



BTO Research Report No. 120

**A Guide to the Provision
of Refuges for Roosting Waders.**

by

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November 1993

**A report by the British Trust for Ornithology
under contract to English Nature**

BTO, The Nunnery, Thetford, Norfolk IP24 2PU
Registered Charity No. 216652

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EXECUTIVE SUMMARY

This report aims to guide the provision of refuges for waders during the non-breeding season and comprises a review of the generic literature on studies of movements of waders between sites within estuaries and analyses of Wash Wader Ringing Group data.

The study objectives were to:

1. Selectively review the literature on intra-estuarine movements of waders to generate hypotheses to be tested by analyses of Wash Wader Ringing Group data.
2. Analyse Wash Wader Ringing Group data for selected species to examine the relationship of movements between major roost sites in the Wash.
3. Carry out a detailed analysis of wader movements to and from the Terrington roosts.
4. Use the results of 1-3 to recommend the location, size and distance between roost refuges for different species of waders around the Wash.
5. Recommend any necessary further research on species for which it was not possible to fulfil objective 4.
6. Identify general principles for refuge provision on other estuaries.

The review concentrates on a handful of studies which have investigated individual estuarine complexes, notably the Moray Firth, the Firth of Forth and the Wash. The findings of these studies have been compared and causative factors explored, drawing on appropriate research into wader, and more broadly waterfowl, ecology. The subsequent species accounts, are for the ten main wader species occurring at the Wash. These have been priority species for the Wash Wader Ringing Group's activities since the early 1960s and so at least some ringing data are available for analyses. A discussion of disturbance and its effects on mainly waders follows. The review is completed by a discussion about refuges, based on studies of their provision and effectiveness. These studies have concentrated on wildfowl, principally quarry species.

Differences in intra-estuarine movements are apparent between species of wader and, in some cases, within a species on different estuaries. Refuge provision will thus need to take into account a range of mobility patterns in order to maximise the availability of safe roosts for different species. It is important that undisturbed roosts are close to the birds' main feeding areas, particularly in winter. This is especially important in periods of severe weather when metabolic stress is high. Refuges need to be of a size sufficient to ensure that any disturbance on the periphery does not affect the birds within. Thus roosts require surrounding buffer zones. The roost itself may vary in extent and exact location, depending on season and whether tides are springs or neaps. A roost refuge will thus need to accommodate areas of intertidal mudflat, saltmarsh, sea wall and coastal fields.

The data analyses sought to identify inter-refuge distances for several species of wader by investigating inter-roost movements within the Wash. An initial, large scale analysis was carried out for the whole Wash, and followed by a finer scale analysis of mobility within

Terrington. The large scale analysis approach provided a set of distances from each of several roosts, beyond which the majority of a given species did not move. The finer scale analysis modelled the distribution of waders being retrapped with distance and generated a series of distances which would cater for varying percentages of the total population of a wader species. These distances, when entered on a GIS, allow the best siting of potential refuges and enable buffer zones to be determined. Ultimately, these refuges will need to be tested *in situ*.

Knot and Oystercatcher were found to be the most mobile species on the Wash, whilst Redshank and Grey Plover were identified as being the least mobile. Of the three species for which detailed movements were analysed, the Redshank data were insufficient to allow inter-refuge distances to be calculated.

Based on the results for the least mobile species an inter-refuge distance of 3km would enable 50% of the Grey Plover to be accommodated at roost refuges; similarly, an inter-refuge distance of 9km would provide refuges for 25% of the Grey Plover. The equivalent inter-refuge distances for Dunlin are 6km and approximately 15km, respectively.

The next stage of the process requires agreement on location and size of the refuges and an experimental period to test the effectiveness of designated refuges.

INTRODUCTION

This report could be considered to consist of a review section (Sections 1, 2, 3 and 4), an analysis section (Sections 5 and 6) and a final recommendation section (Section 7). The overall aims of the report can be expressed as:

1. To identify and review the parameters determining the potential refuge locations for the Wash strategy.
2. To consider general principles of refuge provision.
3. To quantify some of the parameters reviewed in 1.

In order to address these aims, the review sections concentrated on those studies which have investigated the extent of intra-estuarine movement of waders in relation to various factors. Additionally, aspects of the fundamental ecology of waders were incorporated where these can assist in determining refuge provision. The results of the little experimental testing of existing refuges, has been examined. Most of these studies refer to wildfowl in relation to shooting, but nonetheless have relevance to establishing refuges for waders.

The interchange between roosting sites is obviously very closely tied up with the mobility of birds between feeding areas. Those species that, for example, utilise a number of feeding grounds within an estuary and move between them according to prey availability, tidal state, weather conditions will also make use of different roosting sites around the estuary. These birds will spend more time flying from feeding ground to roosting site than those which are sedentary and utilise roosting sites adjacent to the feeding site.

This review identifies the factors crucial to determining refuge location and size. The review is followed by an analysis of the Wash Wader Ringing Group data with the specific aim of assessing the overall mobility of various wader species and developing a model which would allow the proportion of birds catered for by varying inter-refuge distances to be assessed and so begins the process of building a framework for refuge provision.

1. METHODS FOR THE STUDY OF INTRA-ESTUARINE MOVEMENTS OF WADERS

The two most common methods used for studying the movements of waders are ringing-recapture and colour-marking, using temporary plumage dyes, leg flags, wing tags or colour rings. These colour-marking methods may be used to identify cohorts or individuals. Additionally, radiotelemetry allows tracking of an individual's movements. Results of these approaches are presented in the following sections.

Ringing-recapture is used mainly as a method for studying the movements of waders between estuaries and on a larger scale between wintering and breeding grounds. It has also been used to study the intra-estuarine movements of waders. Catching birds by cannon-netting or mist-netting on estuaries where waders are regularly ringed will result in recaptures of birds previously caught and ringed. Minton (1975) documented movements of waders within the Wash, from a series of catches on the west coast of the Wash in two winters and observations of the proportion of waders on the east coast that carried rings from the west coast. The different proportions of species amongst the east coast recaptures also gave information about differences in mobility between species. By carrying out ringing-recapture exercises concurrently on opposite sides of an estuary during the non-breeding season it is possible to gain an insight to species' mobility and frequency of movement.

Ringing-recapture can also be used to study movements of waders between winters. Symonds *et al.* (1984) used this method to study the site-fidelity of waders on the Firth of Forth between winters. By ringing waders at a particular site during the first winter and catching birds at the same site in the following winter, the number of *retraps*, *i.e.* recaptures of birds ringed the previous winter at the same site, could be calculated. The proportion retrapped of each species gave information on those species that return to the same site each year and those that utilise different sites within the Firth of Forth from year to year. Clark (1983) also used ringing-recapture to assess the degree of movement of Dunlin between four bays on the south side of the Severn estuary. By making a large number of catches over four winters, it was possible to compare male and female and adult and juvenile differences in within- and between-winter movements.

Several papers in the literature (Furness & Galbraith 1980; Symonds *et al.* 1984; Davidson & Evans 1985; Symonds & Langslow 1986) present data on the movements of waders collected from colour-marking schemes. In these studies birds were caught by cannon-netting at daylight roosts and mist-netting at feeding areas. Non-permanent dyes were used to mark the body and by using different colours in different combinations it was possible to devise a code that distinguished birds from particular marking sites. Thus the movements of each species from each marking site in the estuary could be monitored, and by repeating catches at the same site on a regular basis and marking the birds with a different code each time, any changes in behaviour during the winter could be observed.

The success of colour-marking schemes relies heavily on frequent observations of wader feeding grounds and roosting sites in the estuary in order to count the number of marked birds present. Observer accuracy needs to be high, and the time spent observing sites must be spread as evenly as possible throughout the estuary in order to reduce bias in favour of heavily-watched sites.

The results can be presented as the percentage of marked birds observed at each site out of the total marked from a capture site. This compensates for differences in the numbers of birds marked in each catch, but does not compensate for differences in the frequency of visits to each area. That is why it is important to minimise bias from unequal time spent at sites. If the results include figures for the total numbers of birds observed at sites, marked and unmarked, then it is possible to calculate an *index of dispersal*. This is done by expressing the numbers of marked birds observed per number checked in the observation areas per number originally marked in this way. Thus the index measures the decline in the proportion of marked birds within a flock as they disperse from a particular marking site.

Differences in interpretation of mark/recapture movements can arise because of differences in the distance scale used by separate studies. Whilst absolute distance is unlikely to be biologically important, it is a useful yardstick for assessing whether or not movements which have been defined as local in one study are comparable with those of another. It is important to understand the extent of sites which function as a *home range*. For example, Kirby *et al.* (1988) indicated that the Alt, Ribble and Dee comprised one estuarine complex for the purpose of regular interchange by waders moving between roosting and feeding areas.

Cooper (1988) analysed movements of dye marked waders and recaptures of ringed birds, within the Wash, by determining the half-distance moved (after Coulson & Brazendale 1968), analogous to the principle of radioactive decay, whereby the *concentration* of marked birds decreased by 50%. Using this approach, Cooper demonstrated that Knot were more mobile than either Dunlin or Sanderling, and tended to be more mobile than Oystercatchers.

Colour-marking schemes have inherent weaknesses including the possibility of multiple sightings of the same individual and differences in the visibility of markings due to bird behaviour or the topography of different sites. Statistical analysis of results is not always valid but the data obtained from colour-marking schemes do provide useful information on the movements of birds within estuaries and differences in mobility between species. One way of minimising double counting of colour-marked birds is to synchronise site checks in an estuary, which would require a team of observers.

2. FACTORS AFFECTING MOVEMENT

2.1 Roosts

Some of the regular movements of birds within an estuary may be attributed to flights between feeding areas and roosting sites. The frequency and distance of these movements depends upon the proximity of the favoured roosting sites to suitable feeding grounds and also depends upon the species of wader. The requirement for a suitable roost may entail movement over considerable distances. Davidson *et al.* (1991) provide a summary of findings from several studies. The distance between feeding and roosting areas may be critical at certain times of year, particularly during periods of severe winter weather. As feeding areas change during the course of the winter, waders may roost close to the tide edge or fly the extra distance to a safe roost. There is a trade-off between the risk of predation and energy expenditure.

The availability of a safe roost, close to their feeding areas is important to waders. The provision of a no-shooting islet in the Bassin d'Arcachon led to substantial increases in the numbers of waders roosting and feeding there (Campredon 1979), indicating that it was the lack of such a roost, rather than food availability which had previously limited the numbers of waders using this productive bay.

Symonds & Langslow (1986) in their work on shorebirds on the Moray Firth noted that those species which tended to use the same feeding site were also loyal to the same roosting site. Sedentary species such as Oystercatcher, Redshank and Turnstone regularly returned to the original roosting site where they were marked, whereas mobile species such as Bar-tailed Godwit and Knot tended to roost at the favoured site nearest to their feeding area. Dunlin were also considered to be mobile in the Moray Firth, due to the lack of a suitable roost close to some of the preferred feeding areas causing birds to fly several kilometres between roosting and feeding areas. However, these birds showed a negligible degree of interchange between feeding or roosting areas.

The observations of Symonds & Langslow (1986) on species' differences in mobility between sites are supported by other studies. Symonds (1980) working on waders in the Forth found that Knot were very mobile and made use of any suitable feeding and roosting area. Dunlin also moved between sites, largely as a result of Musselburgh providing the main roost site for Dunlin feeding in the Outer Forth. Both Mackie (1976) and Furness & Galbraith (1980) observed that colour-marked Redshank on the Firth of Clyde remained at the roost site bordering the marking area.

At the Wash, the development of the safe roost by modification of the topography of gravel pits just behind the sea wall on the RSPB reserve at Snettisham gradually led to a shift in roosting behaviour, with substantial numbers of Knot and Oystercatcher, in particular, preferring to roost there rather than fly to Holme or Thornham during high spring tides especially in winter. At the time of the Wash Water Storage Feasibility Study, there was an increasing tendency for waders to roost on the reserve at Snettisham (Prater 1975). Traditionally, Thornham Point was the main roost site for the east Wash wader population (Berry 1971), notably at high water on evening spring tides (HWS) in autumn and winter, but it declined during the 1980s, as Snettisham grew. The changing shore topography at Holme has led to the development of a sandy spit, which is isolated from the mainland on

intermediate tides, providing a safe, island roost. This is favoured by Knot in October/November especially, with up to 100,000 using the site. The area is partially flooded on the highest tides and so Knot often fly on to Thornham or the reserve at Titchwell which now has a suitable roosting area. These changes in roost use reflect changes in topography, either as a result of natural events or management and seasonal changes in feeding distribution.

2.2 Feeding Areas

One of the principle factors affecting the movement of waders within an estuary is the availability of prey. Wader species vary in the main types of prey taken. Thus differences in the behaviour of prey species will result in differences in behaviour of the waders that prey on them, including differences in mobility. Several pieces of work have been carried out in British estuaries to study the movements of certain wader species during the winter and explain differences in mobility.

