energy losses.

Though Purple Sandpipers did not share vigilance with Redshanks, nor Turnstones with Dunlins, the associations may still be beneficial in reducing the risk of predation. By producing large flocks, such associations reduce individual risk (Hamilton 1971, Fox *et al.* 1994) and will increasingly confuse predators (Neill and Cullen 1974, Fox *et al.* 1994). Cresswell (1994) found that for individual Redshank, the probability of being captured by a raptor decreased with increasing flock size. This dilution effect and the increasing confusion of predators, he suggested, are perhaps the most important reasons for flocking in large numbers. Above a certain flock size, individual vigilance levels no longer decrease (Myers 1984, Metcalfe 1984c) and other factors must therefore be important in the formation of very large flocks, such as those seen at roosts. Despite these dilution and confusion effects however, small wader species do not tend to roost with large ones. This is perhaps because large species may be avoided by some species of attacking raptor, whilst once in flight, large species, such as Oystercatcher, tend to form separate flocks.

Changes in the risk of predation cannot explain the seasonal changes seen in the Turnstone / Purple Sandpiper association. Overall disturbance rates do not follow a seasonal pattern, whilst the seasonal changes in the rate of disturbance from raptors do not match those of the association. If the energetic benefits of roosting together were important, one would expect that the two species would roost together more in midwinter, which they do not. However if the species roosted together to exchange information about food locations, one would perhaps expect the changes in association that were seen. The need to know the whereabouts of food would be great in winter, when energetic demands are high and greater still in spring when individuals require to lay down fat reserves for their forthcoming migrations. For the reasons explained previously however, it is unlikely that Turnstones and Purple Sandpipers roosted together for this purpose. The seasonal change in roosting association is perhaps more simply related to species' dominance. In summer, Purple Sandpipers arrive on average, after Turnstones, and as the subordinate species, they may choose to form separate flocks rather than lose out to Turnstones in the search for favourable roost positions. In winter and early spring, Turnstones arrive relatively later and in these situations may choose to join existing flocks of Purple Sandpipers as their dominance would assure them of favourable, central roosting positions. The seasonal change in the association may, however, have also resulted from the lack of Purple Sandpipers at the roost in summer and early autumn: the two species were found to roost together less often when Purple Sandpiper numbers were low.

Summary.

1). Turnstones and Purple Sandpipers associated together frequently at the West Harbour roost. Association indices at West Harbour tended to be highest between species of similar size.

2). There was no evidence that Turnstones and Purple Sandpipers roosted together to exchange information concerning the location of food resources. Neither species followed the other from the West Harbour roost and there was little competition for food between the two over low water.

3). There was little evidence that Turnstones and Purple Sandpipers roosted together for microclimatic reasons. The two species were increasingly found apart as wind speed increased. Purple Sandpipers were found more often at the edge of mixed flocks of the two species, where they would be more exposed to the wind and cold temperatures. Most Purple Sandpipers would therefore not benefit energetically from roosting with Turnstones.

4). Turnstones and Purple Sandpipers probably roosted together in order to decrease the risk of being taken by a predator. Both species shared vigilance with each other and by roosting together in large flocks would also benefit from reduced individual risk and a possible increase in predator confusion.

Chapter 7.

General Discussion.

Chapter 2 of this thesis established that Turnstones and to a lesser degree Purple Sandpipers are usually faithful to the same wintering sites between years and that both species are sedentary on small stretches of coast during each winter. Their minimum annual survival rates were high, though a little lower than those recorded in previous studies. During winter both species spent most of each day either feeding over the low water period or roosting over high water. Chapters 3 and 4 revealed how numbers using a particular roosting or feeding site and the time spent roosting varied for both species according to tide levels, weather conditions and season. From further study of behaviour at an individual level, it was apparent that feeding and roosting behaviour were inextricably linked and should not be considered separately.

7.1. The association between feeding and roosting behaviour in non-breeding shorebirds; the importance of dominance status.

Previous studies have shown how the time that shorebirds spend roosting varies seasonally according to the birds' food requirements. During winter, when daylength is short and when individuals put on weight as protection against food shortages and energy losses in cold weather (Johnson 1985, Summers *et al.* 1992), feeding becomes a priority and the time spent roosting over the high tide period is relatively small (Heppleston 1971, Goss-Custard and Durell 1983). Just before spring migration, some species increase their feeding time in order to put on fat reserves and roosting time is again reduced (Zwarts *et al.* 1990, Robinson 1992); similar changes in behaviour occur before autumn migrations (Handel and Gill 1992). Piersma (1983) has shown that in a spring and summer roost of Black-tailed Godwits, roosting time was shortest in June when, because of the demands of breeding, the godwits needed a 'long working day'. Similar changes in behaviour were seen in the present study. Turnstones, and more particularly Purple Sandpipers, arrived at the roost latest during the period of weight increase around or just prior to midwinter and again in spring, just before their northward migrations.

The time that is spent roosting varies between species. Small species, such as Dunlin and Sanderling, have been found to roost for shorter periods than large species, such as Curlew and Oystercatcher (Greenhalgh 1975), as the latter species do not need to feed for as much of the tidal cycle (Hale 1980). Variation in the time spent feeding and roosting has additionally been seen within species. Robertson and Dennison (1979) found that groups of Turnstones occupying different zones of an estuarine complex fed for different lengths of time before coming to their roosts. Such variation may relate to differences in the quality of the feeding habitat in the different zones or differences in the feeding abilities of the different groups of Turnstones. These factors may be connected: subordinate, less efficient Oystercatchers, for example, occupy less favoured feeding zones as a result of exclusion from preferred feeding areas by dominants (Ens and Goss-Custard 1984). Goss-Custard and Durell (1983) also found that young Oystercatchers were seen less often at high water roosts during winter than adults and more often at high water feeding sites.

In all these studies, however, the emphasis is on how much of the tidal cycle is needed for feeding: little consideration is given to the benefits or disadvantages of roosting. Whilst feeding provides birds with energy, roosting may allow them to save energy and an understanding of roosting behaviour is therefore important in analysing how birds balance their daily energy budgets. Energy may be saved over high water by using roosts close to feeding grounds (see Caccamise and Morrison 1986), avoiding disturbance and by using sheltered sites or the shelter found in large flocks. At West Harbour, for example, shorebirds could save considerable energy by roosting at the base of sheltered sides of the island, where wind speeds were much reduced. Roosts may be even more profitable, energetically, if they additionally act as 'information-centres' (Ward and Zahavi 1973), providing birds with knowledge of the locations of profitable food sources.

As shown in the present study, however, the decisions of which roost to use or whether to use sites that provide foraging opportunities over high water are, to a certain degree, dependent upon an individual's dominance. Competition for favourable sites over high water is high and may, as at low water in Oystercatchers (Ens and Goss-Custard 1984), lead to the avoidance of preferred sites by subordinates. Individuals that were subordinate at the main West Harbour roost, (including first-winter birds), were found at the edge of flocks more frequently, where they were more exposed to the wind and cold (Whitlock 1979) and were at greater risk of being taken by a predator (Kus *et al.* 1984). As a probable result of this, subordinates used the West Harbour roost less frequently than dominants (at least in some seasons), and preferred sites that, although not sheltered from poor weather and disturbance, were closer to low water feeding grounds and also offered high water feeding opportunities. Such behaviour would be particularly advantageous for individuals that were also subordinate whilst feeding and that needed to forage over high water to balance their energy budgets. In the present study, in two of three years for Turnstones and one of two years for Purple Sandpipers, roosting dominance was correlated with dominance on 'home feeding areas'; Whitfield (1985a) similarly found that roosting dominance rank was related to feeding dominance rank in his study of wintering Turnstones. Behaviour over the high water period must therefore be considered along with feeding behaviour when attempting to understand how individuals balance their energy budgets.

Dominance may ultimately be important in determining an individual's survival (*e.g.* Johnson et al. 1980, Kikkawa 1980). Individuals that are subordinate whilst foraging may have lower intake rates (Ens and Goss-Custard 1984, Whitfield 1985a) and may not be able to maintain their daily energy budgets as a result. For Turnstones, Whitfield (1985a) provided some evidence that the survival of individuals may indeed be partly determined through their dominance status on feeding grounds. In comparison to other shorebird species however, Purple Sandpipers need to forage for a relatively short period of the tidal cycle to maintain their energy budgets (Dierschke 1993) and so even if subordination does result in lowered intake rates, it is unlikely to affect an individual's survival. Subordination may, however, also increase an individual's likelihood of being taken by a predator. Kus *et al.* (1984) found that juvenile Dunlins were found at the edge of flocks more often than adults and, partly as a consequence of this, were caught more frequently by hunting falcons. Several studies have found that subordinate or juvenile birds are found more often at the periphery of roosting flocks (Swingland 1977, Weatherhead and Hoysak 1984, Still *et al.* 1987, Jenni 1993, the present study) and a similar situation is likely to occur in feeding flocks. By avoiding large roosts and foraging in small flocks over high water, subordinate Turnstones and Purple Sandpipers are likely to be at an even greater risk of predation. Subordination may, in a number of ways therefore, decrease the probability of an individual's survival.

7.2. Variety within and between high water 'roost' sites.

The above discussion emphasises how the high water roosting and feeding needs of shorebirds vary according to season, species and the individual. 'Roost' sites are needed that offer shelter from severe weather, protection from disturbance and predators, that give birds the opportunity to sleep, preen and bathe and that offer feeding opportunities over the high water period. In addition, these 'roost' sites should be as close as possible to low water feeding areas. Within each site there should be as much space as possible: as shown at West Harbour, birds are often segregated according to species and a roost site should be large enough to accommodate such segregation.

In reality, few single sites are likely to have all these qualities and a number of sites may be used by the same individuals as a result. In the present study, 'Headland' residents had the choice over high water of staying on the Headland, where feeding opportunities were varied, limited shelter was available from winds from most directions, but where disturbance rates were high, or flying 1-2 km to West Harbour, where there was greater shelter, less disturbance, but fewer feeding opportunities. Few high water sites were available on the Headland on spring tides however and birds usually flew to West Harbour as a result. Differences in the quality and use of shorebird roost sites have been recorded before by Furness (1973b), Swennen (1984) and Davidson and Evans (1986), the latter emphasising the importance that some sites should provide feeding opportunities to birds over high water.

As high water 'roost' sites do vary in their quality, it is clearly important, from a conservation perspective, that a number should be available to the shorebirds wintering in an area. These sites should preferably be close together, allowing birds to move if disturbance levels at one site become too high. Between them they should also provide high water feeding opportunities throughout the year. If birds are under threat, for example, from industrial development, protection of a complex of roost sites may be needed: it may be of limited value to protect one roost if another close by becomes increasingly disturbed or lost to development.

7.3. Effects on shorebird numbers of the loss of the West Harbour roost site and its replacement with an artificial island.

This final section discusses the effects on shorebird behaviour of the loss through redevelopment of the roost site at West Harbour and its replacement with the artificial island (see 1.3.2 for an overview).

The maximum numbers of four species: Purple Sandpiper, Turnstone, Oystercatcher and Knot, roosting at West Harbour have declined in the years since the harbour's redevelopment, whilst Redshank numbers have recently increased. The decline in Purple Sandpiper numbers at West Harbour is long-term and appears to be linked to a local population decline. In comparison to other studies, over-summer return rates of Purple Sandpipers to Hartlepool, particularly in 1993, were low. The suggestion that some birds moved to new wintering areas was supported by the sighting of one colour-ringed individual, a resident at Hartlepool in winter 1992/93, in Scotland in December 1993. Also, coincident with the decline at Hartlepool, Purple Sandpipers have increased at a number of sites further north on the Durham coast, probably due to improved feeding conditions following cessation of colliery waste dumping there (R.T. McAndrew, pers. comm.).

Turnstone minimum annual survival rates in the area (Table 2.3) were slightly lower than others previously reported in Britain (Evans and Pienkowski 1984, Metcalfe and Furness 1985). The slightly lower rates recorded at Hartlepool and the slight decline in the maximum numbers recorded feeding at Hartlepool Headland do not, however, explain the size of the (c.50%) decline in Turnstone numbers seen at the West Harbour roost. This decline appears to be due to the birds' decreasing preference for the site, rather than to a decline in total numbers in the area.

The maximum number of Turnstones recorded spending high water on Hartlepool Headland has also fallen slightly. Studies of colour-ringed birds revealed that individuals that used the Headland over high water on neap tides also frequently used the West Harbour roost on spring tides (see 5.3.1.5). Some individuals that now use the West Harbour roost less frequently may, therefore, also have abandoned the Headland as a high water site. Roosts such as those at Steetley and Crimdon further to the north and Seaton Sands to the south probably now accommodate those individuals lost to West Harbour.

The declines in the numbers of Oystercatcher and Knot roosting at West Harbour may also be due to a change in roost site preference, since numbers of both species feeding on Hartlepool Headland appear to be stable.

Building work had no detectable impact on the numbers of Purple Sandpipers and Turnstones roosting at West Harbour during 1991/92, despite being the most frequent disturbance factor that year. Other disturbance factors may, however, be important in explaining the changes in wader numbers seen subsequently.