Symonds & Langslow (1986) studied the movements of 8 wader species within the Moray Firth and attempted to explain the inter-species differences in mobility observed. They suggested that the availability of invertebrates that dwell in the sediments varies more than that of surface-living prey such as mussels (*Mytilus edulis*), and hence those waders that feed on invertebrates in the sediment may be forced to change feeding sites more often due to lack of prey than those species that feed on surface-dwellers. They based their reasoning on the observation that small invertebrates living in mud tend to vary their depth and activity in the substrate whereas surface-dwellers are much more sedentary and are often attached to the substrate. However, mussel spatfall varies, leading to cyclical shortages which can have deleterious effects on birds which feed on them.

Species such as Knot which feed on below-surface invertebrates which, from the colour-marking schemes carried out in the Moray Firth, were found to be more mobile than Oystercatchers and Turnstones which feed on sedentary surface invertebrates such as mussels, limpets and periwinkles. Mobility during the midwinter period was defined in terms of the percentage of sightings of marked birds outside the original feeding area and outside the original firth. The Moray Firth is divided into three smaller firths: the Beaully Firth, the Cromarty Firth and the Dornoch Firth. Those species described as mobile tended to move frequently between feeding sites, though within this category there were variations in behaviour with Knot and Bar-tailed Godwits moving around the entire Moray Firth but Dunlin only moving within the firth they were marked in. Species categorised as sedentary such as Oystercatchers and Redshank tended to remain at the feeding site adjacent to the marking area and those few that were observed to move did not leave that particular area of the Moray Firth. The greater mobility of Redshank compared with Oystercatcher in the Forth and Moray could be ascribed to differences in prey; Redshank fed on small invertebrates in the mud that show marked fluctuations with respect to tide, temperature, weather conditions *etc.* (Symonds *et al.* 1984).

Similarly Symonds *et al.* (1984) found differences in the mobility of waders on the Firth of Forth and ascribed these in part to differences in prey availability. Oystercatchers feed on mussels on the Forth as well as on the Moray and they were observed to be very sedentary, with only 1.5% of sightings of marked birds outside the marking area. Redshank and

Dunlin, which feed on invertebrates in the soft sediments, exhibited greater movement away from the marking area with 7.3% and 27.5% of sightings respectively away from the marking area. Those Redshank and Dunlin that were observed to move tended to stay within whichever section of the Forth they were marked in *i.e.* the Inner or the Outer Forth and interchange between these two sections was small. Knot, which had the greatest mobility of the seven species studied (43% of sightings away from marking area), feed on small bivalve molluscs in the sediment such as *Macoma balthica* (*e.g.* Goss-Custard *et al.* 1977a) which show great spatial and temporal variation. Knot were observed to move around the entire estuary and thus not only moved more frequently but also further than any of the other waders studied. There was considerable intermixing of Knot from different marking sites.

The behaviour of prey species and the effect this has on their availability therefore influences wader movements within an estuary on a daily basis. On a seasonal basis, weather conditions can affect prey availability and cause large-scale movements of waders to less-preferred parts of the estuary. Evans (1981) reported that extensive removal of prey species populations can occur when wave action causes sediment-scour on sandy and muddy shores (see also Clark 1983; Ferns 1983 and Clark 1989). This decline in prey availability would be expected to lead to changes in the foraging location of waders that feed from the upper layers of mud and sand. It was suggested that the mobility of Knot within and between estuaries may be a strategy to identify several potentially suitable feeding sites, in case their food sources are removed from one site by wave action.

Those species which feed on sedentary prey on hard substrates such as rocky shores or mussel beds would not be expected to experience the large fluctuations in food supply that can occur on sandy or muddy shores (Metcalf & Furness 1985). Rocky shores are far less likely to suffer sudden erosion by wave action as a result of inclement weather, except in severe storms, and invertebrate prey species in this habitat such as barnacles and periwinkles, are firmly attached to the substrate, as are mussels on mussel beds. In addition, cold temperatures have less effect on the availability of rocky shore invertebrate communities since they cannot burrow into the substrate. With this great temporal stability of rocky shore prey one would expect the wader species that feed on them to be fairly sedentary. This is borne out by studies on Turnstones feeding on rocky shores and mussel beds in the Firth of Clyde which showed a high level of site-fidelity in colour-marking schemes (Metcalf & Furness 1985).

The above studies have shown how prey species and substrate type determine prey availability which in turn influence wader movements in estuaries, and have highlighted some of the differences in mobility between species. Prey availability can also account for differences in mobility of the same species on different estuaries. Symonds *et al.* (1984) in their study of movements on the Forth compared their dataset with that of Minton's (1975) report of the large-scale ringing study on the Wash and found discrepancies in the observed behaviour of Oystercatchers on the two estuaries. On the Wash a high degree of interchange was found for Oystercatchers, between the east and west shores, whereas on the Forth there was little movement of this species away from marking areas. The discrepancy could be related to differences in prey taken at the two sites. At the Wash, the main prey taken by Oystercatchers is *Cerastoderma edule*, with *Mytilus edulis* and *Macoma balthica* of lesser importance. On the Forth, *Mytilus edulis* is believed to be the principle prey of Oystercatchers. The distribution of spat settlement in *Cerastoderma* and *Macoma* is

far more variable than in *Mytilus* and therefore the patchy distribution of invertebrate prey could account for the greater mobility of Oystercatchers on the Wash.

Cooper (1988) analysed the movements of dye marked waders and recaptures of ringed birds within the Wash and had similar results to Minton (1975). Cooper demonstrated that Knot were more mobile than either Dunlin or Sanderling, and tended to be more mobile than Oystercatchers. Although not significant, Oystercatchers tended to be more mobile than Dunlin or Sanderling. The order of decreasing mobility observed within the Wash was Knot, Oystercatcher, Sanderling, Dunlin, Turnstone. Apart from differences between species, there were seasonal differences in the degree of movement within species (Langston 1987). For example, Oystercatchers moved between sites in autumn, but were much more localised in winter, which could account, at least in part, for the discrepancies between studies on the Forth (Symonds *et al.* (1984) and Wash (Minton 1975). Dunlin and Turnstone were generally localised in their movements between feeding and roosting areas, whilst Knot were highly mobile throughout the estuary in all seasons.

Three underlying reasons were given for movement in the Wash (Cooper 1988):

1. Maximisation of food intake whilst minimising interference from other feeding birds caused waders to spread along the tide edge to feed on the incoming tide, as the intertidal area diminished.
2. Flights to spring tide roosts, where birds feel "safe", may involve birds in lengthy flights. However, as winter progresses, when birds feed for more of the tidal cycle, they may continue to feed or form roosts closer to their feeding areas.
3. Flights to find new food resources are made as the profitability of existing feeding areas is reduced.

Goss-Custard & Durell (1990) in their work on Oystercatchers feeding on mussels in the Exe estuary observed differences in mobility within the same species on the same estuary. Movement occurred on a seasonal basis as a behavioural adaptation to increasing numbers of Oystercatchers and decreasing foraging efficiency. It was observed that as Oystercatchers arrive on the Exe in late summer from breeding grounds, high densities of birds occur on the preferred mussel beds. As bird densities rise, dominant behaviour increasingly affects mean daily intake rate (Goss-Custard & le V. dit Durell 1987). Subordinate birds are unable to maintain an adequate intake rate because they cannot defend territories and suffer theft of food by dominant birds (Goss-Custard & le V. dit Durell 1988). Many Oystercatchers leave the preferred mussel beds, in reverse order of dominance, as densities rise and feed in less preferred areas of the estuary. Thus increases in feeding density can affect subsections of a wader population and cause movements within an estuary to alternative feeding grounds. Expansion of feeding bird distributions as a result of influxes of birds has also been documented for the Wash (Goss-Custard 1977; Goss-Custard *et al.* 1977b).

There are inter-specific differences in distribution of feeding effort across different tidal levels. For example, at low tide, Dunlin feed at all tidal levels in the Wash, but in winter they start to feed as soon as the tide turns and so make considerable use of the upper levels. But Bar-tailed Godwit feed mostly at the mid to lower shore levels (Goss-Custard *et al.* 1987; Goss-Custard *et al.* 1988).

Most studies have concentrated on diurnal behaviour and so changes in location at night are under-recorded. There is evidence from several studies that in certain situations regular movements of birds occur within an estuary as a result of night feeding. Dugan (1981) carried out a study on nocturnal foraging in Grey Plover wintering on the Tees Estuary. By using radio-tags he was able to follow the movements of Grey Plover during the hours of

darkness and found that some birds frequently changed feeding sites at night, moving across the estuary from their daytime feeding areas to mudflats not used during the day. It was reasoned that the movement of Grey Plovers to different feeding grounds at night might be a response to the behaviour of their prey and was likely to be part of a strategy to maximise biomass intake. The main prey of Grey Plovers on the Tees are *Nereis* spp. and observations of the activity of these invertebrates revealed that they become more active, and more available to predators, at night (Pienkowski 1983). By moving to areas where *Nereis* have become available at night, Grey Plovers are able to increase their rate of biomass intake which will have declined during the day with the decline in activity of their preferred prey.

A second example of wader movements at night influenced by changes in prey availability comes from work by Ruiz *et al.*(1989) on a wintering Dunlin population at Bodega Bay, California. During the winter, more than half of the Dunlin population started to exhibit regular crepuscular movements, leaving the daytime feeding areas for sites outside the Bay. It was suggested that the mobile population moved inland every evening to feed on fields, and that this was a response to a dramatic decline the previous year in the abundance of shorebird prey at Bodega Bay. However, since crepuscular movements of other wader species at Bodega Bay have been observed before and after the decline in prey, the movements of Dunlin may be a regular seasonal occurrence whatever the local food conditions.

Thus waders may regularly move within, or out of, an estuary at night in order to take advantage of food resources outside their normal daytime feeding areas. The two examples of night feeding and the other work on wader movements outlined reveal the strong influence of food resources on wader movements. The shifting, unstable environment of an estuary means that many wader species, particularly those that feed on mud and sand, suffer frequent declines in the availability of prey and they must be able to respond to these declines in order to maintain their rate of biomass intake. Moving to feeding grounds with a greater abundance of prey when conditions deteriorate in their original feeding grounds ensures that their rate of intake is maintained. This movement could be essential to the survival of waders in winter because the principal cause of wader mortality in winter is food shortage (Goss-Custard & le V. dit Durell 1990).

2.3 Tidal and circadian cycles

Within an estuary the tidal state influences wader behaviour and causes regular movements of birds, associated with the tidal cycle. Work on wader feeding ecology and behaviour has involved studying the movements of species on estuaries in relation to the tidal cycle and this is illustrated in the following examples from the literature.

Fleischer (1983) studied the movements of Ruddy Turnstones in relation to tidal oscillations and observed that tides strongly influence Turnstone foraging behaviour. At high tide birds flocked, but with increasing time after high tide the flocks dispersed. Movement of the Turnstones was related to food resources. As the tide fell, birds followed the water's edge, remaining fairly close together, and fed on small invertebrates and pieces of carrion that were left by the ebbing tide. At low tide Turnstones switched to feeding on crabs and dispersed over the mudflats. As the tide rose they congregated at the water's edge again to feed on the abundant invertebrates there and moved back up the shore with the flood tide.

Thus tides affected the movements of Turnstones by altering food availability and foraging area within the feeding site.

Some feeding areas are available at different tidal states. Davidson & Evans (1985) considered observations of waders feeding in the Orwell Estuary and noted that one particular area, Fagbury Flats, was one of the few feeding grounds in the estuary to remain uncovered at high tide. Regular movements of Grey Plovers, Oystercatchers, Turnstones and Ringed Plovers were observed as these birds returned to Fagbury after foraging areas elsewhere were inundated. This movement pattern extended their foraging time. Though densities of birds at Fagbury rose at high tide and foraging efficiency was therefore likely to decrease, the benefits of gaining extended feeding time obviously outweighed the costs of moving back to Fagbury.

The Wash Water Storage Feasibility Study indicated that increased diurnal feeding times, most noticeable in Knot and Dunlin in winter, were related to difficulties in obtaining adequate food (Goss-Custard *et al.* 1977b). It seems likely, therefore, that increased diurnal feeding time and the associated use of upper-shore feeding areas, which were little used or unused in autumn, during winter flood and ebb tides are responses to reduced availability of prey.

In contrast, Sanderling feed most actively during the flood and ebb tides throughout the non-breeding season because their preferred prey species are activated by the advancing tide washing over them. Cyclical patterns of site use by this species have been identified at Teesmouth from studies of an individually colour-ringed population (Cooper 1988). These movements were related to the availability of a suitable high tide roost site and of different feeding habitats, such as outcrops of rock exposed at low tide, the mid-tide band of *Nerine cirratulus* activated by the flood tide, and the upper sandy shore deposits of tidal wrack left by high spring tides accompanied by strong onshore winds. The seasonality of these patterns of movement was associated with the total numbers of Sanderling present and the stage of the annual cycle, for example autumn post-nuptial moult, winter, *etc.*

High tide movements to alternative feeding grounds have been observed amongst wildfowl species as well as waders. Bryant & Leng (1975) studied Shelduck on the Firth of Forth which feed mainly on *Hydrobia ulvae* in that area. Movements of Shelduck on a daily basis were observed at high water when their preferred feeding areas became inundated. They moved to shallower areas with poorer *Hydrobia* resources to continue feeding. When the tide ebbed they moved back to the main feeding grounds. These high water movements will be more pronounced during spring tides when a greater area of mudflat will be inundated to a depth that prevents feeding.

2.4 Seasonal Movements

The time of year is another factor influencing the frequency and extent of movements by waders within estuaries. Observation of species throughout an entire winter has shown that behavioural changes take place during the winter in relation to periods of migration in the spring and autumn.

Symonds (1980) found that in January birds marked in the Outer Forth estuary began to arrive in the Inner Forth, suggesting that the behaviour pattern had changed and birds were

becoming more mobile about the Forth, in preparation for the spring migration. Similarly movements in October could represent passage through the estuary by migrant birds to their main wintering site. For Dunlin in particular, Clark (1983) noted that on the Severn they tended to be sedentary from December to February, remaining at the same feeding site, but from October to December and February to March they were much more mobile and moved between bays. Post-nuptial moult lasts until October with onward migration taking place in October/November (Pienkowski & Pienkowski 1983). Thereafter, the winter is a period of relative stability, until February/March when movements increase again. Other species show some deviation from this pattern, but the general principles are the same.

Supporting evidence for the greater mobility of waders within estuaries during migration periods comes from Symonds & Langslow (1986) who observed that during the spring the normally sedentary Oystercatchers, Ringed Plovers and Redshanks increased the frequency of their local movements in the Moray Firth. Most of the records of these species moving between firths are from the spring period. Some areas not previously used as feeding grounds by waders were reported to have become important for feeding Oystercatchers, Redshanks, Knot and Dunlin. These colour-marking studies also revealed that Oystercatchers were much more mobile during the autumn than in midwinter and sightings of marked Oystercatchers throughout the Moray Firth during this period confirmed that many were dispersing through the area to their main wintering sites. Similarly more movement of Bar-tailed Godwits was noted during the autumn than later in midwinter.

Seasonal differences in wader mobility are also documented for the Wash (Cooper 1988) with most species being more localised in winter than during autumn or spring, for example Oystercatcher.

2.5 Severe Weather

In order to survive, a bird must balance its energy expenditure with its food intake. Mechanisms leading to either a reduction in food intake or to an increase in energy expenditure are likely to lead to an imbalance. At its most extreme, this imbalance leads to starvation and death. Each bird has to adapt its behaviour to maximise its chance of survival. Migration to temperate climates during the non-breeding season, is advantageous because of the highly productive estuarine systems and the relatively low likelihood of a total freeze. However, severe weather does occur, to varying degrees and has potentially significant energetic costs. These may be addressed by increasing foraging time, reducing the distance moved between feeding and roosting areas or cold weather movements, but there are constraints on these behaviours.

Foraging time may be increased by using more of the areas available during different stages of the tidal cycle, extending feeding time into the hours of darkness (see Section 2.2), or reducing the time spent in other activities such as roosting, aggression or vigilance. Roosting closer to the feeding grounds is one way of reducing energy expenditure, whilst enabling greater foraging time. Under different weather conditions, different behaviours change priority. Vigilance behaviour decreases at times of increased feeding time, in winter, and this decrease is more pronounced in periods of severe weather (Metcalf & Furness 1984; Roberts 1990). During the severe weather of February 1991, at the Wash, waders were

noticeably less responsive to people at close proximity, maximising their foraging time at the expense of increased risk of predation (pers. obs.).

Typically, waders display a weight cycle in which winter body weight peaks in mid-winter, December/January (Johnson 1985, Langston unpubl.), to offset likely reductions in food availability in colder weather. Weights generally decrease during the remainder of the winter. The rate of weight decrease may be accelerated by periods of severe weather, as demonstrated for Curlew on the Wadden Sea (Steltlopergroep F.F.F 1983), because metabolic rate increases. The timing of severe weather determines the degree of effect on body condition. A study of Mallard wintering in Texas (Whyte & Bolen 1984), demonstrated that a period of low temperatures and snowfall in November did not prevent the pattern of early winter weight increase, whereas similar weather in mid-December to mid-February resulted in the mobilisation of lipid reserves to compensate for increased energy demands, thereby resulting in more rapid weight loss than usual at that time of year. These findings are comparable with studies of wader energetics.

In February 1991, a period of low temperatures at the Wash caused the intertidal area to freeze. This coincided with high tide occurring towards the middle of the day, so the waders were prevented from feeding on the intertidal areas for most of the short daylight period. Large scale mortality resulted and it is estimated that about 68% of the Redshank wintering on the Wash died (Clark 1993b). Over 2,500 corpses were collected, which were very emaciated leading to confirmation of starvation as the cause of death. Redshank had used most of their reserves, laid down in early winter, by February and so a freeze at this time had more severe consequences than it would have had earlier in the winter. Additionally, Redshank are generally one of the more vulnerable species to severe weather (Davidson 1982; Davidson & Evans 1982; Davidson & Clark 1985; Clark & Davidson 1986).

In periods of severe weather the availability of feeding areas which enable the extension of feeding time over high water may be of critical importance, for example the use by waders of Fagbury Flats on the Orwell estuary (Davidson & Evans 1985). During a period of severe weather on the Forth, when the mudflats were completely frozen over, the Shelduck left this preferred site and moved further downstream to more saline water where the effects of the freeze were less severe (Bryant & Leng 1975).

The consequences of severe weather in estuaries appear to lead to increases in the frequency and distance of movements by waders (Cooper 1988), principally those species that feed on soft substrates and experience marked fluctuations in their food supply. These species rely on alternative feeding grounds that provide hard weather refuges in order to survive until they can return to their preferred feeding sites. However, if movement to another site results in no improvement in food availability, birds may not have sufficient reserves to move again, leading to increased mortality. This appears to have happened at the Wash in 1991, as there is evidence to suggest that the Dunlin which died included birds which had moved from the Wadden Sea to escape the severe weather there (Clark *et al.* 1993).

Extremes of weather conditions can cause large-scale movements of birds primarily between estuaries during the winter. These cold weather movements are particularly notable in species such as Lapwing and Wigeon. Waders are affected by severe weather such as low temperatures, gales and ice primarily through reduced availability or loss of food resources. The extent to which different species are affected varies according to the type of substrate

upon which they feed. As previously mentioned, strong wave action can result in sediment removal and thus the loss of prey species (Evans 1981). Those waders, such as Sanderling, that feed on vagile invertebrates in mobile soft sediments are more likely to have to find alternative feeding areas after bad weather than those species that feed on invertebrates attached to the substrate *e.g.* Oystercatchers feeding on mussels.

Cold weather also affects the availability of invertebrates on muddy substrates by causing them to burrow into the sediment, and those species of wader feeding on mudflats will be forced to change feeding grounds, either within the same estuary or outside it (Dugan 1982; Metcalfe & Furness 1985). Waders that forage on mussel beds and rocky shores are less affected by cold weather because their prey cannot burrow into the substrate. There is also evidence that rocky shore prey species have a lower mortality rate in severe weather than those of mud and sand (Metcalfe & Furness 1985). Thus the food resources on rocky shores are much more stable in severe weather than those of mudflats and the waders utilising them such as Turnstones and Oystercatchers, will be far less likely to change feeding areas than waders feeding on soft sediments. However, there are exceptions if cold weather coincides with poor stocks of mussels and cockles for example. In such circumstances alternative feeding areas may be sought (Clark 1993a).

2.6 Disturbance

Disturbance here refers to human-induced activities, excluding land take and other aspects of site development, which disrupt behaviour patterns. There are many forms of disturbance; the main categories which occur in areas used by waterfowl in particular and which have been the subject of investigations of their impact, are discussed below. There is generally a lack of direct evidence linking disturbance with population changes in waders (Cayford 1993), although there is a substantial body of evidence demonstrating immediate impacts on bird behaviour, for example increased use of some feeding areas by night, as has been found for Pintail and Dunlin on the Mersey estuary, to avoid daytime disturbance (Rehfish *et al.* 1991, Rehfish in prep.).

Disturbance varies in intensity, frequency, predictability, spatial distribution and duration (Cayford 1993). This variability contributes to the varied responses by individuals and different species, and at different times and localities. This is manifested in the variable approach distances recorded by different studies.

Smit & Visser (1993) provided an overview of the effects of disturbance on shorebirds around the Wadden Sea. They identified the main bird/man interactions which lead to disturbance as:

Roosting birds Foraging birds

Tourism - Walking people
Surfing & sailing

Farming
Hunting, egg collecting
Military activities

Lugworm digging
Walking on intertidal area
Civil aircraft
Military activities
Fisheries
Leisure boats

Small aircraft and walkers (also Scott 1989) were considered to have a major impact, resulting in birds flying up at large distances. Curlew and Redshank were found to be the least tolerant of people approaching on foot; Golden Plover were the most tolerant. When approached to within 250m, Oystercatchers reacted to disturbance in 57% of incidents, whilst Curlew did so in 76% of cases. However, disturbance by walkers was usually short-lived, lasting for 38 seconds per hour for Oystercatchers and 57 seconds per hour for Curlew. Similar results were found for birds approached from water. Kayaks/canoes and sailing boats caused more disturbance to roosting waders than motor boats and wind surfers, probably because they tend to pass closer to the shore (Koepff & Dietrich 1986, cited in Smit & Visser 1993), but a few zigzag movements of a single windsurfer caused dabbling ducks to leave the area of open water. This highlights the different effects resulting from the location and type of activity on different groups/species of waterfowl. Van der Meer (cited in Smit & Visser 1993) produced a formula to calculate the size of area vacated by birds in response to different sources of disturbance, taking into account various parameters. This could be a useful tool to adapt for use in monitoring disturbance-related behaviour and the effectiveness of refuges.

Habituation plays an important role in birds' response to disturbance. In areas of high disturbance, a disturbance event elicits less response. The nature of the activity also affects the response. A stationary person was tolerated more than a moving one, or than a group of people moving. Flying is an obvious response to disturbance, but feeding birds may cease feeding whilst increasing their vigilance and so reduce their foraging time. A flight response by a roosting bird leads to additional energy expenditure. In terms of avian energetics, both reactions are potentially detrimental to survival, in extreme conditions.

Individual disturbance events may not be critical to a bird's survival. But cumulatively, as a result of interfering with food intake or by increasing susceptibility to predation, or under certain conditions, such as periods of severe weather, disturbance may lead to reduced survival (*e.g.* NCC/RSPB 1988, English Nature 1992). This may manifest itself through an inability to balance the energy budget on the chosen feeding area or through birds deserting the area and not finding sufficiently good conditions for survival elsewhere. A study of foraging behaviour by Sanderlings (Burger & Gochfield 1991) demonstrated an increase in crepuscular and nocturnal foraging to compensate for reduced diurnal foraging time, as a result of a dramatic increase in the numbers of people using the Florida beaches, *i.e.* within 100m of feeding birds, between 1986 and 1990. The reduction in daylight feeding was due to Sanderling also spending more time in alert behaviour and flying or running in response to disturbance during daylight and dusk.

Belanger & Bedard (1990) found that a 35% increase in nocturnal foraging, by staging Snow Geese, was required to compensate for man-induced disturbance leading to cessation of diurnal feeding. This represents a substantial energetic cost to these geese, at a time of high energy requirements.

2.6.1 Recreation

Recreation takes many forms, of which shooting is one now but is generally considered separately, perhaps because of its long history as a way of life and for subsistence. Other forms of recreation are a more recent development, particularly in terms of the dramatic increases as a result of modern lifestyles (Owen *et al.* 1986). Recreation may take the form of

a short stroll, jogging, or be a more formally organised activity, such as sailing or water-skiing. It is the level of intensity of recreational pursuits which is likely to lead to the greatest impact on birds. There have been contradictory findings by different studies, indicative of the variable impact of different activities and the lack of comparability in the methods used.

Using data from Tuite (1982), Owen *et al.* (1986) identified birdwatching, fishing, sailing and windsurfing, and informal recreation as the most common recreational activities on inland waters. Informal recreation included walking, jogging and picnicking *etc.*. Davidson *et al.* (1991) reviewed a wide spectrum of human activities on estuaries, including recreational activities. They identified the same forms of recreation as being prevalent on estuaries.

Burger (1981) found that close proximity to roosting birds and fast-moving activities, such as jogging, caused maximum disturbance, with waders flying out of the area, to other marshes, and wildfowl moving on to open water. Windsurfing was identified as a major source of disturbance in the Wadden Sea (Koepff & Dietrich 1986, cited in Smit & Visser 1993), owing to large numbers of participants at once. The authors found that the average flight distances, in response to water-based recreation, were as follows: Curlew 269m, Knot 249m, Bar-tailed Godwit 226m, Grey Plover 192m and Dunlin 122m. Oystercatchers were generally more tolerant of close approach than other species.