Although, in general, disturbance frequency and intensity were not proven to affect Purple Sandpiper numbers on subsequent days, it was noted that, after a departure of birds from the roost on one day caused by a Merlin, there was a large decrease in the numbers of birds present the following day. Zegers (1973) noted that intense ringing activities which caused shorebirds to leave their roosts, also resulted in declines in the numbers seen at roosts on subsequent days. An increase in disturbance from factors that frequently cause roost departures, *e.g.* raptors, rats, helicopters and boats in this study, may thus lead to more frequent drops in roost numbers. The increased rate of disturbance seen in the present study from boats, some of which entered the outer harbour as well as the marina, may partly explain the decline seen in the numbers of some species roosting at West Harbour. Disturbance by rats may be particularly important if it occurs at dusk to birds intending to roost overnight. Conversely, the increase in numbers of Redshank seen at the West Harbour roost in winter 1993/94 is probably also related to disturbance. An alternative Redshank roost within Hartlepool docks was subject to increased disturbance from building work from autumn 1993 onwards, the same period during which Redshank numbers at West Harbour were seen to increase. Disturbance clearly has an important effect on numbers and it is interesting to note, therefore, that disturbance has been used as a management tool in the control of bird 'pests', most notably gulls (*e.g.* Gosler *et al.* 1995).

Although West Harbour as a whole has declined in importance as a roost site, the island is now by far the preferred site for all waders within it. Purple Sandpipers, for example, hardly used the beams provided for them on the inner pier and instead roosted on the island for almost 80% of their time. Turnstones (and Knots), however, have often used other sites around the harbour (Table 3.12), increasingly so since the island's completion, and their relative aversion to the island may be partly responsible for the overall decline seen in their numbers at West Harbour. All the species preferred to roost on the sides of the island, perhaps as the island's castellated cap prevented birds standing there from seeing possible approaching danger. The sides of the island were also particularly advantageous in allowing birds to shelter from the wind. Some birds, notably Knot, did roost on the top of the island occasionally, however, despite being more exposed to the wind and possibly subject to an increased risk of predation.

Interestingly, the peak count of 686 Turnstones in September 1991, the largest assembly ever recorded in the Hartlepool area, occurred when the island consisted of a rubble core. The facing of large irregular blocks, provided subsequently, may prevent the birds from packing together as closely as they used to (and would prefer to) and could account for their sensitivity to wind strength. On the old piers, they roosted in large numbers irrespective of wind strength (R.T. McAndrew, pers. Comm.).

The island also offers protection from some disturbance factors, though not, unfortunately, from boats or raptors. The proportion of disturbances within the harbour attributable to man (9.4%) was low in comparison with other studies, *e.g.* the 20 - 34% recorded by Kirby *et al.* (1993), whilst disturbance from dogs was totally absent. Only one of 24 disturbances attributable to man affected waders on the island, a further seven affecting waders on the inner pier. It is concluded that the artificial island has provided a satisfactory roost site, which might be used even more if boats and water-skiers could be kept away from it over the high water period.

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Appendix 1.

To test whether ageing of Turnstones in the field was accurate, comparison was made between the 'adjudged' ages of birds that were subsequently found to be colour-ringed and their 'actual' ages, *i.e.* those based on ageing when birds were caught. Data were taken from September to December 1993, after a sample of first-winter Turnstones had been caught and colour-ringed. As the table below shows, ageing in the field was very accurate: only one of 20 Turnstones initially classified as a first-winter bird was an adult and only three of 60 Turnstones classified as adult birds were first-winters ($\chi^2 = 56.510$, d.f. = 1, $P < 0.001$).

		Actual age	
		First-winter	Adult
Adjudged age	First-winter	19	1
	Adult	3	57

Appendix 2.

2.1. Biometric data for Turnstones.

The following data were used to investigate whether the mass and wing-length of Turnstones were correlated and whether these measurements differed between adult and first-winter birds.

i. Data from a catch on Seaton Sands on 26 February 1992.

Age	Wing-length (mm)	Mass (g)
6		108
5		100
6		108
6		110
6		111
6		96
6		102
6		107
6		106
6		113
6		108
5		105
5	145	104
5	152	99
5	149	100
5	143	98
5	148	107
6	155	100
5	149	116
6	148	105
5	153	101
5	145	99
6	153	102

Age	Wing-length (mm)	Mass (g)
6	148	107
6	159	107
5	153	100
6	152	101
6	151	112
6	155	102
5	147	110
5	148	94
5	151	105
5	148	103
6	148	99
5	153	104
6	153	104
5	145	94
5	145	102
5	152	102
6	154	96
6	156	110
6	160	100
6	156	100
6	153	104
6	159	97

where 5 = a bird born the previous summer; 6 = a bird born in a year before then.

ii. Data from a catch at West Harbour on 23 September 1993.

Age	Wing-length (mm)	Mass (g)
4		107
4	152	106
4	155	101
4		109
4		114
4		117
4	155	118
4	162	117
4	155	106
4		118
4	155	113
4	158	109
4		117

Age	Wing-length (mm)	Mass (g)
4		109
4		110
4		107
3	156	103
3	158	94
3	153	100
3	152	129
3	150	88
3	154	99
4	157	117
4		103
4		113
3	150	86

where 3 = a bird born that year; 4 = a bird born in a previous calendar year.

2.2. Biometric data for Purple Sandpipers.

The following data were used to investigate whether the mass, wing-length and bill-length of Purple Sandpipers were correlated and whether these measurements differed between adult and first-winter birds. Data are from a catch at West Harbour on 4 March 1993.

Age	Wing-length (mm)	Mass (g)	Bill-length (mm)
6	132	63	27.5
6	125	46	24.1
6	128	63	28.7
5	132	64	29.7
5	130	58	29.1
5	127	60	29.0
6	130	66	30.7
6	126	54	23.9
6	132	78	35.9
6	131	70	33.7
6	128	56	25.2
5	128	64	31.0
5	129	63	30.4
6	126	56	29.1
6	134	63	29.8
6	139	78	36.2
6	130	60	29.2
5	130	64	28.4
5	131	63	27.2
6	136	78	34.7
6	135	66	29.7
6	132	68	29.5
6	127	58	29.1
6	127	58	28.2
6	130	64	29.6
5	132	62	27.7
5	123	52	25.0
6	136	74	33.0
6	128	60	27.2
6	126	56	24.2
6	133	66	33.0

where 5 = a bird born the previous summer; 6 = a bird born in a year before then.

Appendix 3.

3.1. Recoveries and controls of Turnstones associated with the Hartlepool area.

Date ringed	Age	Location	Date found	Location	Distance (km)
14/10/88	6	Vlieland, Holland	26/2/92	Seaton Sands	431
8-10/93[a]	6	Vlieland, Holland	22/10/93	Hartlepool Headland	431
26/2/92	6	Seaton Sands	1/5/93	Vlieland, Holland	431
26/2/92	6	Seaton Sands	2/6/93	Kilen, Greenland	2979
26/2/92	6	Seaton Sands	7/1/93	Hartlepool Headland	3
26/2/92	6	Seaton Sands	13/1/94	Hartlepool Headland	3

[a] - colour rings read.

3.2. Recoveries and controls of Purple Sandpipers associated with the Hartlepool area.

Date ringed	Age	Location	Date found	Location	Distance (km)
13/12/72[a]	4	Jurmo, Finland	14/4-11/5/92 & 15-28/4/93	Hartlepool	1483
10/11/79	2	Rhos-on-sea, Clwyd	29/12/88	Steetley, Hartlepool	226
10/11/79	2	Rhos-on-sea, Clwyd	29/12/88	Steetley, Hartlepool	226
27/11/87	3	Steetley, Hartlepool	20/3/92	Hartlepool Headland	1
29/12/88	4	Steetley, Hartlepool	27/1/94	Seaton Sands	5
4/3/93[a]	5	West Harbour	4/7/93	Farne Islands, Northumberland	107
4/3/93	6	West Harbour	11/11/93	South Gare	7
4/3/93[a]	6	West Harbour	31/12/93	Portobello, Lothian	188

Appendix 4.

The table below summarises data obtained on the night-time activities of Turnstones and Purple Sandpipers at Hartlepool.

Date	Time	Time of High / Low Water	Height of High / Low Water	State of Light	Location	Number of Birds	Activity
3/12/91	1600	HW 1333	4.8m	Dusk	West Harbour	c.50 Turnstone c.50 P. Sandpiper	Roosting
3/12/91	1615	HW 1333	4.8m	Dusk	Inscar beach	100+ Turnstone	Roosting
24/2/92	1700	HW 2000	4.7m	Dusk	Carr House Sands	300+ Turnstone	Roosting
24/2/92	1720	HW 2000	4.7m	Dusk	West Harbour	30+ P. Sandpiper	Roosting
26/2/92	1800	HW 2215	4.0m	Dusk	Carr House Sands	c.560 Turnstone	Roosting
13/11/92	1711	HW 1711	5.2m	Dark	West Harbour	225+ P. Sandpiper	Roosting
15/11/92	1900	HW 1845	4.9m	Dark	West Harbour	30+ P. Sandpiper	Roosting
11/12/92	1600	HW 1600	5.3m	Dusk	West Harbour	19 Turnstone 223 P. Sandpiper	Roosting
12/2/93	1840	HW 1937	5.1m	Dark	West Harbour	22 P. Sandpiper	Roosting
12/2/93	1900	HW 1937	5.1m	Dark	Carr House Sands	c.80 Turnstone	Roosting
15/11/93	1620	HW 1615	5.6m	Dusk	Carr House Sands	c.80 Turnstone	Roosting
20/1/93	1900	LW 2046	1.4m	Dark	Hartlepool Headland	Only a few Purple Sandpipers present	Unknown

West Harbour was only used as a night roost at high water and typically only by Purple Sandpipers. Numbers, even of this species, were low if high water was much more than two hours after sunset. Turnstone, roosting diurnally at West Harbour at high tide, were often seen to leave and fly south in the direction of Carr House Sands as dusk approached. This area and Seaton Sands, further to the south, clearly formed a major night roost for the species. Observations of colour-ringed Turnstones at the Carr House roost revealed that both Headland residents and visitants were using the site in addition to the local residents. This, and the high counts of birds recorded here in February 1992, suggest that Turnstone came to this night roost from a fairly large area.

No Turnstone and only a few Purple Sandpipers were seen during the low water survey of Hartlepool Headland on the night of 20 January 1993. The activity of these Purple Sandpipers was not determined. Steetley pipes to the north-west are used by Purple Sandpipers as a night roost over high tide (E. Wood pers. comm.), and birds may also be present there at night over low water. The recovery of a ringed Turnstone, one of three killed at night by a domestic cat on 7 January 1993, probably somewhere in the vicinity of Steetley or Parton Rocks (Appendix 3; C. Bantoft pers. comm.), does suggest that at least some Turnstone remain in the area over night.

Appendix 5.

The following table shows the rates of disturbance to shorebirds at the West Harbour roost for three month periods from July 1991. The rate was calculated as the number of disturbances per hour of observation.

Date	Building work	Man	Boats[a]	Gulls	Predators[b]	Other birds[c]	Unknown	Total	Observation time (mins.)
J-S 1991	0.722	0.034	0	0.206	0.034	0	0	1.032	1745
O-D 1991	0.578	0	0.145	0.940	0	0	0	1.662	830
J-M 1992	0.119	0.048	0.024	0.143	0.024	0.071	0	0.428	2525
A-J 1992	0	0.121	0.040	0.283	0	0.242	0	0.687	1485
J-S 1992	0.204	0	0.178	0.561	0.127	0.076	0	1.147	2355
O-D 1992	0.064	0.321	0	0.578	0	0.064	0	1.027	935
J-M 1993	0	0.086	0.301	0.946	0.043	0.086	0.688	2.151	1395
A-J 1993	0	0.581	0.194	0.194	0	0	0.194	1.161	310
J-S 1993	0	0.168	0.280	0.056	0.056	0.112	0.056	0.729	1070
O-D 1993	0	0.138	0	0.207	0.207	0	0.069	0.621	870
J-M 1994	0	0.086	0.514	0.171	0	0.086	0.600	1.543	700
A-J 1994	0	0.250	0.375	0.5	0	0	0.250	1.375	480

[a] - boats and helicopters; [b] - raptors, skuas, crows and rats; [c] - Oystercatchers, eiders, Cormorants, partridges and pigeons.

The following are disturbance rates to Turnstones and Purple Sandpipers alone from non-building work factors.