There is evidence that territorial bird's food intake rate may drop to zero due to disturbance forcing vacation of its territory. After the disturbance event, the feeding rate was observed to increase markedly to compensate for the lost foraging time (Belien & Van Brummen 1985, cited in Smit & Visser 1993).

The effects of man-related disturbances on staging Brent Geese were investigated during the spring of 1990, on the Westerhever saltmarsh of the Wadden Sea (Stock *in press*). The birds responded in two ways: in their spatial distribution, and in reactive movement. During the early morning and late afternoon, when there were few tourists, the geese used most of the available saltmarsh. However, as numbers of tourists increased, during the day, the geese kept to the undisturbed south east corner of the saltmarsh. The amplitude of the response by the geese varied according to the source of disturbance. In order of decreasing impact, these were tourist activities, small aeroplanes and helicopters, high-flying aeroplanes. Temporal changes in site use, in relation to the presence of tourists, was also noted in waders on the Wadden Sea (Smit & Visser 1993).

Angling is a widespread activity that can occur throughout the year (Owen *et al.* 1986), and can be potentially disturbing to birds (NCC/RSPB 1988), but studies to date display conflicting results. On Grafham Water, Cooke (cited in NCC/RSPB 1988) noted a marked increase in the numbers of waterfowl towards and after the end of the fishing season. Watmough (1983) also found a rapid increase in numbers of ducks on Foremark Reservoir, after the trout fishing season ended, as a result of redistribution.

On the Dee, recreational disturbance has led to a shift in the roosting behaviour of waders in Liverpool Bay, notably Knot, Dunlin and Bar-tailed Godwit. Increased numbers of these species now roost on the Alt. Daily movements occur, indicating the importance of both feeding areas and "safe" roosts (Mitchell *et al.* 1988). Walkers and dogs were considered to

be the main sources of disturbance. This is, in part, due to walking (with or without a dog) being the most common coastal activity.

A combination of refuges and zonation of activities can be used to combat disturbance effects. Such measures are most readily implemented through coordinating bodies for different activities. However, even for an affiliated sport such as sailing, only a relatively low proportion of participants are club members. Public notices need careful phrasing, education and enforcement measures to be effective.

2.6.2 Shooting

Shooting is one of the most important sources of disturbance (Jepsen 1972 & 1978; Meltofte 1983, in Jepsen & Brown 1990) and at a high level can lead to desertion of an area, thereby creating larger waterfowl exclusion zones than other recreational activities (Watmough 1983). There is also the problem of ingestion of lead shot by birds feeding in areas which are shot over (Mudge 1983). Most assessments of the effectiveness of refuges have been made in relation to disturbance due to shooting.

Bell & Fox (1991) provide an extensive review of disturbance to wildfowl in particular. Owens (1977) identified a learning curve for Brent Geese which, although a non-quarry species, reacted to disturbance at 500m in wildfowling areas, but would tolerate approach to 150m distance in a nearby undisturbed locality. The time of year may affect the extent of disturbance too. Madsen (1988) observed flight distance by Brent Geese at 211m in September, which increased to an average of 367m when shooting disturbance increased in October. Reactions may vary depending upon the type of disturbance. Campredon (1981), working in the Camargue, found that over 80% of diurnal disturbance was due to predators, whilst Man accounted for just over 3% of incidents. However, whilst predators tended to cause local displacement, persistent disturbance by Man caused the total desertion of the site by Wigeon. Many studies of disturbance effects due to shooting indicate a positive relationship between the number of times birds are disturbed and their tendency to move. Birds, particularly quarry species, tend to be more "jumpy" during the shooting season. The question is whether a heightened response to such sources of disturbance is ultimately detrimental to survival as a result of loss of feeding time, greater energy expenditure and the potential for drawing the unwanted attention of predators etc.

Morning and evening flights of wildfowl, close to first and last light, are generally the preferred times for wildfowling. Waders, although no longer quarry species, are more susceptible to disturbance in twilight or darkness. Thus the timing of disturbance can be important. The severe winter weather at the Wash in February 1991, came towards the end of the foreshore shooting season (28 February) and so there was heightened wildfowling activity. This was unfortunate timing since, although as a result of the conditions the waders' tolerance level to human proximity was diminished, they really needed undisturbed feeding conditions at this time. Because the body condition of the wildfowl which were shot was good many wildfowlers did not perceive the critical level of disturbance to waders. This highlights the need for good channels of communication and the importance of localised, voluntary restraint by wildfowling clubs. After 14 days of freezing weather a statutory wildfowl ban is instigated. However, the severe weather of February 1991 lasted for 12 days, so the measures in place for announcing wildfowling suspensions on a national scale were not implemented (Stroud 1992).

2.6.3 Aircraft

The height of flight by aircraft affects the level of disturbance caused to waterfowl: >300m 8%; 150-300m 66%; <150m 70% of cases. This probably accounts for the fact that low-flying military jets cause the highest rate of disturbance (84%) (citation of Heinen in Smit & Visser 1993). Bird species reacted at the following rates: Brent Geese (88-92%), Curlew (15-78%), Shelduck (70%), Redshank (50%), Bar-tailed Godwit (36%).

In particular, a jet flying low on a curving/banking flight path elicits a marked response by birds. This type of flight is often associated with military target practice from the air. Military target practice can be a major source of disturbance, depending on the timing of this activity in relation to the timing of roost formation. Smit & Visser (1993) found that the effects were notable if the roost had formed before commencement of military exercises, whereas once shooting had started, birds would still form a roost in or near the affected area. At the Wash, the bombing ranges at Holbeach/Dawsmere and Friskney/Wainfleet are in regular use. Personal observations indicate that disturbance is caused on some occasions, but this has not been quantified.

Air Exclusion Zones have been implemented successfully, for example over Minsmere and Havergate in Suffolk (H.O Defence). The former NCC recommended that low flying should not take place in the vicinity of important wildfowl and wader wintering sites on those days when a cold weather ban on shooting is in place.

2.6.4 Bait Digging

On the Ythan estuary bait diggers led to little dispersal by Dunlin and Turnstone, which permitted approach to approximately 8m and 15m respectively (Scott 1989). However, Oystercatchers and Redshank were more prone to disturbance, vacating the area and not returning for 20-25 minutes. Zwarts (1974) estimated that an area of $5-20 \times 10^4 \text{ m}^2$ around one bait digger could be vacated by feeding birds (cited in Heiligenberg 1987). There may also be at least local depopulation of lugworms (*Arenicola marina*), although recruitment from adjoining sediments will occur. Upheaval of the sediments, caused by bait digging, may increase mortality of size groups not selected for bait, as was indicated for cockles (*Cerastoderma edule*) in north Norfolk (Jackson & James 1979).

3. SPECIES ACCOUNTS

3.1 Oystercatcher

Results from the principal studies on the movements of waders within estuaries seem to indicate that the degree of mobility of Oystercatchers is not consistent between estuaries, and may be related to food supply. On the Forth and Moray Firth, Oystercatchers were found to be very sedentary with few marked birds observed outside the original feeding site, particularly in mid-winter, whereas they exhibited a high degree of mobility within the Wash. Seasonal variation is apparent in all the studies examined.

3.2 Ringed Plover

Little work has been done on the movements of Ringed Plover around estuaries but they were observed to be loyal to selected feeding areas throughout the winter on the Moray Firth (Symonds & Langslow 1986). In this study they appeared to be more sedentary than Redshanks or Oystercatchers. However, flights of several kilometres between preferred feeding areas and a safe roost were indicated in one area of the Moray. This species, in common with other waders, tends to display greater mobility in spring, preparatory to departure for the breeding grounds.

3.3 Grey Plover

Most studies have found that Grey Plover are not very mobile within estuaries. They remained at the same sites after colour-marking in the Forth (Symonds 1980; Symonds *et al.* 1984) and remained localised within the Wash (Minton 1975). There is evidence of greater mobility in certain conditions. Dugan (1981) found that Grey Plover used different feeding areas at night because of a decline in prey availability at their daytime sites. Also, large itinerant flocks of Grey Plover occur occasionally on British estuaries such as the Severn in winter (Clark 1989).

3.4 Knot

All the work on waders described above has found that Knot are the most mobile species within estuaries and move frequently between feeding and roosting sites. It was suggested in the Forth study that the great mobility of Knot may be a strategy to overcome the problems of variable prey availability and distribution. Through wide-ranging movements within an estuary they can locate suitable feeding areas and when prey availability falls in one area they can exploit alternative food resources elsewhere.

3.5 Dunlin

Symonds (1980) reporting colour-marking work in the Forth stated that the majority of marked Dunlin were loyal to a particular feeding area and that those that moved tended to remain at the new site. On the Wash, there was very little interchange of Dunlin between the four sections of the Wash and mist-netting on the west coast revealed that few retrapped birds had moved more than 2km from the site of ringing (Minton 1975, Cooper 1988).

However, the work on the Forth (Symonds *et al.* 1984) categorised Dunlin as ranging more widely than the sedentary Turnstone, Grey Plover, Oystercatcher and Redshank.

Most studies demonstrate a high degree of site faithfulness by the majority of Dunlin in winter. The main exception is the Outer Forth where the greater mobility can be attributed to the scarcity of suitable roosts.

3.6 Sanderling

There are varying degrees of mobility exhibited by individuals of this species, from those which remained localised within a small area to others which range widely, as demonstrated by studies of an individually colour-ringed population at Teesmouth (Cooper 1988; Langston in prep.) This variability stems from marked changes in the availability of their main prey which is prone to removal in storm induced erosional events. However, Sanderling will take advantage of periodic wrack deposits and some individuals will move considerable distances, apparently in search of improved feeding conditions. Movements may also be associated with roosts. In the Wash, most Sanderling occur along the eastern shore, or at Gibraltar point, and move regularly between Snettisham/Wolferton and Titchwell (Cooper 1988). Sanderling are very site faithful, and return to the same site year after year, as indicated by recapture histories for individuals at the Wash and resightings of colour-ringed birds at Teesmouth.

3.7 Bar-tailed Godwit

Bar-tailed godwits are categorised as itinerant by Symonds *et al.* (1984) with 22.9% of sightings of marked birds in the Forth occurring outside the marking area. In the Moray Firth they were also observed to be very mobile with movements between firths, though not as mobile as Knot (Symonds & Langslow 1986). One of the marking sites in the Moray complex was at Nigg Bay in the Cromarty Firth, and out of the Bar-tailed Godwits marked here 25% were sighted in neighbouring firths, compared to 58% of marked Knot.

3.8 Curlew

In midwinter, Curlew on the Moray Firth remained close to the area in which they were colour-marked and were loyal to selected feeding areas (Symonds & Langslow 1986) similar results were obtained by Evans (1988) working at Tynninghame and Scoughall, in eastern Scotland. There is little other information about local movements of Curlew, but they regularly use inland sites in the hinterland of estuaries.

3.9 Redshank

Redshank have been found to be fairly sedentary waders within estuaries, with regard to both feeding sites (Symonds & Langslow 1986) and roosting sites (Mackie 1976; Furness Galbraith 1980). In the Moray Firth and the Firth of Forth they appear to be slightly more mobile than Oystercatchers with a greater number of Redshanks observed moving between feeding sites, though the majority did not move away from the original marking area. The Redshank at the Wash are also mainly sedentary with a few birds seen to change location from one side of the Wash to the other (Minton 1975). Davidson & Evans (1985) working on the Orwell Estuary reported that most Redshank colour-marked at Fagbury remained at

Fagbury, although a few were seen feeding at another site. In North Wales, movements by Redshank are generally localised (Moss 1985).

Generally, Redshank are site faithful, remaining localised in their wintering areas.

3.10 Turnstone

The work done on wader movements has found Turnstones to be one of the most sedentary and site faithful species (Minton 1975; Sutherland 1981; Dodd & Moss 1983; Cooper 1988). Most feed on rocky shores and mussel beds and thus have a localised distribution within estuaries (Symonds & Langslow 1986). Because they feed on hard substrates their prey tend to show a lot less fluctuation than those of soft shores and Turnstones are able to remain at the same feeding site instead of being forced to move by changes in prey availability (Metcalf & Furness 1985). Whitfield (1985) found pronounced site fidelity to feeding areas and very small home ranges, including roost sites, for Turnstone.

3.11 Summary

Local conditions on an estuary affect the extent of mobility of waders within it. Whilst most species displayed similarities in their extent of movement in different estuaries, the availability of a safe roost and preferred feeding areas sometimes led to considerable distances being travelled between the two. This even applied to species which showed little interchange between low tide feeding areas or between roosting areas.