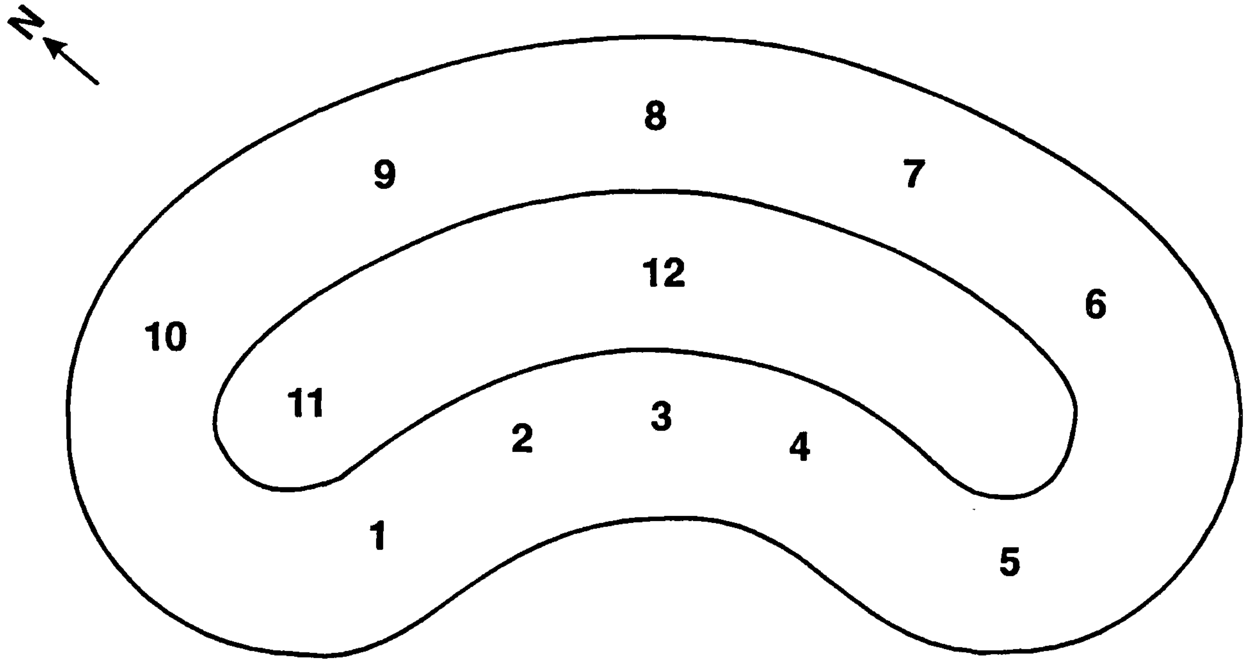
Date	Turnstone	Observation time (mins.)	Purple Sandpiper	Observation time (mins.)
J-S 1991	0.261	1380	0	1380
O-D 1991	0.741	810	0.385	780
J-M 1992	0.166	2525	0.190	2525
A-J 1992	0.646	1485	0.729	1070
J-S 1992	0.866	2355	0.255	2355
O-D 1992	0.834	935	0.642	935
J-M 1993	1.161	1395	2.065	1395
A-J 1993	0.968	310	0.968	310
J-S 1993	0.561	1070	0.480	1000
O-D 1993	0.426	705	0.552	870
J-M 1994	1.091	495	1.371	700
A-J 1994	1.125	480	1.412	425

Appendix 6.

The following table shows the wind speed measurements taken around the West Harbour roost island during low tide on 9 March 1992. Measurements are in metres per minute. The positions around the island at which the readings were taken are shown in the diagram overleaf; 'a' refers to a position that would be at the bottom of the island's slope at high tide (*i.e.* at the high tide mark), 'b' to a position midway up the slope and 'c' to a position on the top of the slope (*i.e.* around the island's rim). Positions 11 and 12 are on the island's top, below the level of the castellated rim.

Position	Measurements	Mean
1a	187, 165, 136	163
1b	177, 186, 196	186
1c	237, 231, 245	238
2a	171, 126, 189	162
2b	387, 371, 355	371
2c	374, 358, 331	354
3a	291, 214, 248	251
3b	263, 306, 329	299
3c	321, 316, 306	314
4a	206, 201, 181	196
4b	273, 250, 235	253
4c	256, 261, 328	282
5a	168, 203, 253	208
5b	225, 118, 111	151
5c	308, 267, 390	322
6a	84, 121, 161	122
6b	80, 96, 55	77
6c	156, 160, 153	156
7a	86, 98, 90	91
7b	76, 54, 31	54
7c	358, 385, 346	363
8a	35, 33, 48	39
8b	23, 20, 31	25
8c	159, 227, 179	188
9a	19, 16, 23	19
9b	22, 40, 24	29
9c	58, 43, 38	46
10a	34, 16, 23	24
10b	52, 29, 45	42
10c	66, 53, 55	58
11	76, 91, 118	95
12	183, 178, 169	177

Position of wind measurements taken around the
West Harbour Island on 9 March 1992



Appendix 7.

7.1. Turnstone behaviour at the West Harbour roost.

There were no correlations between the percentages of Turnstones engaged in each activity and the height of high tide:

Activity	Correlation (r_s) with height of high tide	Significance
Standing	0.048	0.724
Agonistic behaviour	-0.031	0.818
Preening / Bathing	0.193	0.151
Sleeping	-0.082	0.546
Feeding	-0.152	0.259
Running[a]	-0.193	0.149

[a] - running, walking and flying; $n = 57$.

The following tables show the mean percentages of birds engaged in defined activities at the West Harbour roost, either at hourly intervals relative to high tide or in relation to season.

i. In relation to time:

Time relative to high water	Standing	Agonistic behaviour	Preening / bathing	Sleeping	Feeding	Running	Number of samples
-3 hours	8.8	0	72.5	16.0	0.4	2.3	4
-2 hours	10.0	1.2	33.3	47.9	6.0	1.5	12
-1 hour	9.9	0.3	14.3	73.2	0	2.1	14
0	5.3	0.8	17.3	62.6	11.3	2.6	21
+1 hour	2.1	0	26.3	69.6	1.4	0.6	3
+2 hours	10.5	3.8	18.3	66.4	0	1.0	2
+3 hours	33.3	0	23.8	42.9	0	0	1

i. In relation to season:

'Season'	Standing	Agonistic behaviour	Preening / bathing	Sleeping	Feeding	Running[a]	Number of samples
August / September	10.0	1.0	31.2	55.9	0.2	1.7	26
October / November	4.0	0.3	21.2	61.8	11.2	1.5	13
December / January	2.9	1.3	16.8	38.9	35.0	5.1	4
February / March	15.0	1.5	16.2	65.5	0.6	1.3	5
April / May	7.6	0	17.7	69.3	2.6	2.8	9

7.2. Purple Sandpiper behaviour at the West Harbour roost.

Only the percentage of Purple Sandpipers recorded running at the West Harbour roost was correlated with the height of high tide:

Activity	Correlation (r_S) with height of high tide	Significance
Standing	0.106	0.485
Agonistic behaviour	0.209	0.164
Preening / Bathing	-0.047	0.757
Sleeping	-0.141	0.351
Feeding	0.161	0.284
Running	0.298	0.044

$n = 46$.

i. In relation to time:

Time relative to high water	Standing	Agonistic behaviour	Preening / bathing	Sleeping	Feeding	Running[a]	Number of samples
-2 hours	20.6	2.2	10.6	64.1	0.9	1.6	10
-1 hour	15.6	1.0	5.4	74.9	1.3	1.8	15
0	8.3	0.5	5.6	84.5	0.7	0.3	18
+1 hour	0.5	0	7.6	91.9	0	0	3

i. In relation to season:

'Season'	Standing	Agonistic behaviour	Preening / bathing	Sleeping	Feeding	Running[a]	Number of samples
August / September	10.5	0.3	10.5	78.1	0.2	0.5	16
October / November	6.0	0.8	6.6	85.6	0.9	0.2	11
December / January	16.9	0.7	3.3	74.4	3.1	1.6	5
February / March	26.4	2.5	3.8	63.9	1.5	1.9	9
April / May	7.2	1.1	4.1	84.9	0	2.7	5

Appendix 8.

The following table shows the percentages of Turnstones and Purple Sandpipers seen feeding at high water at West Harbour and at Hartlepool Headland.

		Purple Sandpiper				Turnstone			
		West Harbour		Headland		West Harbour		Headland	
Date	Height of high tide (m)	%	*n*	%	*n*	%	*n*	%	*n*
18/7/93	4.9			100	8				
27/7/93	4.6	0	11	0	8	0	34	100	8
21/11/93	4.3			12.5	80	100	16	80.0	30
29/11/93	5.1	0	11	0	14	92.9	28	56.8	44
7/12/93	4.5	0	54	27.3	44	75.0	28	67.2	58
21/12/93	4.3	45.5	101	64.0	25	77.3	22	94.4	71
11/1/94	5.2					0	41	90.2	41
19/1/94	4.2	33.3	15	57.8	45	100	22	76.9	39
27/1/94	5.1					26.3	19	100	26
4/2/94	4.4	0	102	52.5	40			94.9	79
10/2/94	5.2					0	171	0	6
21/2/94	4.0	29.0	69	60.3	58	78.6	14	93.0	57
27/2/94	5.6					0	125	72.3	47
9/3/94	4.6					0	23	0	27
15/3/94	5.1					0	20	100	11
22/3/94	4.0			4.3	139	100	7	38.0	100
23/3/94	4.2			61.1	18			75.0	44
19/4/94	4.2	0	10	1.4	72	34.2	38	16.0	50
21/4/94	4.4	0	11	79.2	48	80.0	10	100	30
26/4/94	5.6					0	51	100	7
3/5/94	4.5	0	40	100	13	1.8	57	83.3	24

where *n* = the number of birds counted.

Appendix 9.

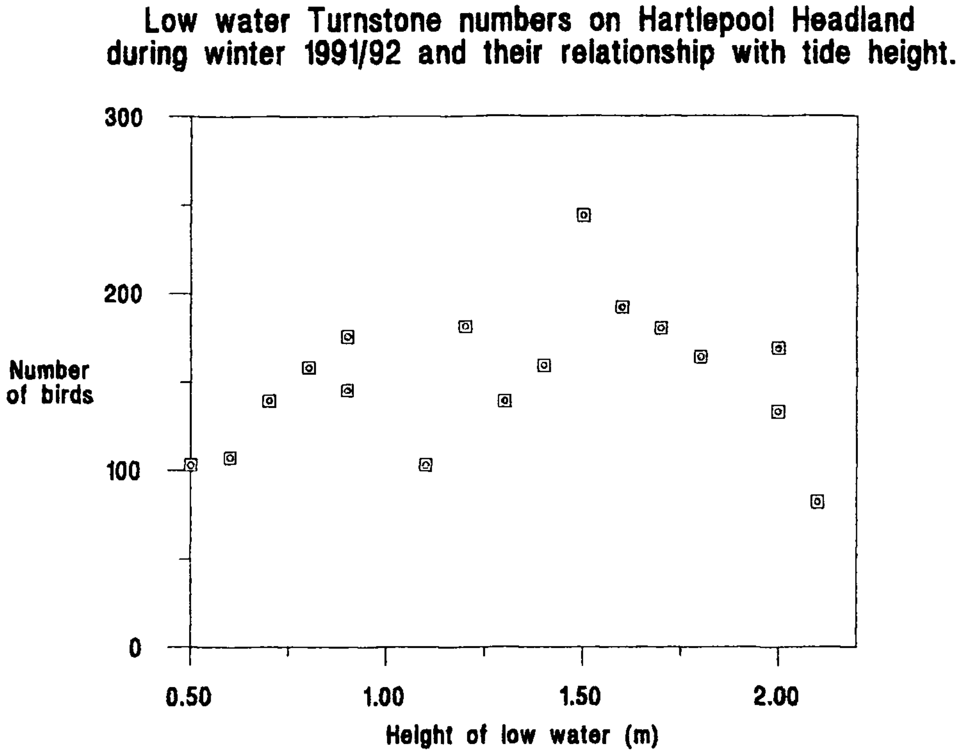
The table below shows the numbers of Turnstones counted on low water surveys of 'south Seaton pipe' during the winters of 1991/92 and 1992/93.

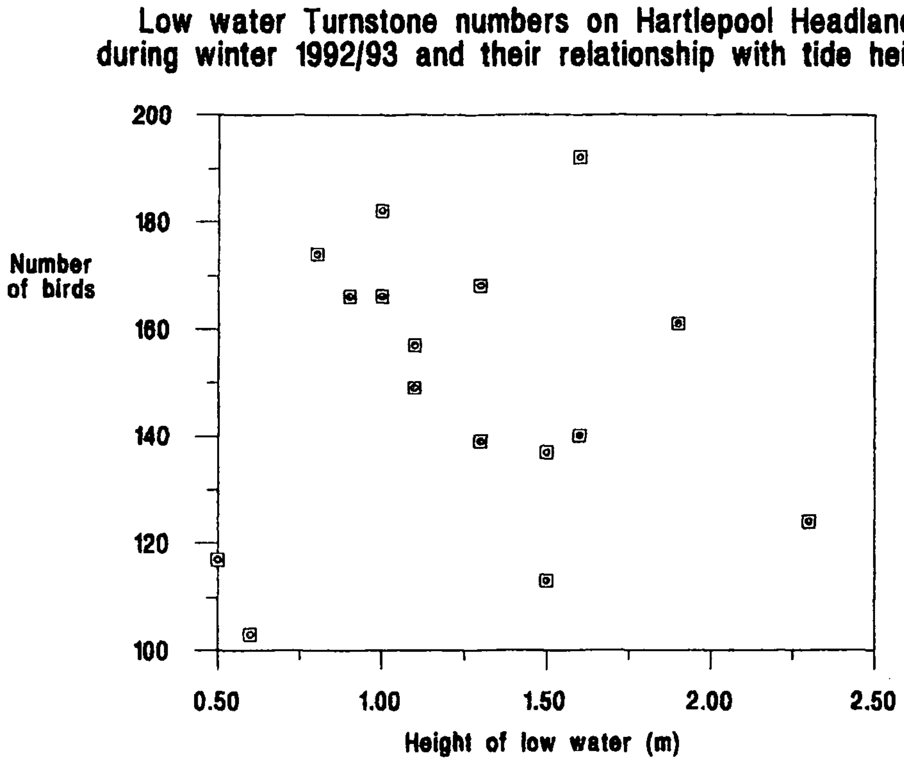
Date	Number of Turnstones
30/10/91	9
5/11/91	11
14/11/91	16
21/11/91	1
28/11/91	23
5/12/91	8
12/12/91	7
20/12/91	3
7/1/92	17
13/1/92	26
20/1/92	0
26/1/92	6
4/2/92	0
10/2/92	4
19/2/92	2
25/2/92	5
5/3/92	4
13/3/92	0
18/3/92	1
27/3/92	0

Date	Number of Turnstones
27/10/92	4
3/11/92	9
10/11/92	5
16/11/92	0
26/11/92	10
30/11/92	7
10/12/92	8
16/12/92	11
1/1/93	6
7/1/93	2
15/1/93	3
21/1/93	1
28/1/93	0
8/2/93	0
15/2/93	0
22/2/93	0
8/3/93	0
16/3/93	1
23/3/93	0
31/3/93	0

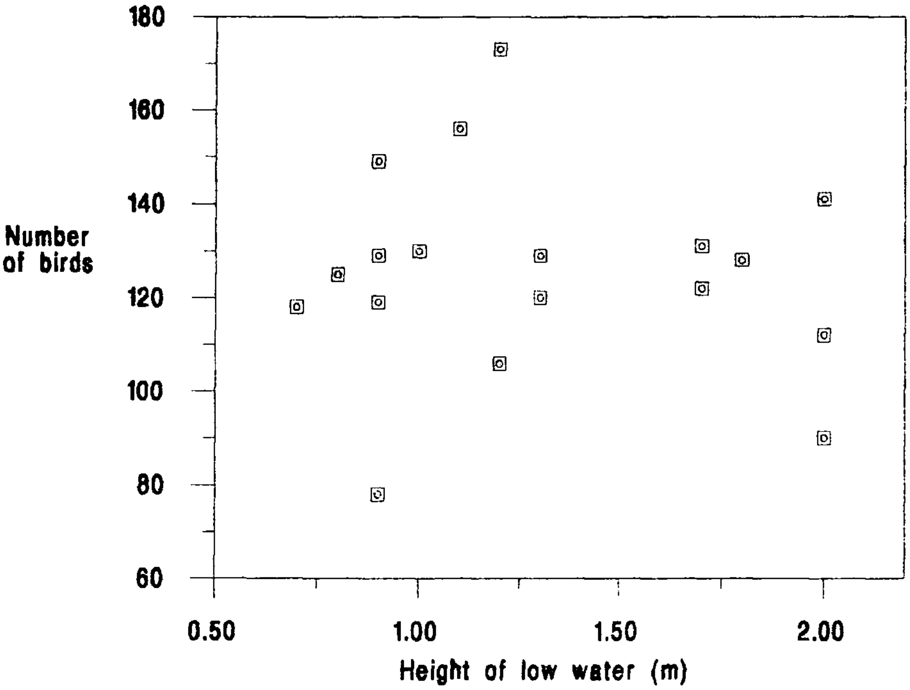
Appendix 10. Low water feeding numbers during winter and their relationship with the height of low tide.

10.1. Turnstone.

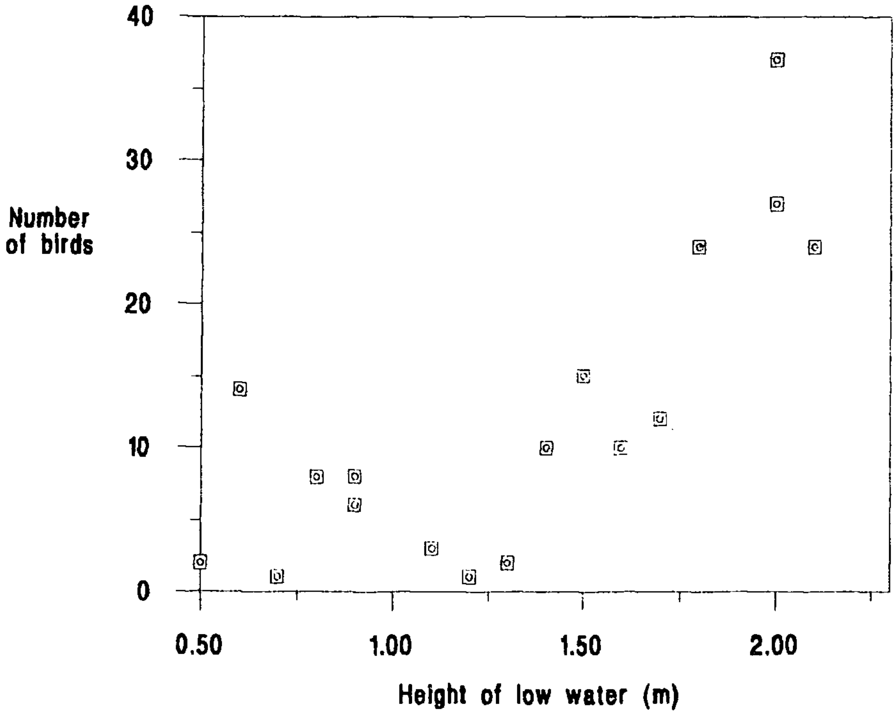




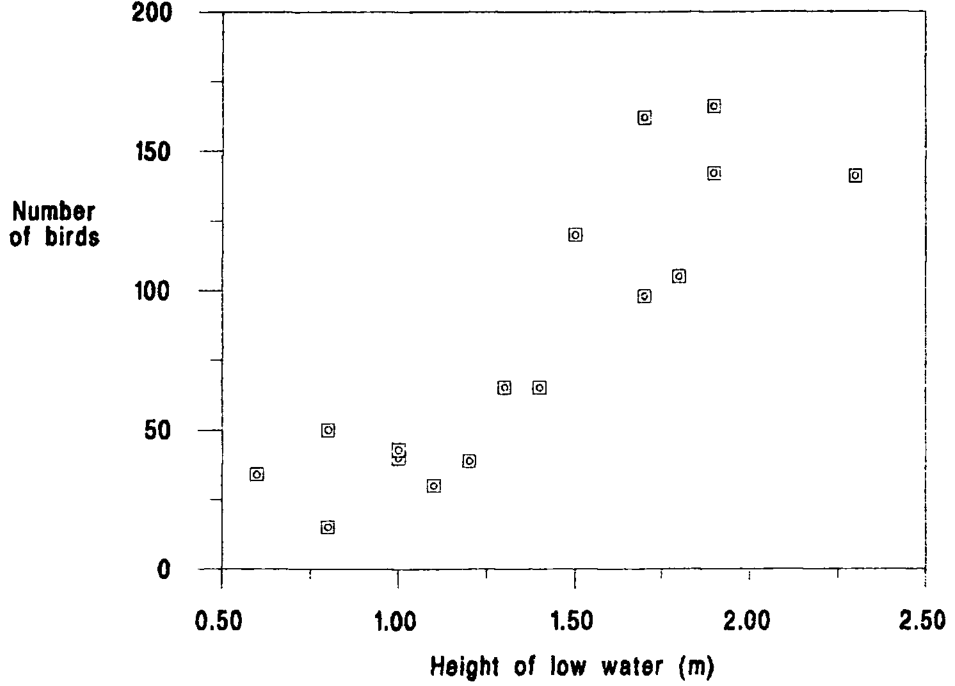
Low water Turnstone numbers on Hartlepool Headland during winter 1993/94 and their relationship with tide height.



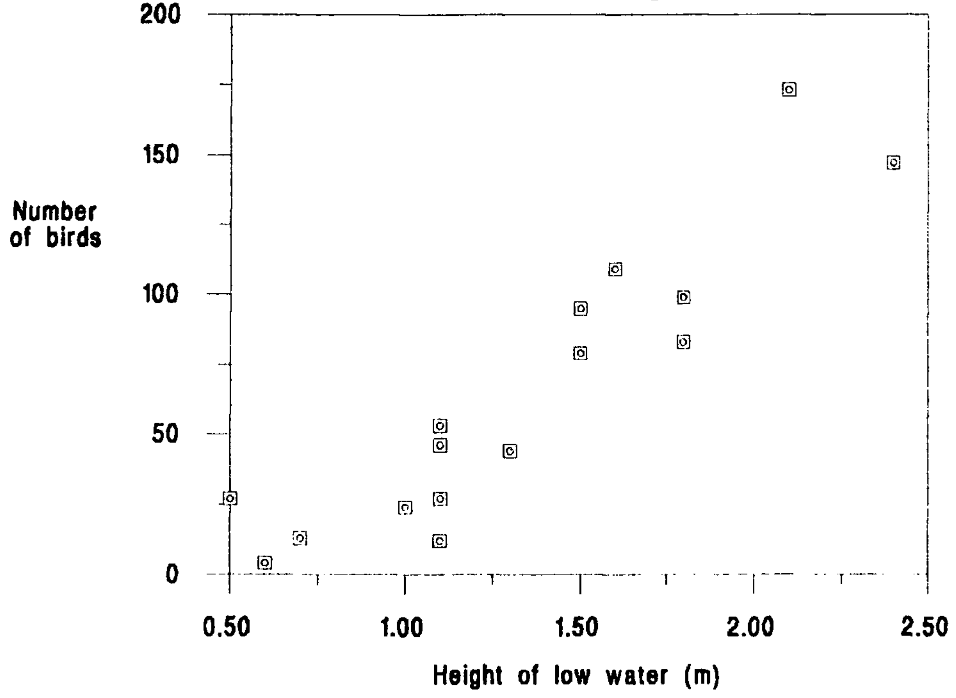
Low water Turnstone numbers in the area between Blackhall and Steetley during winter 1991/92 and their relationship with tide height.



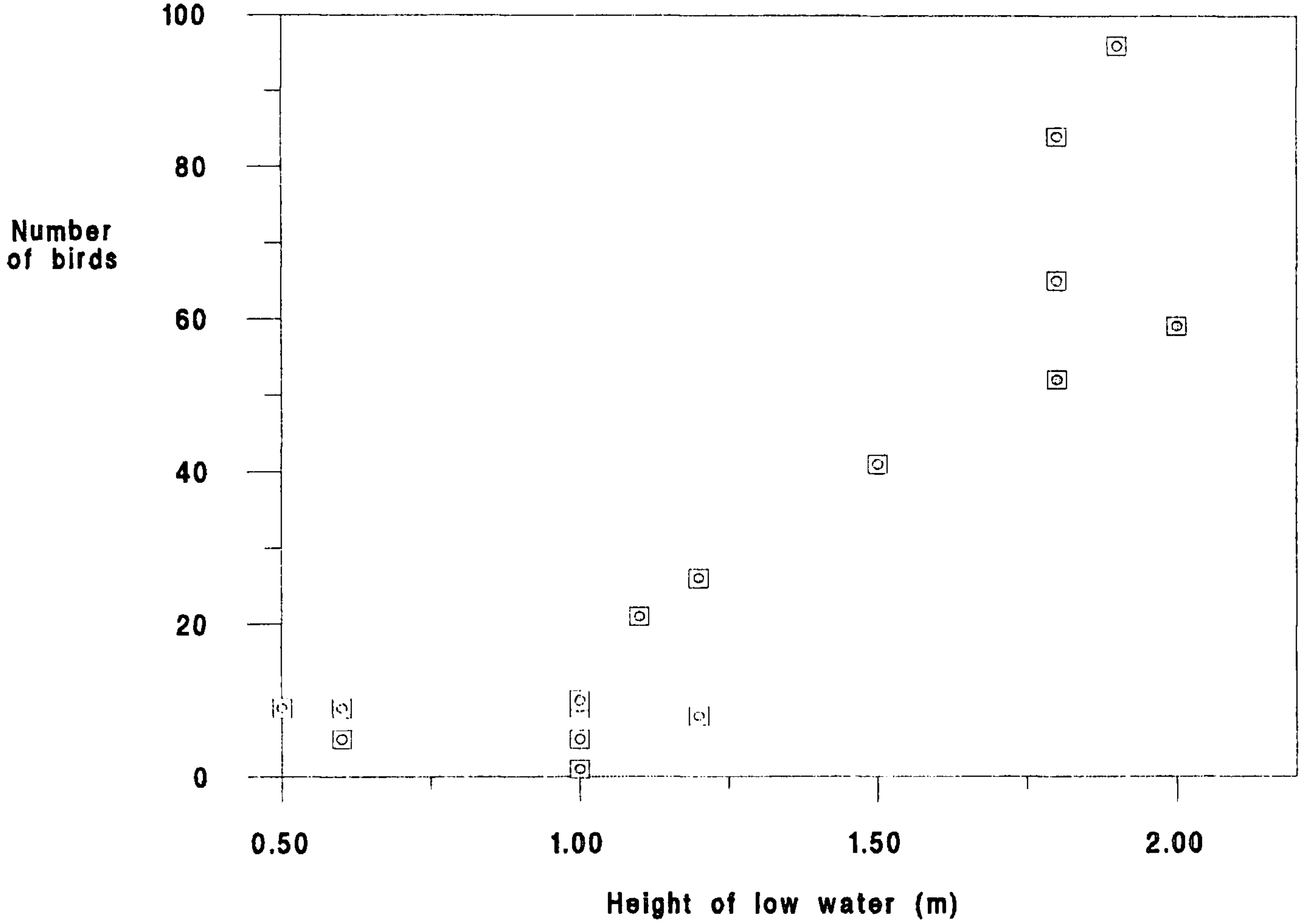
Low water Turnstone numbers in the area between Inscar and North Gare during winter 1991/92 and their relationship with tide height.