4. REFUGES

There is little information about the effectiveness of refuges for waders. Consequently, this review concentrates on wildfowl which have been central to most studies of refuges. In 1960 the Wildfowl Conservation Committee was established and as a result of this a policy for wildfowl conservation was drawn up (Bell & Fox 1991). One of the aims of this policy was to create a number of refuges throughout the country in order to safeguard some of the main sites of species with a limited distribution. It was also intended that these refuges would provide a reservoir of wildfowl that would benefit "sportsmen and naturalists alike". As a result of this policy and the growing public interest in conservation, a system of refuges has been established over the last 30 years across the country. Many of these sites have statutory designations such as SSSI or National Nature Reserve (NNR) and thus the Government's conservation body (country responsibilities now assumed by English Nature, Countryside Council for Wales and Scottish Natural Heritage, under the provisions of the Environmental Protection Act 1990) has a direct say in their management. Several voluntary bodies are involved in the management of refuges including the RSPB, Wildfowl and Wetlands Trust, local wildfowling clubs and the British Association for Shooting and Conservation (BASC).

Perhaps inevitably, as one of the most active and long-standing activities on estuaries, wildfowling has been the subject of closest scrutiny. This also stems from the fact that it is easier to monitor than most other activities because of the affiliation of many wildfowling clubs to local clubs and, in turn, the British Association for Shooting and Conservation. This has also led to wildfowling clubs having an active role in refuge designation; at the Wash, wildfowling clubs have recognised low tide feeding refuges for wildfowl since the early 1960s, but these do not necessarily coincide with the main feeding areas for waders. Through sporting leases to shooting rights over the foreshore and saltmarshes at the Wash, wildfowling clubs have a measure of control over who shoots and can implement BASC's Wildfowling Code of Practice'. They can also set bag limits, call for voluntary suspensions locally and take disciplinary action against members who flout the code (Laws 1987).

In order to maximise the effectiveness of refuges, their purpose and definition must be clear at the outset. Refuges may consist of Shooting Regulated Zones or Core Wildlife Zones; the former confers time dependency, either by time of year or time of day/tidal state, whilst the latter gives priority to the wildlife interests at all times. It may be that a proposed refuge is intended to protect wintering waterfowl and is of low wildlife interest at other times of year. Alternatively, the refuge may be important for breeding, passage migrants and wintering species and so will need to maintain its designation at all times of year. Indeed, refuges may not even achieve their main importance in every winter, if they are subject to large influxes in periods of severe winter weather.

The Trilateral Co-operation on the Protection of the International Wadden Sea (Enemark 1990) ably demonstrates the implementation of nature conservation measures for an ecological entity. The co-operating countries of the Netherlands, Germany and Denmark, have implemented zonation of activities throughout the Wadden Sea area to augment international legislation, with special emphasis on protection of areas important as "nesting, feeding, breeding or moulting grounds for waterfowl", both in themselves and in their interdependencies.

An example of a refuge scheme set up with the primary objective of conserving waterfowl is that of the Strangford Lough Wildlife Scheme (SLWS) in Northern Ireland (Jepsen and Brown 1990). The SLWS was founded in 1966 with the signing of a 25 year covenant between the National Trust and the Wildfowling Association of Great Britain & Ireland (WAGBI, now BASC), through which control of shooting and co-ordination of management were established. Seven refuges were designated within Strangford Lough in which wildfowling, and as far as possible all other human activities were prohibited all year round in order to limit disturbance to birds. Voluntary restraints on wildfowling continued in additional areas. In 1987 an eighth refuge was added. The National Trust has rights, as a result of ownership and leases, to exercise controls and to implement management over much of the foreshore. Strangford Lough is of international importance as a migrating, wintering and breeding site for waterfowl. The main aim of the refuge scheme was to provide disturbance-free zones for overwintering waterfowl including light-bellied Brent Geese, Knot and Redshank which occur at levels of international importance.

The large and convoluted coastline of Strangford Lough, with its many islands, and the small staff for enforcement of restrictions have led to some problems, although this has been alleviated in part by the appointment of voluntary wardens. Quarry species such as Mallard, Teal and Wigeon responded well to the creation of refuges, using them most during daylight hours; night shooting is not permitted (BASC 1990). The enlargement of two refuges in 1983 resulted in a positive response by Wigeon and Brent Geese which indicates that size could be very important in determining the quality of an area as a waterfowl refuge. The positive response of birds to the experimental expansion of some refuges between 1983/84 and 1986/87 may have been a symptom of the increasing levels of disturbance as a result of greater recreational pressures in Strangford Lough. Although wildfowling and access to certain nesting islands are still prohibited in the refuges, recreational activities which have an impact upon birds are increasing both within and outside refuge areas. Despite the creation of the refuges, which currently cover about 10% of the total area of the Lough and include intertidal feeding areas and roosts, wildfowl numbers have fluctuated over the period 1966-1988 and for some species, such as Wigeon, numbers have declined. The reasons for this decline are not clear, but large scale shifts in centres of populations in a short space of time have been demonstrated at several sites as a result of refuge designation and management (Fox *et al.* 1990). The National Trust are implementing management for waterfowl at Anne's Point and it will be important to determine what effect this has on the Greyabbey Refuge which encompasses this area.

Owen & Salmon (1985) demonstrated significant increases nationally in the numbers of most wildfowl species on reserves between 1960 and 1983, and some decreases at unprotected sites. They also identified increases in unprotected areas after the end of the shooting season. This greater use of refuges may have several causes which are not mutually exclusive: a) an increase in refuge area, b) an increase in refuge area plus a re-distribution of birds to sites with refuges, c) an increase in total population because of refuge creation, as a result of reserve management. There could be a learning process involved in the timing of use of refuges to coincide with least disturbance on the site. On some shooting areas, food reserves will be exploited after the end of the open season, when those at other sites may be depleted. The degree to which species respond to the creation of refuges varies; dispersed species, such as Mallard, Goldeneye and Pochard, are found in smaller proportions on reserves compared to gregarious species, such as Wigeon, that tend to be found in high concentrations. There have been few quantified studies of refuges, and these are concerned

mainly with wildfowl. It is generally considered likely that conditions on the wintering grounds can be limiting to population growth in waterfowl and so refuges are an important component of enhancing survival to breed again.

One study involving experimental manipulation of refuges was carried out in Denmark by the DMU (Madsen 1992), on the Nibe Bredning experimental reserve, between 1989 and 1991. The introduction of this reserve scheme led to a decrease in the number of hunters and a ban on mobile punts. There was no commensurate increase in stationary punts. The study hypothesis was that if hunting is disruptive, the experimental restrictions should demonstrate increased numbers of waterfowl, particularly quarry species, in the area, particularly on the reserve. Increases in numbers were observed for swans, light-bellied Brent Geese and Wigeon, but only Wigeon changed their local distribution to concentrate on the reserve. The shortfall of this study is its duration; swans and geese tend to be traditional in their choice of roosting areas especially and so may take several years to adapt to changing circumstances. Additionally, increases at Nibe Bredning were accompanied by increases in the flyway populations of these species. However, the no shooting zones at Nibe Bredning provided a refuge which was used when disturbance increased in the adjoining areas. This was documented to benefit hunters too as the overall numbers of birds in the area were higher. The provision of the reserve led to Wigeon staying longer in the autumn and indeed the increased numbers of Wigeon present are considered to be the result of a redistribution during migration. Nibe Bredning is now the single most important site for Wigeon in Denmark. It remains to be seen whether food becomes the limiting factor and how long it takes for the reserve to reach capacity.

In 1979, the NCC started management of Banks Marsh on the Ribble, which became a NNR in 1981, and subsequently designated approximately 800ha of saltmarsh as a refuge for feeding Wigeon. They continued to lease the shooting rights to the local wildfowling club, but imposed a system of permit shooting only. The wildfowling club continued its voluntary restrictions. By 1984 night shooting was stopped. Traditionally, this area had been the best area for wildfowling and so there was some opposition to the restrictions on wildfowling. However, the population of Wigeon, in particular, has undergone a spectacular increase, apparently sustaining larger bags than before, whilst a lower proportion of the Ribble's Wigeon are cropped (Figure 4.1; Fox *et al.* 1990; Bell & Fox 1991). This increase was due, in part, to management of a suitable grazing sward for the Wigeon. The Ribble refuge has also attracted increased numbers of Teal and Shelduck. The increase in the relative importance of the Ribble has been greater than the national trend for these species and so the national increases in numbers of Wigeon and Teal in winter are only partly responsible for the increases on the Ribble. As stated in Bell & Fox (1991), ideally the population trends shown for refuges, such as the Ribble, need to be compared with trends at non-refuge sites in order to examine the influence of changes to the national population. Their work did not permit the identification of the factors which make an ideal refuge.

However, they did make initial recommendations for refuge establishment and assessment, to allow for conservation and sustainable cropping, paraphrased as follows: 1. Agree objectives for refuge management and criteria to measure success; 2. Collect detailed information on numbers and distribution of birds at low and high tide and on usage by human activities; 3. Formulate refuge regime for an agreed trial period; 4. Monitor bird and human usage to assess degree of success of refuge; 5. Retain flexibility to modify initial plan.

Bell & Fox (1991) examined the distribution of Wigeon on the Ouse Washes, the Ribble and Exe estuaries in relation to the end of the shooting season. At Welney, on the Ouse Washes, Wigeon extended their range over both shot and unshot fields, with many more birds moving on to previously little used fields which had been within the shooting area. The vegetation characteristics of fields were also found to be subordinate to disturbance for Wigeon by Owen (1973). On the Ribble, Wigeon were deterred from using shooting areas in the early part of the shooting season, but over the season as a whole there was no demonstrable effect. Since Wigeon feed predominantly at night on the Ribble, the cessation of night shooting there may well ensure that they have a sufficiently long, undisturbed feeding time so that they are less affected by shooting disturbance in daylight hours. On the Exe, dogs were the most frequent source of disturbance, but the birds resettled each time. Wildfowling was the main cause of desertion, resulting in loss of feeding time. Dawlish Warren LNR provided a refuge from disturbance, but feeding conditions there were not as good as elsewhere on the estuary, where disturbance limited feeding by Wigeon and Brent Geese.

There are inherent practical difficulties in ensuring that sources of human-induced disturbance are minimised or removed, particularly with limited staff resources and where participants are not affiliated to recognised associations. Additionally, in the case of waterfowl, refuge boundaries may need to be elastic because they will not always be recognised as such. The exception will be if the refuge adjoins an area which is used for an activity which causes disturbance to birds, in which case they can adapt to an invisible border. This is recognised in the deployment of scaring techniques on cereal crops, alongside areas managed for geese, which will adjust to the proximity of bird scarers outside their "refuge" (Vickery pers. comm.). This contrasts markedly with the acute awareness of sudden or unusual sources of disturbance to which geese are very responsive. Birds are more likely to adapt to disturbance in adjoining areas if there is an area of open water adjacent to the site which can serve as an unofficial refuge if the birds are forced to move by activities on the shore, including shooting (Bell & Fox 1991).

The wintering population of Pink-footed Geese, in north Norfolk, has increased dramatically from scattered records early this century to a recent peak of nearly 43,000 birds (Seago 1989; Gill 1990). Of the three roosts in this area, Snettisham accounted for about half this number of geese. Records of Pink-footed Geese became more regular in the 1950s and the increase in numbers has been most marked since 1968/69. In 1966, discarded, sprouting sugar-beet tops were first recognised as an important food source for the geese. This apparent dietary switch (Gill pers. comm.) seems to have been the main factor responsible for the population increase. Sugar-beet provides the main dietary component from October to January/February. The wildfowl refuge on the intertidal area offshore from Snettisham/Wolferton is an important roosting area for Pink-footed Geese. The refuge is approximately 1200ha in area and the geese often roost well out on Peter Black and Ferrier Sands (Seago 1989). They feed regularly on old water meadows, for example at Heacham, from February to March, or, as demonstrated in early 1990, on the saltmarsh after the end of the wildfowling season. Whilst the roosts contain large concentrations of geese, the birds disperse widely to feed in smaller groups (Gill 1990). In view of the change in diet, it is difficult to say how important the availability of a *safe* roost at Snettisham has been to the population increase. The wildfowling clubs around the Wash have recognised low tide refuges for wildfowl since the early 1960s. Even when the Snettisham intertidal area is inundated, the geese will roost out on the open water in this area (Seago 1989).

Conclusions of the review

Studies of intra-estuarine movements of waders demonstrate fairly similar patterns for most species on different estuaries, but there may be marked differences between species in any one estuary. For example, Knot are identified in all documented studies as being highly mobile, whilst Turnstone are at the opposite end of the spectrum and sedentary. These differences are largely associated with the feeding ecology of the species and their roosting requirements. There are also seasonal effects which are particularly pronounced during inclement weather or periods of disturbance.

Refuges, provided that they are large enough to ensure that disturbance events on the periphery do not affect birds within them, can be very successful in providing both undisturbed roosting and feeding areas. A positive response to refuge provision can be enhanced by appropriate management.