Low water Turnstone numbers in the area between Inscar and North Gare during winter 1992/93 and their relationship with tide height.

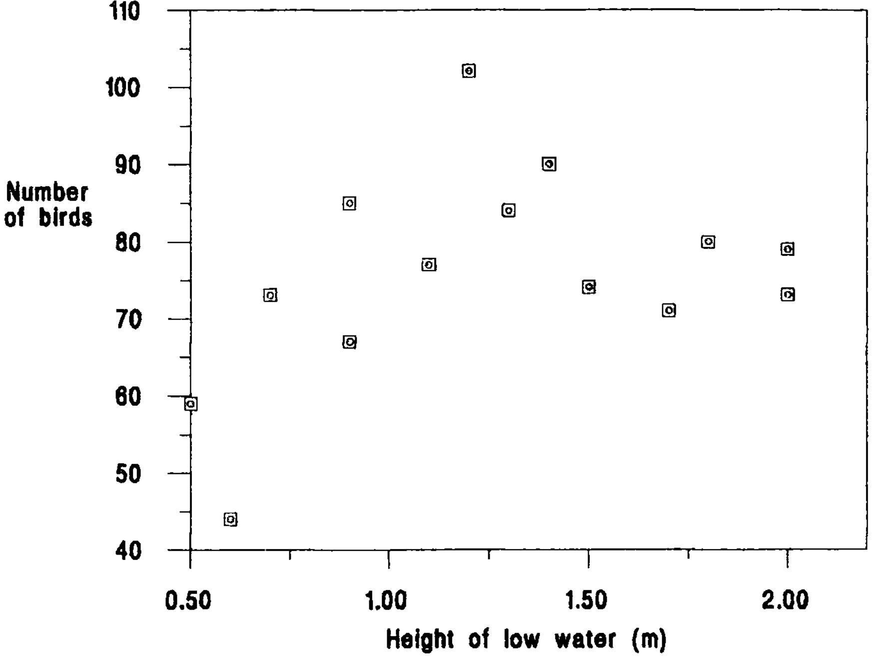


Low water Turnstone numbers in the area between Inscar and North Gare during winter 1993/94 and their relationship with tide height.

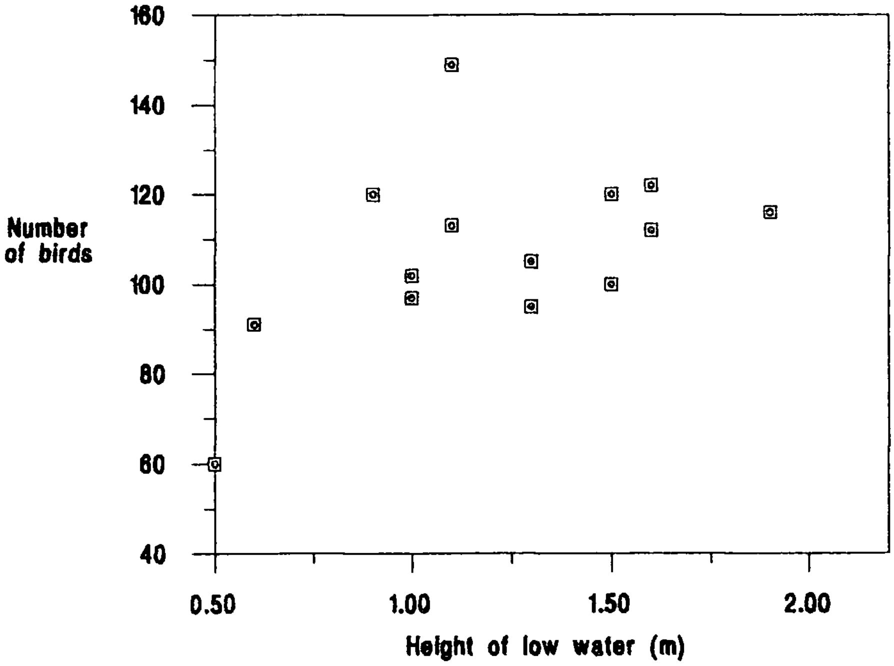


10.2. Purple Sandpiper.

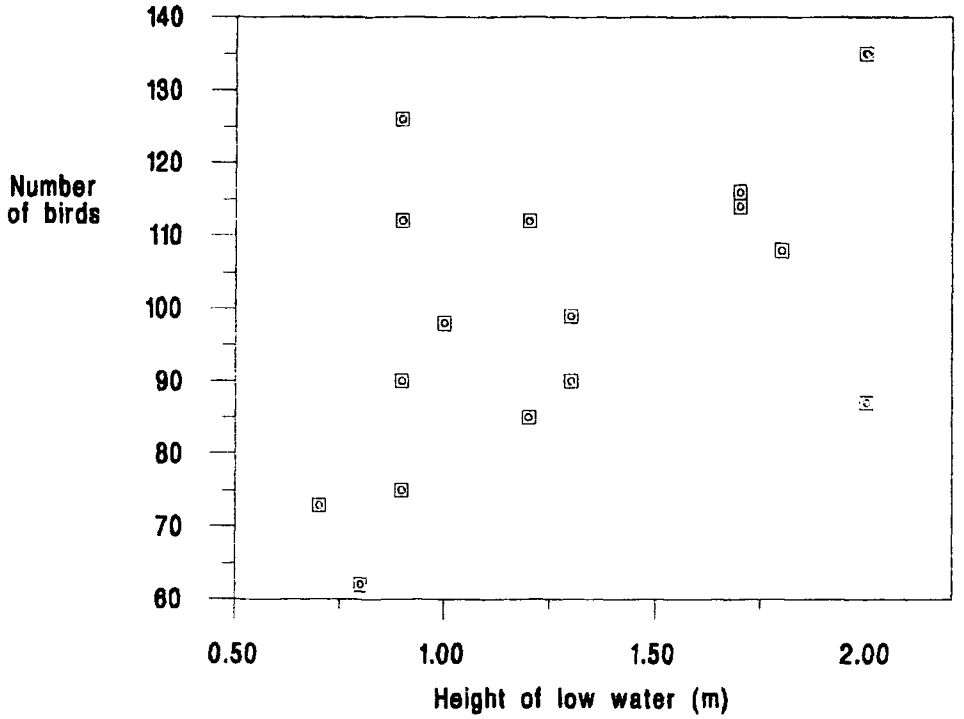
Low water Purple Sandpiper numbers on Hartlepool Headland during winter 1991/92 and their relationship with tide height.



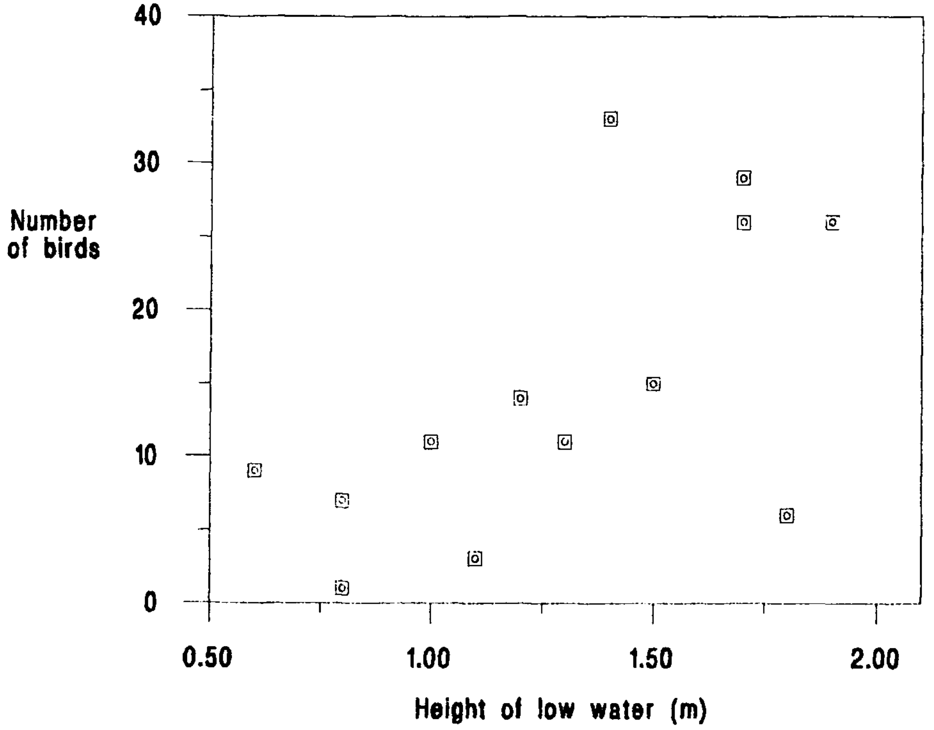
Low water Purple Sandpiper numbers on Hartlepool Headland during winter 1992/93 and their relationship with tide height.



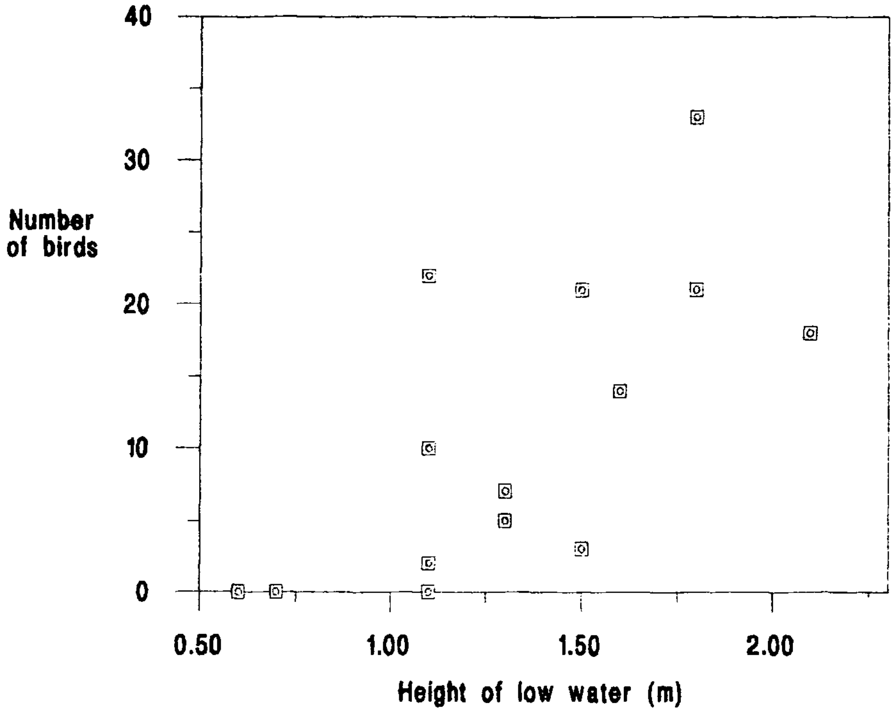
Low water Purple Sandpiper numbers on Hartlepool Headland during winter 1993/94 and their relationship with tide height.



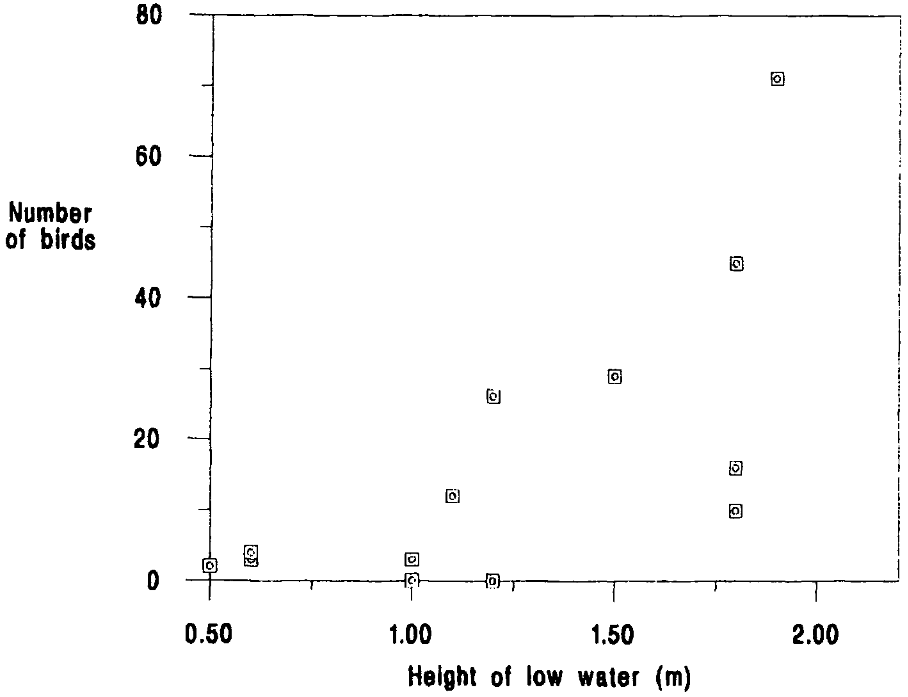
Low water Purple Sandpiper numbers in the area between Inscar and North Gare during winter 1991/92 and their relationship with tide height.



Low water Purple Sandpiper numbers in the area between Inscar and North Gare during winter 1992/93 and their relationship with tide height.



Low water Purple Sandpiper numbers in the area between Inscar and North Gare during winter 1993/94 and their relationship with tide height.



Appendix 11.

11.1. Turnstone dominance hierarchies on low water feeding areas.

i. Hartlepool Headland 1991/92.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
RW YO	100	5	Adult	R
OY Wm	100	5	Adult	V
RW WG	75.0	8	Adult	R
LR LY	66.7	18	Adult	R
LO WY	50.0	4	First-winter	V
LW LR	44.4	9	Adult	R
LG YL	33.3	6	First-winter	R
LO YG	28.6	7	First-winter	R
LO RG	27.3	11	Adult	R
LR GY	27.3	11	Adult	R
RW RO	25.0	4	Adult	V
LO YR	25.0	4	Adult	R
RG RO	25.0	8	Adult	R
LY LG	25.0	4	First-winter	R
Y	0	4	Adult	R
LG WO	0	4	First-winter	V

Under colour-ring identity, B = blue, G = green, L = lime, O = orange, R = red, W = white, Y = yellow and m = metal.

e.g. RW YO is red over white on the left leg below the joint and yellow over orange on the right leg below the joint; a metal ring was above the joint on the right leg unless otherwise stated.

Under residence status, R = a resident and V = a visitant, P = a passage bird.

Interactions between colour-ringed birds:

Winner	Loser	n	
RW YO	LR LY	2	x
LR LY	LG WO	1	x
LR GY	LO YR	1	x
LY LG	LG YL	1	y

where x = interaction went with rank order; y = interaction went against rank order.

ii. West Harbour to North Gare 1991/92.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LW RL	100	4	Adult	R
LO YW	85.7	7	Adult	R
LO RL	80.0	5	Adult	R
GR GR	66.7	6	Adult	R
LO OL	50.0	6	Adult	R
O_aL OR$_{ov}$	42.9	7	Adult	R
LR YL	33.3	8	Adult	R
LY LR	27.3	11	First-winter	R
LO YR	25.0	4	Adult	V
RY GO	20.0	5	Adult	V
LG WO	20.0	5	First-winter	V
LO WY	20.0	5	First-winter	R
LG YO	0	4	First-winter	R
RW RG$_{ov}$	0	7	Adult	R

where $_a$ = ring above joint; $_{ov}$ = rings overlapping.

Interactions between colour-ringed birds:

Winner	Loser	n	
LO YW	LO OL	1	x
LO RL	LY LR	1	x
O_a OR$_{ov}$	RW RG$_{ov}$	1	x
LR YL	LO WY	1	x
LY LR	LG YO	1	x
LY LR	LO YW	1	y

iii. Hartlepool Headland 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LR LY	100	11	Adult	R
RW YO	76.9	13	Adult	R
LY LG	71.4	7	Second-winter	R
LR GY	70.6	17	Adult	R
LG LY	66.7	12	-	R
LG WR	61.5	13	Second-winter	R
LG WO	60.0	10	Second-winter	R
LR WL	50.0	4	Adult	V
YG W	50.0	4	Adult	V
LG RY	42.9	7	Second-winter	R
LY LO	41.2	17	Second-winter	R
LO YR	33.3	6	Adult	R
LO YG	21.4	14	Second-winter	R
LG YL	20.0	20	Second-winter	R
LW LO	20.0	5	Adult	V
LW OY	20.0	5	Adult	R
LY LW	20.0	10	Second-winter	R
LY LY	20.0	10	Second-winter	R
RY GY	12.5	8	Adult	R
LG WL	0	4	Second-winter	V
LO OL	0	6	Adult	V
OG G	0	5	Adult	V

Interactions between colour-ringed birds:

Winner	Loser	*n*	
LR WL	LW LO	1	*x*
LY LG	LY LO	3	*x*
LY LO	LG YL	1	*x*
RW YO	RY GY	1	*x*
LG WO	LO YG	1	*x*
LR LY	LO YR	1	*x*
LR LY	OG G	2	*x*

iv. West Harbour to North Gare 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LO YW	100	5	Adult	R
LW RL	92.3	13	Adult	R
LO WY	80.0	5	Second-winter	R
LW LW	80.0	10	Adult	R
LY LR	62.5	8	Second-winter	R
LR YL	57.1	7	Adult	R
LG LR	50.0	4	-	V
O_aL OR_{ov}	50.0	6	Adult	V
LO RL	28.6	7	Adult	R
LR GL	27.3	11	Adult	R
LR GY	25.0	4	Adult	V
LO OL	20.0	5	Adult	R
LG YO	8.3	12	Second-winter	R

Interactions between colour-ringed birds:

Winner	Loser	*n*	
LO WY	LY LR	3	*x*
LG LR	LG YO	2	*x*
LW RL	LR GY	1	*x*
LW RL	LG YO	1	*x*
LW LW	LR GL	1	*x*
LO RL	LR GL	1	*x*
LO OL	LG YO	1	*x*
LW LW	LO RL	1	*x*

v. Hartlepool Headland 1993/94.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LG LY	100	7	Adult	V
WG mN	100	5	Adult	P
LR LY	87.5	8	Adult	R
LO YR	81.8	11	Adult	R
LG WR	75.0	4	Adult	R
LW RW	75.0	8	Adult	R
LR GY	69.2	13	Adult	V
RW YO	60.0	5	Adult	R
LO YG	52.9	17	Adult	R
LG YL	50.0	10	Adult	R
LO OL	50.0	16	Adult	R
LW OY	40.0	10	Adult	R
RW WG	40.0	5	Adult	V
LW YL	36.4	11	Adult	R
LW WO	28.6	7	Adult	R
OG G	28.6	7	Adult	R
LG RY	22.2	9	Adult	R
LG LR	20.0	5	Adult	V
LG LW	16.7	6	Adult	V
LY WG	12.5	16	First-winter	R
LW LR	10.0	10	Adult	V
RO YG	9.1	11	Adult	R
LY WO	5.9	17	First-winter	R
LG YW	0	4	Adult	V
LY RW	0	6	First-winter	R
RO RG	0	4	Adult	V

Interactions between colour-ringed birds:

Winner	Loser	*n*	
RW WG	LO OL	1	*y*
LO YR	LG LR	2	*x*
LO YG	OG G	1	*x*
LO OL	LO YG	2	*y*
OG G	LO YG	1	*y*
LR GY	LO OL	1	*x*
OG G	LW OY	1	*y*
LY WR	LY RY	1	*x*
LO YG	LY WO	1	*x*

Winner	Loser	*n*	
LW RW	RO YG	2	*x*
LO YG	RO RG	1	*x*
LG YL	LY WG	1	*x*
LG YL	LY RW	2	*x*
LY WG	LY RW	2	*x*
LR LY	LO OL	1	*x*
RW YO	LW WO	1	*x*
LW WO	LY WG	1	*x*

11.2. Purple Sandpiper dominance hierarchies on low water feeding areas.

i. Hartlepool Headland 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
GO WLm	100	8	First-winter	R	L	F
OW WGm	75.0	4	Adult	R	L	F
RL WGm	62.5	8	Adult	R	M	
GR WGm	55.6	9	Adult	R	L	F
GL WLm	50.0	4	Adult	R	M	
LR WGm	42.9	7	Adult	R	M	
WG WGm	40.0	5	Adult	R	M	
GW WGm	33.3	18	Adult	R	M	
RW WGm	25.0	4	Adult	V	M	
OL WGm	16.7	6	Adult	R	M	F
LG WGm	0	4	Adult	R	S	M
OG WGm	0	6	Adult	R	S	M

e.g. GO WLm is green over orange on the left leg below the joint, white above the joint on the right leg, lime over metal below the joint on the right leg.

Under bill-length size class, L = large, M = medium and S = small; under sex F = female and M = male.

ii. West Harbour to North Gare 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
GR WGm	81.8	11	Adult	V	L	F
RG WGm	71.4	7	Adult	R	L	F
GL WLm	70.0	10	Adult	V	M	
LG WLm	69.2	13	First-winter	R	M	
LO WLm	62.5	8	First-winter	R	M	
RO WGm	57.1	7	Adult	R	M	
RY WGm	40.0	5	Adult	R	M	F
LO WGm	25.0	4	Adult	R	M	
LR WGm	25.0	4	Adult	V	M	
OG WLm	25.0	4	First-winter	R	M	
WL WGm	0	4	Adult	R	L	F
GO WLm	0	4	First-winter	V	L	F

Interactions between colour-ringed birds:

Winner	Loser	*n*	
RO WGm	WL WGm	1	*x*
GL WLm	LG WLm	1	*x*
RG WGm	LO WLm	1	*x*
LO WLm	OG WLm	1	*x*
LG WLm	OG WLm	1	*x*
LG WLm	GO WLm	1	*x*

iii. Headland 1993/94.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
RL WGm	100	8	Adult	R	M	
GW WGm	63.6	11	Adult	R	M	
GY WLm	63.6	11	Second-winter	R	M	
OL WGm	61.5	13	Adult	R	M	F
LW WGm	50.0	6	Adult	R	S	M
RY WGm	50.0	6	Adult	V	M	F
WR WGm	42.9	7	Adult	R	S	M
LR WGm	27.3	11	Adult	R	M	
OY WGm	25.0	4	Adult	R	M	F
YL WGm	25.0	4	Adult	R	M	
OG WLm	20.0	10	Second-winter	R	M	
OG WGm	14.3	7	Adult	R	S	M
GR WLm	14.3	7	Second-winter	R	M	F
GW WLm	0	4	Second-winter	V	M	

Interactions between colour-ringed birds:

Winner	Loser	*n*	
GW WGm	LR WGm	3	*x*
RL WGm	OL WGm	1	*x*
LW WGm	OG WGm	1	*x*
OL WGm	YL WGm	2	*x*

iv. West Harbour to North Gare 1993/94.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
OR WGm	88.9	9	Adult	R	M	
GY WGm	66.7	12	Adult	R	S	M
LR WGm	50.0	8	Adult	V	M	
OG WLm	50.0	8	Second-winter	V	M	
LO WLm	50.0	14	Second-winter	V	M	
RW WGm	42.9	7	Adult	R	M	
RY WGm	33.3	9	Adult	R	M	F
WO WGm	33.3	12	Adult	R	S	M
WL WGm	25.0	4	Adult	R	L	F
OL WLm	25.0	8	Second-winter	R	S	M
GW WLm	12.5	8	Second-winter	V	M	

Interactions between colour-ringed birds:

Winner	Loser	n	
OR WGm	GW WLm	2	x
GY WGm	LO WLm	3	x
GY WGm	OG WLm	1	x
OG WLm	LO WLm	1	z
OR WGm	WO WGm	1	x
OR WGm	OL WLm	1	x
WO WGm	RY WGm	1	z
OL WLm	WO WGm	2	y
LR WGm	GW WLm	1	x
GY WGm	GW WLm	1	x
RY WGm	RW WGm	1	y
RW WGm	OL WLm	1	x
RW WGm	WO WGm	2	x

where z = an interaction between two equally ranked birds.

Appendix 12.

The tables below relate the dominance of individual resident Turnstones to their age in years. (Dominance is expressed as the percentage of encounters won).

i. Dominance on 'home' feeding areas.

	Age (in years)											
	1	2	3	4	5	6	7	8	9	10	11	12
LG RY		42.9	22.2									
LG WO		60.0										
LG WR		61.5	75.0									
LG YL	33.3	20.0	50.0									
LG YO	0	8.3										
LO OL							50.0	20.0	50.0			
LO RG		27.3										
LO RL		80.0	28.6									
LO WY	20.0	80.0										
LO YG	28.6	21.4	52.9									
LY LG	25.0	71.4										
LY LO		41.2										
LY LR	27.3	62.5										
LY LW		20.0										
LY LY		20.0										
LY RW	0											
LY WG	12.5											
LY WO	5.9											
LY WR	50.0											
OG G										28.6		
RG RO								25.0				
RW YO										100	76.9	60.0
RY GY										12.5		

ii. Dominance at the West Harbour roost.

	Age (in years)											
	1	2	3	4	5	6	7	8	9	10	11	12
LG RY		36.4	50.0									
LG WO	50.0	63.0										
LG WR		0	0									
LG YG		0										
LG YL		14.3										
LG YO	0	0										
LO OL							0	41.7	50.0			
LO RG		28.6										
LO RL		66.7	57.1									
LO YG			0									
LY LG		20.0										
LY LO		30.8										
LY LR		0										
LY LW		25.0										
LY LY		16.7										
LY RW	0											
LY RY	16.7											
LY WG	28.6											
OG G									33.3	50.0		
RW YO											53.3	54.5
RY GY									100	50.0		
RY OG								20.0	55.6			

Appendix 13.

13.1. The relationship between dominance on 'home' feeding areas and survival in Turnstones.

i. Dominance over winter 1991/92 and survival over summer 1992.