Few studies have tested the effectiveness of refuges rigorously and most of those concentrated on the effects of refuges on principally wildfowl quarry species. The main impetus for such studies was the desire to reconcile conservation with sustainable hunting. Some species, notably Wigeon, can show a rapid response to refuge provision. Similarly, there is evidence to show that shot-over areas are used more after the end of the shooting season. Even the relatively small level of disturbance created by visitors to a reserve can lead to a short-term decline in the total bird presence. However, the main difficulty in many of these studies has been to disentangle the effects of disturbance from other factors such as food resources and the availability of safe roosts.

Refuge provision necessitates the identification of key areas for the species of conservation interest, in this case roost locations for waders. The next stage requires the estimation of the distances which birds move between these sites, particularly for those species which move the shortest distance between roosts. These factors can be used to determine the minimum inter-refuge distance which will ensure refuge accessibility to a pre-determined proportion of the population of the most sedentary species. By providing for the least mobile species, the consequent refuge locations will accommodate the more mobile species.

These principles were applied to the following analyses of Wash Wader Ringing Group data. This data set was used because it offers the most comprehensive set of ringing data for a British estuary.

5. LARGE SCALE ANALYSIS: THE WASH

5.1 Introduction

Habitats must be considered in terms of their heterogeneity in time and in space (May 1974). This is a valuable concept when considering wader movements within the confines of a well defined area as represented by the Wash, an area comprising many discrete habitats ranging from fields to estuarine mudflats the characteristics of which will depend on the season and resources (Southwood 1977).

Waders normally roost near their feeding grounds but these change with seasonal, physical and biological conditions. It is thus reasonable to have as a starting hypothesis that waders will vary their roosting sites within a localised area depending on, for example, tidal levels, disturbance, vegetation growth and temperature, as well as varying their roosting sites on a larger scale depending on, for example, seasonal prey switching and long-term disturbance.

The movements between wader roosts were thus analysed at two levels. This chapter deals with large scale movements between roosts such as might occur if waders moved from one part of the Wash to another fulfilling objective 2, while the following chapter concentrates on small scale movements between roosts in adjacent catching sites.

5.2 Methods

The Wader Study Group archive of Wash Wader Ringing Group data included all the waders to have been ringed or handled on the Wash. Each wader catching site was systematically coded from 1984, prior catches having only been given approximate coordinates. Five wader species, Oystercatcher *Haematopus ostralegus*, Grey Plover *Pluvialis squatarola*, Knot *Calidris canutus*, Dunlin *Calidris alpina* and Redshank *Tringa totanus* found in internationally important numbers on the Wash (Ramsar Convention Bureau 1988; Smit & Piersma 1989) were included in the analysis as they were caught in large enough numbers to make an analysis of their movements feasible. Within the United Kingdom, the Wash has the highest average peak winter counts of Grey Plover and Knot, the second highest counts of Oystercatchers and Dunlin and the sixth highest counts of Redshank. Although other species, such as Bar-tailed Godwit *Limosa lapponica* and Curlew *Numenius arquata*, are also found in internationally important numbers on the Wash they were not included in the analysis as they are caught less regularly.

The Wash was divided into five sections (Figure 5.2.1), the East Wash (TF760450-TF605230), Terrington (TF603230-TF492250), Holbeach (TF491250-TF343337), Benington (TF343339-TF435500) and Friskney (TF435501-TF560580). In each section several major ringing sites are established (Figure 5.2.2).

Grey Plover, Dunlin, Knot and Redshank were considered to be juvenile if in their first year of life, Oystercatcher were considered juvenile in their first and second years of life. These age classes are based on the ability to age birds on plumage and soft part colouration.

The total wader catch was calculated for each species in each section from the whole Wash data set. The total catch of each wader is represented by circle size and a number in parentheses. For example, in the East Wash section of the Wash, 6305 adult Oystercatchers

were caught (Figure 5.3.1.1). The sums of the waders caught more than once (retrapped) on the whole Wash either in the same year (within-year), or one year apart (between-year), or at any time interval were also calculated and given as the *total number of birds handled at least twice* in the species figures *i.e.* 462 Oystercatchers were handled at least twice in the same year (Figure 5.3.1.1). The proportion of the pie-charts filled and the arrows between the pie-charts relate only to birds handled at least twice, those birds that can give evidence of movement. The relative filling in the pie-chart in each section represents the proportion of waders handled once in the section that were subsequently handled again in the same section *i.e.* about 75% of the birds handled at least twice and caught at least once in the East Wash section were handled a second time in the East Wash section (Figure 5.3.1.1). The numbers of individuals moving between sections are represented as a proportion of the total birds handled at least twice and the movements are shown by arrows *i.e.* 8% of 462 Oystercatchers handled twice, or 37 individuals, moved from the East Wash to Terrington or *vice versa* (Figure 5.3.1.1).

The analysis varied slightly as a function of the size of the data set. Sufficient Oystercatchers, Knot, Dunlin and Redshank were caught to be able to represent the within- and between-year movements of both adult and juvenile birds on the Wash estuary. Due to a smaller sample size, the Grey Plover analysis was carried out using the pooled juvenile and adult movements, and a further analysis included all recorded movements, including movements more than one year apart. The between-year analysis only included birds handled at a one year interval, whenever sample size allowed, as this had the advantage of lessening mortality factors which can bias any ringing recovery analysis.

The median and mean distances between sites where waders were first handled and subsequently recaptured were also calculated for the birds caught since the establishment of accurate site codes in 1984 (*e.g.* Figure 5.3.1.5). The median value is the distance travelled by fifty percent of the birds.

5.3 Results

5.3.1 Oystercatcher

Of 17189 adult Oystercatchers caught, 44.6% were from Friskney and 36.7% from the East Wash (Figure 5.3.1.1). Within-year most adult birds at Friskney, the East Wash, Terrington and Benington were retrapped on the same section. Inter-section adult movements were recorded between the East Wash and Terrington, the East Wash and Friskney, Terrington and Friskney, Friskney and Benington, Benington and Terrington, Friskney and Holbeach and the East Wash and Holbeach.

Of 7387 juvenile Oystercatchers caught, 34.3% were from Friskney, 32.0% from Terrington and 28.7% from the East Wash (Figure 5.3.1.2). Within-year most juvenile birds at Friskney, the East Wash and Terrington were retrapped on the initial catch section, at Benington most juveniles were from or retrapped in another section. Inter-section juvenile movements were recorded between the East Wash and Terrington, the East Wash and Friskney, Terrington and Friskney, Friskney and Benington and Benington and Terrington. No birds ringed or controlled at Holbeach were handled twice.

Between-year most adult Oystercatchers at Friskney, the East Wash, Holbeach and Terrington were retrapped on the initial catch section, at Benington most adults were from or retrapped in another section (Figure 5.3.1.3). Inter-section adult movements were recorded between the East Wash and Terrington, Terrington and Friskney, Friskney and Benington, the East Wash and Friskney, the East Wash and Holbeach, the East Wash and Benington and Terrington and Benington.

Between-year most juvenile Oystercatchers at Friskney, the East Wash and Terrington were retrapped on the initial catch section, at Benington and Holbeach most or all juveniles were from or retrapped in another section (Figure 5.3.1.4). Inter-section juvenile movements were recorded between the East Wash and Terrington, the East Wash and Friskney, Terrington and Friskney, Friskney and Benington, Terrington and Benington, Holbeach and the East Wash, Holbeach and Friskney and Terrington and Holbeach.

The median and mean within-year distances moved by adult Oystercatchers between subsequent catches were 9.50km and 8.69km, while the juveniles moved less than 1km and 5.15km respectively (Figure 5.3.1.5, Table 5.3).

5.3.2 Grey Plover

Of the 4125 Grey Plovers caught, 36.5% were from the East Wash, 30.6% were from Terrington, and 16.5% from Friskney (Figure 5.3.2.1). Most birds were retrapped within-year in the same section. Inter-section adult movements were recorded between the East Wash and Terrington and Friskney and Benington. No birds ringed or controlled at Holbeach were handled twice.

Most Grey Plovers were retrapped between-year in the same section (Figure 5.3.2.2). Inter-section adult movements were recorded between Holbeach and Terrington and Terrington and Friskney. No birds ringed or controlled at Benington were handled twice.

When the between-all-years and within-year data are combined most Grey Plovers were retrapped in the initial catch section except at Holbeach (Figure 5.3.2.3). Inter-section adult movements were recorded between the East Wash and Terrington, Friskney and Benington, the East Wash and Friskney, Terrington and Friskney and Terrington and Holbeach.

The median and mean within-year distances moved by adult Grey Plovers between subsequent catches were less than 1km and 2.34km, while the juveniles moved less than 1km and 0.82km respectively (Figure 5.3.2.4, Table 5.3).

5.3.3 Knot

Of the 28941 adult Knot caught, 70.6% were from the East Wash and 25.5% from Friskney (Figure 5.3.3.1). Within-year most adult birds at the East Wash and Friskney were retrapped on the same section. Inter-section adult movements were recorded between the East Wash and Friskney, Terrington and Friskney and the East Wash and Terrington. No adult Knot ringed or controlled at Holbeach or Benington were handled twice.

Of the 4975 juvenile Knot caught, 57.5% were from the East Wash, 17.0% from Holbeach and 15.9% from Friskney (Figure 5.3.3.2). Within-year most juvenile birds at the East Wash were retrapped on the initial catch section, while at Friskney and Terrington most juveniles were from or retrapped in another section. Inter-section juvenile movements were recorded between the East Wash and Friskney, the East Wash and Terrington, Terrington and Friskney and the East Wash and Benington. No juveniles ringed or controlled at Holbeach were handled twice.

Between-year most adult Knot at the East Wash and Friskney were retrapped on the initial catch section, at Benington and Terrington adults were from or retrapped in another section (Figure 5.3.3.3). Inter-section adult movements were recorded between the East Wash and Friskney, the East Wash and Terrington and Terrington and Friskney. No adults ringed or controlled at Holbeach were handled twice.

Between-year most juvenile Knot at the East Wash were retrapped on the initial catch section, at Friskney and Terrington most or all juveniles were from or retrapped in another section (Figure 5.3.3.4). Inter-section juvenile movements were recorded between the East Wash and Friskney, the East Wash and Terrington and Friskney and Terrington. No juveniles ringed or controlled at Holbeach were handled twice.

The median and mean within-year distances moved by adult Knot between subsequent catches were less than 1km and 6.23km, while the juveniles moved 2.50km and 2.50km respectively (Figure 5.3.1.5, Table 5.3).

5.3.4 Dunlin

Of the 79657 adult Dunlin caught, 44.4% were from Terrington, 26.5% from the East Wash, 15.9% from Benington and 9.9% from Friskney (Figure 5.3.4.1). Within-year most adult birds at Friskney, the East Wash, Terrington and Benington were retrapped on the same section. Inter-section adult movements were recorded between the East Wash and Terrington, Friskney and Benington, the East Wash and Friskney, Terrington and Friskney, Benington and Terrington, Terrington and Holbeach and Benington and the East Wash.

Of the 17144 juvenile Dunlin caught, 41.3% were from Terrington, 36.9% were from the East Wash, 10.2% from Friskney and 9.7% from Benington (Figure 5.3.4.2). Within-year most juvenile birds at Friskney, the East Wash and Terrington were retrapped on the initial catch section, at Benington and Holbeach all or most juveniles were from or retrapped in another section. Inter-section juvenile movements were recorded between the East Wash and Terrington, Friskney and Benington, the East Wash and Friskney, the East Wash and Benington, Terrington and Friskney, Benington and Terrington, the East Wash and Holbeach and Benington and Holbeach.

Between-year most adult Dunlin were retrapped on the initial catch section (Figure 5.3.4.3). Inter-section adult movements were recorded between the East Wash and Terrington, Friskney and Benington, Terrington and Friskney, the East Wash and Friskney, the East Wash and Benington, Terrington and Benington and Terrington and Holbeach.

Between-year most juvenile Dunlin were retrapped on the initial catch section except at Holbeach where most or all juveniles were from or retrapped in another section (Figure 5.3.4.4). Inter-section juvenile movements were recorded between the East Wash and Terrington, Friskney and Benington, the East Wash and Friskney, Terrington and Benington, Benington and the East Wash and Benington and Holbeach.

The median and mean within-year distances moved by adult Dunlin between subsequent catches were less than 1km and 2.04km, while the juveniles moved 1.50km and 5.19km respectively (Figure 5.3.1.5, Table 5.3).

5.3.5 Redshank

Of the 9604 adult Redshank caught, 51.9% were from Terrington, 24.5% from the East Wash, 10.7% from Benington and 10.2% from Friskney (Figure 5.3.5.1). Within-year most adult birds were retrapped on the same section except at Friskney where most adults were from or retrapped in another section. Inter-section adult movements were recorded between the East Wash and Terrington, Terrington and Friskney, Benington and Terrington, the East Wash and Benington and Benington and Holbeach.