Colour-ring identity	Dominance (% of encounters won)	Survival over summer 1992
RW YO	100	S
LW RL	100	S
LO YW	85.7	S
LO RL	80.0	S
RW WG	75.0	S
GR GR	66.7	D
LR LY	66.7	S
LO OL	50.0	S
LW LR	44.4	S
O_aL OR_{ov}	42.9	S
LR YL	33.3	S
LO YG	28.6	S
LR GY	27.3	S
LY LR	27.3	S
LO YR	25.0	S
RG RO	25.0	S
LO WY	20.0	S
LG YO	0	S
RW RG_{ov}	0	D

where S = 'survived' and D = 'died', *i.e.* did not return to the study area.

ii. Dominance over winter 1992/93 and survival over that winter and over summer 1993.

Colour-ring identity	Dominance (% of encounters won)	Survival over winter 1992/93	Survival over summer 1993
LO YW	100	S	D
LR LY	100	S	S
LW RL	92.3	D	
LO WY	80.0	S	S
LW LW	80.0	S	S
RW YO	76.9	S	S
LY LG	71.4	D	
LR GY	70.6	S	S
LG LY	66.7	S	S
LY LR	62.5	S	D
LG WR	61.5	S	S
LG WO	60.0	D	
LR YL	57.1	S	S
LG RY	42.9	S	S
LY LO	41.2	D	
LO YR	33.3	S	S
LO RL	28.6	S	D
LR GL	27.3	S	S
LO YG	21.4	S	S
LO OL	20.0	S	S
LG YL	20.0	S	S
LW OY	20.0	S	S
LY LW	20.0	S	S
LY LY	20.0	S	D
RY GY	12.5	D	
LG YO	8.3	D	

13.2. The relationship between dominance on 'home' feeding areas and survival in Purple Sandpipers.

i. Dominance over winter 1992/93 and survival over summer 1993.

Colour-ring identity	Dominance (% of encounters won)	Survival over summer 1993
GO WLm	100	D
OW WGm	75.0	D
RG WGm	71.4	D
LG WLm	69.2	D
RL WGm	62.5	S
LO WLm	62.5	S
RO WGm	57.1	D
GR WGm	55.6	D
GL WLm	50.0	D
LR WGm	42.9	S
RY WGm	40.0	S
WG WGm	40.0	D
GW WGm	33.3	S
LO WGm	25.0	D
OG WLm	25.0	S
OL WGm	16.7	S
LG WGm	0	D
OG WGm	0	S
WL WGm	0	S

ii. Dominance over winter 1993/94 and survival over summer 1994.

Colour-ring identity	Dominance (% of encounters won)	Survival over summer 1992
RL WGm	100	D
OR WGm	88.9	S
GY WGm	66.7	D
GW WGm	63.6	S
GY WLm	63.6	S
OL WGm	61.5	S
LW WGm	50.0	S
WR WGm	42.9	D
RW WGm	42.9	S
RY WGm	33.3	S
WO WGm	33.3	S
LR WGm	27.3	D
OL WLm	25.0	S
OY WGm	25.0	S
YL WGm	25.0	S
WL WGm	25.0	D
OG WLm	20.0	S
GR WLm	14.3	S
OG WGm	14.3	S

Appendix 14. Tests for biases in data concerning segregation at the roost.

14.1. Turnstone.

The following tests investigated whether individuals from different groups were present on days of different high tide levels. If such differences existed, bias would be produced in the subsequent analyses, as individuals would be the nearest neighbours of birds from their own group more often than expected. Visitant Turnstones were found to use the West Harbour roost on days of higher average high tide levels than residents (Mann-Whitney $z = 2.710$, $P < 0.01$). Visitants were therefore excluded from the test which investigated whether there was segregation between individuals from different areas. Individuals classified on the basis of feeding area as 'Headland', 'West Harbour to North Gare' or 'North and South' residents were seen at West Harbour over high water on days of similar tidal levels (Kruskal-Wallis $\chi^2 = 3.327$, d.f. = 2, n.s.).

14.2. Purple Sandpiper.

As with Turnstones, initial tests investigated whether individuals from different groups were present at the West Harbour roost on days of different high tide levels (data are taken from late winter / early spring 1993). Individual Purple Sandpipers resident over low water on the Headland and between West Harbour and North Gare were seen at the West Harbour roost on days of similar high tide levels (Mann-Whitney $z = 0.217$, n.s.), as were adult and first-winter individuals ($z = 0.336$, n.s.) and individuals from different bill-length size classes (Kruskal-Wallis $\chi^2 = 4.849$, d.f. = 2, n.s.). No individuals were therefore omitted from any of the analyses.

Appendix 15.

15.1. Turnstone dominance hierarchies at the West Harbour roost.

i. 1991/92.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LR RL	100	4	Adult	V
LW RL	100	4	Adult	R (S)
RW RW$_{ov}$	100	4	Adult	V
RY GY	100	5	Adult	R (N+S)
GR GR	81.8	11	Adult	R (S)
OW m	75.0	4	Adult	P
LO RL	66.7	15	Adult	R (S)
RY B	66.7	9	Adult	R (S)
LG WO	50.0	6	First-winter	R (N+S)
LR RW	50.0	4	Adult	R (S)
LG LY	33.3	6	-	R (N)
LO RG	28.6	7	Adult	R (N)
LO YR	25.0	4	Adult	R (N)
LW LR	20.0	5	Adult	R (N)
LW LY	20.0	5	Adult	-
RY OG	20.0	5	Adult	R (-)
RW RG$_{ov}$	14.3	7	Adult	R (S)
LG YO	0	6	First-winter	R (S)
LO OL	0	4	Adult	R (S)
OR WG$_{ov}$	0	4	Adult	V
RG GW$_{ov}$	0	4	Adult	P
RG WY	0	9	Adult	R (S)

where, under residence status, R = resident, V = visitant, P = passage bird, N = Headland resident, S = West Harbour to North Gare resident and N+S = North and South resident.

Interactions between colour-ringed birds:

Winner	Loser	*n*	
LG WO	LG YO	1	*x*

ii. summer 1992.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters
LG YG	80.0	10
LG LY	75.0	4
LY LO	50.0	10
LY LG	14.3	7
LY LW	14.3	7
LG YL	0	4
LG YO	0	4
LY LR	0	5

Winner	Loser	*n*	
LG YG	LY LO	1	*x*
LG YG	LY LR	1	*x*
LG LY	LG YO	1	*x*
LY LG	LG YL	1	*x*
LY LW	LG YL	1	*x*

iii. 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
LW RL	80.0	10	Adult	R (S)
RY B	80.0	15	Adult	V
LO YW	77.4	31	Adult	R (S)
LG WO	63.0	27	Second-winter	R (N)
LR WR	62.5	8	Adult	V
LG LY	58.1	31	-	R (N)
LO RL	57.1	7	Adult	R (S)
RW$_{ov}$ RG$_{ov}$	55.6	9	Adult	R (S)
RY OG	55.6	9	Adult	R (N+S)
RW YO	53.3	15	Adult	R (N)
LY RL	50.0	8	Second-winter	V
RY GY	50.0	6	Adult	R (N)
LG LR	42.9	7	-	R (N+S)
LO OL	41.7	12	Adult	R (S)
LG RG	40.0	5	-	R (S)
LO YR	39.1	23	Adult	R (N)
OR WG$_{ov}$	37.5	8	Adult	V
LG RY	36.4	11	Second-winter	R (N)
LR LY	33.3	6	Adult	R (N)
OG G	33.3	6	Adult	R (N+S)
LY LO	30.8	13	Second-winter	R (N)
LR YL	30.0	10	Adult	R (S)
LW WG	27.3	11	Adult	R (-)
LW LW	26.7	15	Adult	R (S)
LW OY	25.0	8	Adult	R (N)
LY LW	25.0	4	Second-winter	R (N)
LY LG	20.0	5	Second-winter	R (N)
LY LY	16.7	6	Second-winter	R (N)
LG YL	14.3	7	Second-winter	R (N)
LG RW	12.5	8	Second-winter	V
LG WL	12.5	8	Second-winter	V
LR GY	12.5	8	Adult	R (N)
LG WR	0	4	Second-winter	R (N)
LG YG	0	16	Second-winter	R (N+S)
LG YO	0	4	Second-winter	R (S)
LR RW	0	6	Adult	V
LY LR	0	11	Second-winter	R (S)
RG GW$_{ov}$	0	5	Adult	P

Interactions between colour-ringed birds:

Winner	Loser	*n*	
LG LR	LG WR	1	*x*
LW LW	LG YO	1	*x*
LY LO	LG YG	2	*x*
LG WO	LY LO	1	*x*
LY RL	LR RW	2	*x*
LW RL	OG G	1	*x*
LO YW	LW LW	2	*x*
OR WG$_{ov}$	LG YL	1	*x*
LO YR	LG RW	1	*x*
LO YR	RW YO	1	*y*
LR WR	LY LR	2	*x*
LR WR	LG RG	1	*x*
LG RG	LW WG	1	*x*
LW WG	LG YG	1	*x*
RY B	LR LY	1	*x*
LR YL	LG YO	1	*x*
RWov RGov	LG YG	1	*x*

iv. 1993/94.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
RY B	94.1	17	Adult	V
LW WL	88.9	9	Adult	R (N+S)
LO YR	77.3	22	Adult	R (N)
LW RW	71.4	7	Adult	R (N)
LG LY	64.3	14	Adult	V
LW WG	60.0	15	Adult	V
RW YO	54.5	11	Adult	R (N)
LW WY	53.8	13	Adult	R (S)
LG RY	50.0	6	Adult	R (N)
LO OL	50.0	4	Adult	R (N)
OG G	50.0	4	Adult	R (N)
LY OY	46.2	13	Adult	V
LG LR	36.4	11	Adult	V
O$_a$L OR$_{ov}$	33.3	6	Adult	R (-)
RY OG	33.3	6	Adult	V
LY WG	28.6	7	First-winter	R (N)
LW OY	25.0	4	Adult	R (N)
LR YL	21.4	14	Adult	R (N+S)
LR LY	20.0	5	Adult	R (N)
LY RY	16.7	6	First-winter	R (N+S)
LG RG	0	6	Adult	R (S)
LG WR	0	6	Adult	R (N)
LO YG	0	6	Adult	R (N)
LR GY	0	4	Adult	V
LW RY	0	4	Adult	R (-)
LY RW	0	5	First-winter	R (N)

Interactions between colour-ringed birds:

Winner	Loser	*n*	
OG G	LG LR	1	*x*
LO YR	LG RY	1	x
LO YR	LR GY	1	x
RY B	O$_a$L OR$_{ov}$	3	*x*
RY B	LR YL	1	*x*
O$_a$L OR$_{ov}$	LR YL	1	*x*
LY OY	LG RG	1	*x*

Winner	Loser	*n*	
LW WG	LR YL	1	*x*
RY B	LY OY	1	*x*
LW WY	LG RG	1	*x*
LG LR	LG RG	1	*x*
OG G	LY RW	1	*x*
LY WG	LY RW	2	*x*
LO YR	LR YL	1	*x*

15.2. Turnstone dominance hierarchy at the high water feeding area at Seaton Sands in 1991/92.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status
RY B	100	4	Adult	R (S)
LO YW	71.4	7	Adult	R (S)
LW RL	69.6	23	Adult	R (S)
LR YL	66.7	9	Adult	R (S)
LG LR	54.5	11	-	-
LO OL	50.0	6	Adult	R (S)
RY OG	44.4	9	Adult	R (-)
LO YR	42.9	14	Adult	R (N)
LW LW	28.6	7	Adult	R (S)
OG G	25.0	8	Adult	R (N+S)
LO WY	25.0	4	First-winter	R (S)
LG WO	0	4	First-winter	R (N+S)
LG YO	0	24	First-winter	R (S)

Interactions between colour-ringed birds:

Winner	Loser	*n*	
RY B	LG YO	1	*x*
LO YW	LW LW	1	*x*
LO YW	LG YO	1	*x*
LW RL	LO YW	1	*y*
LW RL	LG LR	1	*x*
LW RL	LO YR	2	*x*
LW RL	LG YO	1	*x*
LW LW	LG YO	1	*x*

15.3. Purple Sandpiper dominance hierarchies at the West Harbour roost.

i. 1992/93.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
RG WGm	88.9	9	Adult	S	L	F
LR WGm	85.7	14	Adult	N	M	
GR WGm	83.9	31	Adult	N	L	F
LR WLm	83.3	6	First-winter	S	M	
GO WLm	78.6	14	First-winter	N	L	F
OR WGm	66.7	6	Adult	S	M	
GL WLm	66.7	12	Adult	N	M	
GW WGm	63.6	11	Adult	N	M	
OG WLm	61.5	13	First-winter	S	M	
LG WLm	60.0	10	First-winter	S	M	
OW WGm	60.0	5	Adult	N	L	F
RY WGm	58.8	17	Adult	S	M	F
OL WLm	50.0	4	First-winter	S	S	M
LO WLm	47.8	23	First-winter	S	M	
RO WGm	47.4	19	Adult	S	M	
OY WGm	45.5	11	Adult	N	M	F
GY WLm	44.4	9	First-winter	-	M	
WY WGm	42.9	7	Adult	N	L	F
RL WGm	40.0	5	Adult	N	M	
GY WGm	28.6	7	Adult	S	S	M
WO WGm	25.0		Adult	-	S	M
WR WGm	16.7	6	Adult	N	S	M
LW WLm	16.7	6	First-winter	N	M	
LO WGm	12.5	8	Adult	S	M	
WL WGm	8.3	12	Adult	S	L	F
GR WLm	8.3	12	First-winter	N	M	F
LW WGm	0	4	Adult	N	S	M
OG WGm	0	4	Adult	N	S	M
OL WGm	0	7	Adult	N	M	F
RW WGm	0	4	Adult	S	M	
GW WLm	0	5	First-winter	S	M	
LY WLm	0	9	First-winter	S	S	M

Interactions between colour-ringed birds:

Winner	Loser	*n*	
GR WGm	GR WLm	2	*x*
OG WLm	RO WGm	1	x
OG WLm	LO WLm	1	x
RO WGm	WO WGm	2	*x*
LO WLm	RO WGm	2	*x*
RY WGm	LO WLm	1	*x*
LR WGm	WO WGm	1	*x*
GR WGm	RO WGm	1	*x*
GR WGm	GY WLm	2	*x*
OY WGm	GY WLm	1	*x*
GR WGm	WL WGm	1	*x*
GW WGm	RY WGm	2	*x*
GO WLm	OG WLm	1	*x*

Winner	Loser	*n*	
GW WGm	OL WGm	1	*x*
GR WGm	LY WLm	1	*x*
WY WGm	LY WLm	1	*x*
LR WLm	LO WGm	1	*x*
LR WLm	LW WGm	1	*x*
RY WGm	WO WGm	1	*x*
LG WLm	WL WGm	1	*x*
LR WGm	WL WGm	1	*x*
RG WGm	LY WLm	1	*x*
RG WGm	GW WGm	1	*x*
GO WLm	OG WLm	1	*x*
WO WGm	GY WLm	1	*y*

ii. 1993/94.