Of the 2125 juvenile Redshank caught, 44.5% were from Terrington and 28.1% from the East Wash (Figure 5.3.5.2). Within-year most juvenile birds at the East Wash, Terrington, Holbeach and Benington were retrapped on the initial catch section, at Friskney all juveniles handled twice were from or retrapped in another section. Inter-section juvenile movements were recorded between the East Wash and Terrington, Terrington and Friskney and the East Wash and Benington.

Between-year most adult Redshank at Friskney, the East Wash, Benington and Terrington were retrapped on the initial catch section (Figure 5.3.5.3). Inter-section adult movements were recorded between the East Wash and Terrington, Terrington and Friskney, Friskney and Benington, the East Wash and Benington and Terrington and Benington. No adult Redshank ringed or controlled at Holbeach were handled twice.

Between-year most juvenile Redshank at Friskney, the East Wash, Benington and Terrington were retrapped on the initial catch section, at Holbeach all juveniles were from or retrapped in another section (Figure 5.3.5.4). Inter-section juvenile movements were recorded between the East Wash and Friskney, the East Wash and Terrington, Terrington and Friskney, the East Wash and Benington and Benington and Holbeach.

The median and mean within-year distances moved by adult Redshank between subsequent catches were less than 1km and 0.75km, while the juveniles moved less than 1km and less than 1km respectively (Figure 5.3.5.5, Table 5.3).

Species	Within-year distances moved	
	Mean (km)	Median (km)
Oystercatcher Adult	8.69	9.50
Juvenile	5.15	<1.00
Grey Plover Adult	2.34	<1.00
Juvenile	0.82	<1.00
Knot Adult	6.23	<1.00

	Juvenile	2.50	2.50
Dunlin	Adult	2.04	<1.00
	Juvenile	5.19	1.50
Redshank	Adult	0.75	<1.00
	Juvenile	<1.00	<1.00

Table 5.3 The mean and median distances moved within the Wash by different species of wader.

5.4 Discussion

5.4.1 Oystercatcher

Most Oystercatchers were section-faithful. Over 82% of adult and over 78% of juveniles were recaptured on the same section both within- and between-year. The median and mean distances moved by adult Oystercatchers were greater than those recorded for juveniles though based on a small sample size.

Oystercatchers moved most between the East Wash and Terrington (5-11%) while between 3 and 5% of birds moved between Friskney and Terrington, between 2 and 5% moved between the East Wash and Friskney and between 1 and 5% moved between Friskney and Benington.

Species		Percentage of total movements that are between-section (%)	
		Within-year	Between-year
Oystercatcher	Adult	17.3	16.5
	Juvenile	20.9	21.1

Fewer movements were recorded between the other sections. Generally there was very little difference in the patterns of the between-section movements of adults and juveniles, between- and within-year. The total number of birds caught showed that Terrington especially, but also Benington, held higher proportions of juveniles than adults than did the other sections. At Terrington there is a major juvenile Oystercatcher roost which attracts birds that have been feeding in the section on the nearby mudflats. Adults more commonly feed on mussels and cockles further out and are less attracted to the Terrington roost. Few Oystercatchers were caught at Holbeach but this is a reflection of the difficulty of catching rather than the numbers of Oystercatchers present.

5.4.2 Grey Plover

Most Grey Plovers were section-faithful. Over 82% of Grey Plovers were recaptured on the same section both within- and between-year. The mean distance moved by adult Grey Plovers was greater than that recorded for juveniles.

Grey Plover	Percentage of total movements that are between-section (%)		
	Within-year	Between-year	All data combined
Adults and juveniles	12.4	4.4	17.2

Between-year individual Grey Plovers moved between Friskney and Terrington and Holbeach and Terrington. Within-year and when all the data were combined showed that most between-section movements were between the East Wash and Terrington with fewer birds moving between Friskney and Benington. The movements between the East Wash and Terrington were often of birds that moulted at Terrington in the autumn and that would winter along the beaches of the East Wash section. The autumn roosts would be in fields and this reflected increased disturbance around the Wash in the summer and autumn. Generally there was very little difference in the between- and within-year patterns of adults and juveniles.

5.4.3 Knot

Most adult Knot were section-faithful though birds moved between Friskney and the East Wash in different years. Juveniles moved more than adults between sections and were particularly mobile in different years. Over 91% of adults were recaptured on the same section both within- and between-year. Juveniles were very mobile between-year but less so within-year. The median distance moved by adult Knot was less than that recorded for juveniles, though the reverse is true for the mean distance. The sample size, especially of juveniles, was small and these results must be treated with caution.

Species		Percentage of total movements that are between-section (%)	
		Within-year	Between-year
Knot	Adult	5.2	8.6
	Juvenile	8.4	32.7

Knot moved most between the East Wash and Friskney (3-25%). A few individuals also moved between Friskney and Terrington and Terrington and the East Wash. Both adults and juveniles were more likely to change section in different years than in the same year, juveniles moving more than adults. Friskney and the East Wash were the two most important sections for Knot on the Wash, though the difficulty of catching at Holbeach lessens the potential catch in the section. The importance of Friskney and the East Wash,

notably Holme and Snettisham/Wollerton, stems from the tendency of most Knot to roost in a few large, single species flocks.

5.4.4 Dunlin

Most Dunlin were section-faithful. Over 91% of adult and over 80% of juveniles were recaptured on the same section both within- and between-year. The median and mean distances moved by adult Dunlin were less than those recorded for juveniles. The species showed every evidence of being site faithful.

Species		Percentage of total movements that are between-section (%)	
		Within-year	Between-year
Dunlin	Adult	8.4	6.7
	Juvenile	19.2	14.1

Dunlin moved most between the East Wash and Terrington (4-10%) and too a lesser extent between Friskney and Benington (2-4%). Within-year some juveniles also moved between the East Wash and Friskney and the East Wash and Benington. Few movements were recorded between the other sections. Generally there was little difference in the patterns of the between-section movements of adults and juveniles but the latter were more mobile. Large numbers of Dunlin were caught in all sections.

5.4.5 Redshank

Adult Redshank were very section-faithful. Over 93% of adult and over 86% of juveniles were recaptured on the same section both within- and between-year. The median and mean distances moved by adult Redshank were both less than 1km. Only one juvenile was caught twice on the Wash in one year since 1984.

Species		Percentage of total movements that are between-section (%)	
		Within-year	Between-year
Redshank	Adult	6.3	3.1
	Juvenile	10.4	13.0

Only three inter-site movements by adult Redshank were made by more than individual birds, juveniles being only slightly more mobile, especially between-year.

6. SMALL SCALE ANALYSIS: TERRINGTON

6.1 Introduction

The previous chapter considered the distances moved by waders between subsequent catches over the whole Wash, large scale movements that could have been brought about by such factors as seasonal prey switching or depletion. The distribution of these distances showed that the average movements of all five wader species were less than 10km. This section seeks to confirm any preference for such short distance movements when the analysis is carried out at a fine scale, with data that allows a more accurate definition of catch sites. This level of analysis should help determine the rate of dispersal of the waders and subsequently the proportion of waders able to reach roosting refuges according to inter-refuge distance. This section fulfils objective 3.

6.2 Methods

The small scale analysis concentrated on the Terrington section of the Wash (Figure 5.2.1) as Terrington had thirteen sites where roosting waders could be caught which enabled a more precise analysis of movements (Figure 6.2.1). Both within- and between-year analyses were carried out on Grey Plover, Dunlin and Redshank as these species were normally caught several times a year at Terrington. All mark-recapture data from 1984 onwards, the date at which catch sites were individually coded, were used in the analysis. The data sets were extended with catch data from 1980/81 onwards whenever the catch site could be accurately located.

The analysis aimed at creating dispersal models for the Terrington waders based on the positions of initial capture and subsequent recapture. A simple comparison of the numbers of retrapped birds with distance would have been misleading as the number of recaptures is dependent on the sizes of each catch. This is demonstrated by the following table which makes the assumption that a constant population is being sampled:

	Initial population size N	Size of first catch c_1	Size of second catch c_2	Number of birds caught twice $\frac{c_1 c_2}{N}$
Example 1	1000	1000	1000	1000
Example 2	1000	1000	100	100
Example 3	1000	100	1000	100
Example 4	1000	100	100	10

The following retrap rate compensated for catch size and allowed a direct comparison to be made of the distances moved between catch sites:

$$\text{Retrap rate} = \frac{r}{c_1 c_2} \times \alpha$$

where r is the number of birds recaptured, c_1 the number of birds in the first catch, c_2 the number of birds in the second catch and α a constant. A complete justification of the method and the assumptions inherent to the method can be found in Appendix I.

The retrap rate was then related to the distance between the relevant catch sites whenever there were enough data. A probability distribution of *the likelihood of a wader travelling a certain distance or further* was derived from the cumulative retrap rate for each species. The probability distribution was such that when the distance to roost was zero the probability of a wader being able to fly that distance was 1. As the distance increased the probabilities tended towards zero (Figure 6.2.2 & e.g. Figure 6.3.1.2). The cumulative probability distribution was generated from the mean retrap rate at each distance; only distances at which at least three paired catches existed, allowing three retrap rates to be calculated, were used. This lessened the likelihood of an aberrant single retrap rate contributing inordinately to the distribution. The distribution was considered linear and taken to be two-tailed as waders could fly to a roost from any direction.

The cumulative probability distribution as calculated is robust, being derived directly from available data, but is limited to the maximum inter-site distance at Terrington of 7.0km. To extrapolate over longer distances, a logarithmic model was fit to the cumulative probability curve using the procedure REG in SAS version 6 (SAS Institute 1989), with the restriction that the intercept should be at zero (this forces a cumulative probability of one when the distance is zero).

Thus the model was:

$$P = e^{ax}$$

where P is the probability of a bird being able to fly the distance x or more to a roost and a is a negative constant.

If the roosts or refuges are D km apart, a wader will need to fly a maximum of $D/2$ km to the nearest refuge. From the model, the proportion of waders to which a roost or refuge is available can be calculated as follows, where $D/2$ is half the inter-refuge distance:

$$\int_0^{D/2} e^{ax} dx = \left[\frac{1}{a} e^{ax} \right]_0^{D/2}$$

Thus, if the refuges were zero kilometres apart, all of the randomly distributed waders could reach a refuge. If the refuges are two kilometres apart, the furthest waders would be expected to fly a maximum of 1km to the nearest refuge; all the waders at the refuge would be able to fly to the refuge (waders at zero distance), and an increasingly small proportion of waders would be able to fly to the refuge as the distance to the refuge increases (Figure 6.2.3). The overall proportion of waders that can make it to the refuge is the sum of the proportions of the waders that can make it to the refuge at each distance away from the refuge, or the integral between zero and $D/2$ of the model as shown above. For a justification of the method see Appendix II.

As a practical solution to the variability in the available data for the different species minimum catch sizes of 10, 150, 100 and 25 were used for Grey Plover, adult Dunlin, juvenile Dunlin and Redshank respectively. Larger catch sizes lessen the likelihood of anomalous results based on very small numbers of retraps. The retrap rate constant, α , was proportional to the minimum catch size. The data for between- and within-year adult Dunlin movements were analysed. Fewer Redshank and juvenile Dunlin were caught than Grey Plover and adult Dunlin and thus further specific analyses would be required to make an analysis of their movements valid. Only enough Grey Plover were caught for a pooled within- and between-year analysis of adult movements to be feasible.

Entries in the tables of recapture matrices, incorporated in the following species accounts, are presented in the format shown in Table 6.2.1.

6.3 Results

6.3.1 Grey Plover

In total, 190 catches of 10 or more adult Grey Plover were analysed (Tables 6.3.2a & 6.3.2b). Only 21 of those catches were within-year, the other 169 being between-all-years. The maximum number of birds retrapped in any one catch was 3 and the largest single catch included in the analysis was of 130 Grey Plover.

The retrap rate tended to decline with distance (Figure 6.3.1.1). The cumulative probability showed that less than 5% of the Grey Plover movements were over about 3.5km (Figure 6.3.1.2). The logarithmic model regression coefficient was -0.8217 ($P < 0.001$) and the model had a coefficient of determination (R^2) of 0.67 ($n=25$) (Table 6.3.1).

6.3.2 Dunlin

Fifty catches of 150 or more adult Dunlin were analysed within-year (Tables 6.3.3.1a, 6.3.3.1b & 6.3.3.1c). The maximum number of retrapped birds was 18 and the largest single catch included in the analysis was of 945 Dunlin. The within-year retrap rate tended to decline with distance (Figure 6.3.2.1). Less than 5% of the adult Dunlin movements were over 5km (Figure 6.3.2.2). The logarithmic model regression coefficient was -0.5002 ($P < 0.001$) and the model had a coefficient of determination of 0.87 ($n=6$) (Table 6.3.1).

12 catches of 100 or more juvenile Dunlin were analysed within-year (Table 6.3.3.2). The maximum number of birds retrapped was 13 and the largest single catch included in the analysis was of 325 juvenile Dunlin. There were not enough data points at each distance to make an analysis of changes in retrap rate according to distance feasible (Figure 6.3.2.3).