Colour-ring identity	Dominance (% of encounters won)	Number of encounters	Age	Residence status	Bill-length size class	Sex
YG WGm	80.0	5	Adult	S	L	F
LR WGm	66.7	12	Adult	N	M	
OY WGm	60.0	5	Adult	N	M	F
GY WLm	60.0	5	Second-winter	N	M	
LO WLm	58.8	17	Second-winter	N+S	M	
RY WGm	55.6	27	Adult	S	M	F
GW WGm	53.8	13	Adult	N	M	
OR WGm	44.4	18	Adult	S	M	
OL WLm	41.4	29	Second-winter	S	S	M
OG WLm	41.2	17	Second-winter	N	M	
GR WLm	40.0	5	Second-winter	N	M	F
WL WGm	37.5	16	Adult	S	L	F
RL WGm	36.4	11	Adult	N	M	
WR WGm	35.3	17	Adult	N	S	M
RW WGm	30.0	10	Adult	S	M	
GY WGm	28.6	14	Adult	S	S	M
LW WGm	28.6	7	Adult	N	S	M
OL WGm	23.1	13	Adult	N	M	F
GW WLm	16.7	12	Second-winter	N+S	M	
YL WGm	12.5	8	Adult	N	M	
WO WGm	11.8	17	Adult	S	S	M
OG WGm	0	9	Adult	N	S	M

Interactions between colour-ringed birds:

Winner	Loser	*n*	
GY WGm	OL WLm	1	*y*
RY WGm	WR WGm	1	*x*
LO WLm	OG WGm	1	*x*
OL WLm	OL WGm	1	*x*
LR WGm	WO WGm	1	*x*
GY WLm	OG WLm	1	*x*
OR WGm	GW WGm	1	*y*
OR WGm	WO WGm	2	*x*
YG WGm	OR WGm	1	*x*
OL WLm	GY WGm	1	*x*
OG WLm	RY WGm	1	*y*

Winner	Loser	*n*	
LO WLm	OL WLm	1	*x*
LO WLm	WO WGm	1	*x*
LO WLm	GW WLm	2	*x*
GW WGm	YL WGm	2	*x*
WL WGm	GY WGm	1	*x*
WL WGm	GW WLm	1	*x*
GY WGm	WL WGm	1	*y*
YL WGm	WL WGm	1	*y*
OG WLm	OL WLm	1	*y*
OL WLm	RY WGm	1	*y*
OL WLm	WR WGm	1	*x*

Appendix 16.

16.1. Turnstone roost attendance and season.

i. The following table shows the proportion of surveys on which individual Turnstones were seen at the West Harbour roost during autumn, winter and spring. The number of surveys for which an individual was present in the study area is shown in parentheses. Data are taken from 1992/93.

Colour-ring identity	Autumn	Winter	Spring
LG LR	0.500 (20)	0.214 (28)	-
LG LY	0.524 (21)	0.179 (28)	0.4 (5)
LG RG	0.154 (13)	0.214 (28)	-
LG RY	0.238 (21)	0.429 (28)	0.4 (5)
LG WO	0.810 (21)	0.333 (15)	-
LG WR	0.238 (21)	0.071 (28)	0.4 (5)
LG YG	0.667(21)	0.214 (28)	-
LG YL	0.333 (18)	0.321 (28)	0.4 (5)
LG YO	0.333 (21)	0.067 (15)	-
LO OL	0.650 (20)	0.250 (28)	-
LO RL	0.500 (14)	0.036 (28)	-
LO WY	0.421 (19)	0.107 (28)	0.2 (5)
LO YG	0.100 (20)	0.071 (28)	0 (5)
LO YR	0.278 (18)	0.393 (28)	0.2 (5)
LO YW	0.800 (20)	0.143 (28)	-
LR GL	0.143 (7)	0.036 (28)	-
LR GY	0.250 (20)	0.285 (28)	0.6 (5)
LR LY	0.067 (15)	0.179 (28)	0.2 (5)
LR YG	0.500 (10)	0.071 (28)	-
LR YL	0.571 (21)	0.143 (28)	-
LW LW	0.333 (21)	0.071 (28)	0.2 (5)
LW OY	0.200 (20)	0.357 (28)	0.2 (5)
LW RY	-	O.667 (9)	0.5 (4)
LY LG	0.381 (21)	0 (6)	-
LY LO	0.714 (21)	0.182 (22)	-
LY LR	0.286 (21)	0.071 (28)	-
LY LW	0.429 (21)	0.143 (14)	-
LY LY	0.056 (18)	0.179 (28)	0.4 (5)
OG G	0.476 (21)	0.357 (28)	0.4 (5)
O_aL OR$_{ov}$	0.150 (20)	0 (28)	-
RW YO	0.611 (18)	0.286 (28)	0.2 (5)
RY GY	0.400 (20)	0 (11)	-
RY OG	0.238 (21)	0.143 (28)	-

ii. The following table shows the proportion of surveys on which individual Turnstones (resident on Hartlepool Headland) were seen at high water sites at Hartlepool Headland during autumn and winter. The number of surveys for which an individual was present in the study area is shown in parentheses. Data are taken from 1992/93.

Colour-ring identity	Autumn	Winter
LG LY	0 (9)	0.071 (14)
LG RY	0 (9)	0.071 (14)
LG WO	0 (9)	0 (6)
LG WR	0.222 (9)	0.500 (14)
LG YL	0.444 (9)	0.429 (14)
LO YR	0.111 (9)	0.071 (14)
LW OY	0.333 (9)	0.500 (14)
LY LG	0.444 (9)	0.400 (5)
LY LO	0.222 (9)	0.357 (14)
LY LW	0.222 (9)	0.545 (11)
RW YO	0.111 (9)	0.286 (14)
RY GY	0 (9)	0.250 (8)

16.2. Purple Sandpiper roost attendance and season.

The following table shows the proportion of surveys on which individual Purple Sandpipers were seen at the West Harbour roost during autumn, winter and spring. The number of surveys for which an individual was present in the study area is shown in parentheses. Data are taken from 1993/94.

Colour-ring identity	Autumn	Winter	Spring
GW WGm	-	0.421 (19)	0.200 (5)
LW WGm	0.438 (16)	0.316 (19)	0.250 (4)
OG WGm	-	0.250 (16)	0.200(5)
OL WGm	0.889 (9)	0.421 (19)	-
OY WGm	0.818 (11)	0.263 (19)	-
RL WGm	-	0.286 (14)	0.250 (4)
RW WGm	-	0.316 (19)	0.600 (5)
RY WGm	0.857 (7)	0.632 (19)	0.800 (5)
WO WGm	0.688 (16)	0.579 (19)	0.800 (5)
YG WGm	-	0.667 (6)	0.750 (4)
GR WLm	0.625 (16)	0.158 (19)	0.200 (5)
GW WLm	-	0.471 (17)	0.400 (5)
GY WLm	0.800 (5)	0.421 (19)	0.600 (5)
OG WLm	-	0.579 (19)	0.250 (4)
OL WLm	0.875 (16)	0.579 (19)	1.000 (4)

Appendix 17.

i. The following table shows whether associations between species at the West Harbour roost were related to the number of either species involved.

Association	Number of	Mann-Whitney z	Significance	Numnber of	Mann-Whitney z	Significance
Tu / PS	Tu	0.432	n.s.	PS	3.264	$P < 0.05$
Tu / Oy	Tu	2.209	$P < 0.05$	Oy	2.517	$P < 0.05$
Tu / Rk	Tu	1.839	n.s.	Rk	0.903	n.s.
Tu / Kn	Tu	0.797	n.s.	Kn	1.051	n.s.
Tu / Du	Tu	0.159	n.s.	Du	0.401	n.s.
PS / Oy	PS	0.318	n.s.	Oy	2.616	$P < 0.01$
PS / Rk	PS	1.570	n.s.	Rk	1.070	n.s.
PS / Kn	PS	1.532	n.s.	Kn	2.896	$P < 0.01$
PS / Du	PS	0.217	n.s.	Du	1.589	n.s.

where Tu = Turnstone, PS = Purple Sandpiper, Oy = Oystercatcher, Rk = Redshank, Kn = Knot, Du = Dunlin.

The associations between Turnstone and Purple Sandpiper (χ^2 = 0.604, d.f. = 1, n.s.), Turnstone and Oystercatcher (χ^2 = 0.320, d.f. = 1, n.s.) and Purple Sandpiper and Oystercatcher (χ^2 = 0.699, d.f. = 1, n.s.) were not affected by which species was more numerous at the roost.

ii. The following table shows whether associations between species at the West Harbour roost were related to wind speed.

Association	z or t value (d.f.)	Significance
Tu / PS	$z = 2.774$ [a]	$P < 0.01$
	$t = 0.352$ (38) [b]	n.s.
Tu / Oy	$z = 0.099$	n.s.
Tu / Rk	$t = 0.551$ (20)	n.s.
Tu / Kn	$t = 2.579$ (19)	$P < 0.05$
PS / Oy	$t = 0.879$ (69)	n.s.
PS / Rk	$t = 0.378$ (20)	n.s.
PS / Kn	$t = 0.723$ (20)	n.s.
PS / Du	$t = 1.266$ (14)	n.s.

[a] - on days when Turnstones outnumbered Purple Sandpipers; [b] - on days when Purple Sandpipers outnumbered Turnstones.

Appendix 18.

The following tables record the numbers of Turnstones and Purple Sandpipers in flocks departing mixed roosts of the two species at West Harbour and the number of birds left remaining at the roost. Data are recorded chronologically.

9 September 1993		
Number of birds departing	Number of Turnstones remaining	Number of Purple Sandpipers remaining
2 PS	186	16
2 Tu	184	16
1 Tu	183	16
3 Tu	180	16
3 PS	180	13
1 Tu	179	13
2 Tu	177	13
1 PS	177	12
1 Tu, 2 PS	176	10
6 PS	176	4
6 Tu	170	4
1 Tu	169	4
5 Tu	164	4
3 Tu	161	4
4 PS	161	0

8 October 1993		
Number of birds departing	Number of Turnstones remaining	Number of Purple Sandpipers remaining
1 Tu	22	4
7 Tu	15	4
4 Tu	11	4
3 Tu	8	4
3 PS	8	1
2 Tu	6	1
6 Tu, 1 PS	0	0

where Tu = Turnstone and PS = Purple Sandpiper

22 October 1993		
Number of birds departing	Number of Turnstones remaining	Number of Purple Sandpipers remaining
6 Tu	20	
1 Tu	19	67
1 PS	19	66
2 Tu	17	66
3 Tu	14	66
2 PS	14	64
2 Tu	12	64
10 PS	12	54
1 Tu	11	54
10 PS	11	44
3 Tu	8	44
6 PS	8	38
22 PS	8	16
2 PS	8	14
9 PS	8	5
5 Tu	3	5
1 Tu, 5 PS	2	0

26 October 1993		
Number of birds departing	Number of Turnstones remaining	Number of Purple Sandpipers remaining
2 PS	30	Not recorded
1 Tu	29	
1 Tu	28	
2 Tu	26	
6 Tu	20	
1 Tu	19	
5 PS	19	
1 Tu	18	
6 Tu	12	
2 PS	12	
2 Tu	10	
8 PS	10	
2 Tu	8	
4 PS	8	
4 Tu	4	
3 PS	4	
1 Tu	3	
1 Tu	2	
2 Tu	0	

7 November 1993		
Number of birds departing	Number of Turnstones remaining	Number of Purple Sandpipers remaining
6 PS	Not recorded	7
1 PS		6
2 Tu		6
1 PS		5
1 Tu		5
6 Tu		5
5 Tu		5
3 PS		2
8 Tu		2
2 PS		0