76 duplicate catches of adult Dunlin were analysed between-year (Tables 6.3.3.3a, 6.3.3.3b & 6.3.3.3c). The maximum number of retrapped birds in any one catch was 14 and the largest single catch included in the analysis was of 945 Dunlin. The between-year retrap rate tended to decline with distance (Figure 6.3.2.4). Less than 10% of the adult Dunlin movements were over 5km (Figure 6.3.2.5). The logarithmic model regression coefficient was -0.4698 ($P < 0.001$) and the model had a coefficient of determination of 0.97 ($n=8$) (Table 6.3.1).

6.3.3 Redshank

Only 18 duplicate catches of adult Redshank were analysed within-year (Tables 6.3.4.1a & 6.3.4.1b). The maximum number of retrapped birds was 17 and the largest single catch included in the analysis was of 641 adult Redshank. There were not enough data points at each distance to make an analysis of retrap rate with distance feasible (Figure 6.3.3.1).

35 duplicate catches of adult Redshank were analysed within-year (Tables 6.3.4.2a & 6.3.4.2b). The maximum number of birds retrapped was 32 and the largest single catch included in the analysis was of 641 adult Redshank. There were not enough data points at each distance to make an analysis of retrap rate with distance feasible though the retrap rate did tend to decline with distance (Figure 6.3.3.2).

6.4 Discussion

The retrap rate of individual Grey Plover between-all-years, of adult Dunlin and between-year adult Redshank between roosts tended to decline rapidly with distance. Fewer than 10% of adult Grey Plover and Dunlin selected roosts that were more than 5km apart at Terrington.

The logarithmic models based on the distances between the roosts selected by adult Dunlin, both within- and between-year, generated very similar best-fit lines. Individual adult Grey Plover at Terrington seemed to move less between roosts than adult Dunlin as described by the larger regression coefficient of the former. Thus as the inter-refuge distance increases, the proportion of Grey Plover able to reach the refuges declines more rapidly than the proportion of Dunlin able to reach the refuge (Figure 6.4.1; Tables 6.4.1-6.4.3). If the refuges are to cater for multiple species they should ideally target the least mobile species, in this case Grey Plover, for the more mobile species will always be able to accommodate shorter movements. The following table shows the inter-refuge distances needed for accessibility by 95%, 90%, 75%, 50% and 25% of adult Dunlin and Grey Plover:

Population percentage availability %	Inter-refuge distance <i>km</i>
--------------------------------------	---------------------------------

	Grey Plover overall	Dunlin within-year	Dunlin between-year
25	9	14	16
50	3	6	6
75	1	2	2
90	0.5	0.5	0.5
95	<0.5	<0.5	<0.5

Deciding on a certain proportion of Grey Plover that are to be catered for by a certain inter-refuge distance should guarantee that a greater proportion of adult Dunlin will be able to move as far as the refuges.

Assumptions initially had to be made about the wader distributions, that the birds were randomly mixed, that the population size at each site was constant and that the birds do not leave the section. If the birds were not randomly mixed, but formed aggregations, the number of retraps would be expected to be either very large or very small as the waders caught together in an initial catch would also be caught together in a subsequent catch. This could be a real problem in geese where birds form family groups through some of the winter (Black & Owen 1989; Percival 1991) but the few mathematically sound studies of wader aggregation show no such behaviour in waders (Roberts & Evans 1993) beyond temporary aggregations formed through the needs of feeding or flocking (*e.g.* Colwell & Landrum 1993). The population size at each site will obviously not be constant if for no other reason than that the total population of the Wash varies within the winter and birds will leave the section. The constant population size will only have a major effect if the ratio of ringed to unringed birds in each site varies through the winter and there are no *a priori* reasons for that to be the case. Similarly, the waders leaving the section should not affect the ratios of ringed to unringed birds remaining.

7. ROOST PROVISIONING: DISCUSSION

There has been very little previous work on the dispersal of waders, a trawl through *Wildlife Review* 1991 onwards failing to find a single reference on the subject. The existing literature on wader dispersal only includes analyses based on much smaller data sets that were collected over a shorter period than that used in this analysis.

Tendency to disperse	Site	Author(s)
KN>DN>RK>OC>GV	Firth of Forth	Symonds, Langslow & Pienkowski 1984
KN>DN>RK>OC	Moray Firth	Symonds & Langslow 1986
KN>OC>DN=RK=GV	The Wash	Minton 1975
KN>OC>DN	The Wash	Cooper 1988
OC>KN>GV=DN>RK adults DN>OC>GV>RK juveniles	The Wash	this study ^a
DN>GV adults	Terrington	

GV: Grey Plover DN: Dunlin KN: Knot OC: Oystercatcher RK: Redshank
^a based on median and mean within-year movements

Table 7.1 Summary of findings of studies investigating wader movements within estuarine complexes.

The results of this study (Table 7.2) are similar to those of previous studies on the Wash (Table 7.1), confirming Knot and Oystercatcher as the most mobile species. Juvenile Dunlin also appear very mobile on the Wash throughout the year. However, Cooper (1988) found that a small sample of juvenile Dunlin were sedentary in autumn. The other two studies show Knot to be the most mobile species but Oystercatcher was relatively less mobile on the Firth of Forth and Moray Firth than on the Wash. Redshank are site faithful on estuaries (Minton 1975; Mackie 1976; Furness & Galbraith 1980) and they, Turnstone or Grey Plover are probably the least mobile species on the Wash when median and mean distances moved are taken into account. It would not be possible to catch large enough samples of Turnstone on the Wash to make an analysis of their movements feasible as Turnstone are only found in small concentrations on most sites.

At Terrington, Grey Plover, being less mobile than Dunlin, provide the minimum estimate of inter-refuge distance. If it is assumed that the roosting behaviour of Grey Plover does not change even after the provisioning of refuges, 50% of the present population would be catered for by refuges placed 3km apart, while refuges 9km apart would only cater for 25% of the population (Section 6.4). The former would require some 30 refuges and the latter approximately 10 refuges. The above distances are similar to the mean inter-roost distance along a section of the Alaskan coast of just under three kilometres ($\bar{x}=2.91\text{km}$, $\sigma_{n-1}=2.80$, $n=11$) mapped by Handel & Gill (1992). The number, type, position and effect of the refuges should be considered in relation to the following factors:

Species	Percentage of total movements that are between-section (%)		
	Within-year	Between-year	All data combined
Oystercatcher Adult	17.3	16.5	-
Oystercatcher Juvenile	20.9	21.1	-
Grey Plover Adults & juveniles	12.4	4.4	17.2
Knot Adult	5.2	8.6	-
Knot Juvenile	8.4	32.7	-
Dunlin Adult	8.4	6.7	-
Dunlin Juvenile	19.2	14.1	-
Redshank Adult	6.3	3.1	-
Redshank Juvenile	10.4	13.0	-

Table 7.2 The extent of large scale movements of different wader species between roosts at the Wash.

The approach tolerance will affect the minimum outer buffer zone required to ensure the disturbance-free nature of the refuge cores. The total refuge area needs to be sufficiently large to ensure that birds are not affected by activities in adjoining areas. The tolerance of birds to approach will vary seasonally, according to feeding conditions, according to disturbance levels and between species. The variation between the minimum and maximum tolerance boundaries will be very large, for example during severe weather Dunlin can be approached to within 3-5 metres (pers. obs.) compared to over 100m in more usual conditions (*e.g.* Koepff & Dietrich 1986 cited in Smit & Visser 1993). The most critical time for the waders will be during exceptionally cold winters, as has been seen in Redshank (Clark *et al.* 1993), especially when food stocks are low, as has been the case for Oystercatchers on the Wash (Clark 1993). At such a time of metabolic stress the waders should be as little disturbed as possible. The species least tolerant of disturbance, such as Redshank and Curlew, will take flight at up to 120m when disturbed by walkers on the Wadden Sea but Oystercatchers typically take flight at 400-500m on the Banc d'Arguin, Mauritania (Smit & Visser 1993). It would thus seem reasonable to use a minimum buffer zone around the refuges of at least 250m. If the disturbance is likely to include runners, motorcycles or other fast moving objects the refuge buffer zone ought to be increased. Well-sited fences might obviate the necessity for a reduced buffer zone.

The Wash wader refuge composition should incorporate intertidal, foreshore, saltmarsh and hinterland habitat so as to cater for roosting birds from spring tides to neap tides. The typical, ideal refuge should have a frontage on the Wash mudflats or sandflats and be continuous to a hinterland of fields beyond the high spring tide mark. Sets of fields tend to have year to year attraction, but inevitably the cropping regime affects field roost location preference. Some information on the position, crop type and cropping regimen of the fields most favoured by waders can be extracted from data collected by the Wash Wader Ringing Group (WWRG) which has year to year records of flock locations on fields, including basic crop information. This information should be incorporated into the refuge models, particularly in conjunction with the experimental design for the future manipulation of

refuges. Generally, fields around the Wash are used for autumn roosting, birds displaying a preference for rolled, ploughed, newly sown or stubble fields, *i.e.* fields that are bare or with a low vegetation which allows good all round visibility. The low level of human disturbance to the vast fields around the Wash is mainly in the form of tractors or farm machinery. In autumn the waders moult and are more vulnerable to predation, but because of good food supplies they do not have to roost close to the feeding areas to conserve energy. Consequently, the availability of a *safe* roost means that birds will fly greater distances between their feeding and roosting areas. A few birds continue to use fields through the winter. On the west side of the Wash, there is a tendency for waders north of Benington to roost over spring high tides at Gibraltar Point on wet intertidal areas with sparse vegetation. This behaviour is particularly common in autumn but smaller numbers will roost at Gibraltar Point in winter. This may be related to the low level of use made of saltmarsh by the large flocks of roosting waders in autumn (pers. obs.) presumably because of the high saltmarsh vegetation. Once die back and tidal inundation have knocked back the saltmarsh vegetation, winter roosting develops.

A few examples of Wash scenarios are helpful in illustrating the importance of cropping regime in determining roost location. In the early 1980s, peas were a commonly grown crop on some of the land holdings around the Wash. Cut early, the pea stubble fields were available for roosting by waders returning from their breeding grounds in July/August. Later in the decade, as a result of closure of canneries and freezing plants and the consequently reduced market for peas, several farmers moved away from this crop. Further change in recent years has led to peas becoming a more common crop again. Another vegetation cover type favoured by roosting waders is grass. Grass is particularly common in the few years following reclamation (the last reclamation for agriculture was in 1979, at Butterwick/Freiston). The recent prevalence of wheat has had a significant effect in terms of the availability of suitable roosting fields. In the late 1980s, wheat was widely grown around the Wash, forming in places an almost continuous swathe on fields close to the shore. Before harvesting, the ripening wheat crop was unsuitable for roosting waders which roosted elsewhere, including on sea walls. Once the wheat had been cut, there was an enormous area of stubble with little to distinguish between potential roost sites and birds tended to be dispersed in flocks of a few hundred birds.

Waders can adapt to new roost sites as studies on the provisioning of artificial roosts to compensate for developments or loss of traditional roost sites have shown (Cardiff Bay; Hartlepool docks in progress). There is the proviso that the artificial roost sites must be appropriately located as the flight distance between feeding and roosting areas may become critical to the waders' energy conservation, particularly in winter, when the birds may be experiencing difficulties in maintaining their energy balance. It is also possible to enhance areas set aside for refuges, but opportunities are limited for some open coast waders because of their specialist diets, though such species as Oystercatcher do include earthworms *Lumbricus* spp. in their diet and many waders will augment their feeding with a wide variety of terrestrial and freshwater invertebrates (*e.g.* Cramp & Simmons 1983; Rehfish 1990 and in prep.). Wildfowl are very amenable to habitat manipulation, through the provision of pools, areas of short grass and the artificial supply of food.

Concentration of waders and human activities may occur after refuge creation. If activities are excluded from an area they may just occur elsewhere. There would be little point in restricting human interference in the roost area if it were simply displaced to the wader

feeding grounds. This scenario is unlikely simply because the Wash is so large that it can probably absorb a large number of humans around its shores without any noticeable effect on the waders. More problematical may be that the enhanced attractiveness of an area for wildfowl may poach them from elsewhere. This happened on the Ribble where the decline in Pintail numbers was attributed to the improved habitat at Martin Mere where many Pintail now roost until they feed on the adjacent arable land (Owen *et al.* 1986). In North America *short stopping* effects are well-documented, whereby some species winter further north as a result of refuge provision and management making it more attractive to do so.

SUGGESTED GUIDELINES FOR REFUGE PROVISION FOR ROOSTING WADERS

Results of a detailed analysis of the movement patterns of waders generally concur with earlier studies and demonstrate the pronounced overall similarity in individual species mobility on different estuaries. Thus general principles for the provisioning of refuges for roosting waders can be made, to safeguard the existing wader populations. These principles are presented in a recommended action sequence:

1. The first step is to identify the main roost locations in the estuary, as determined by the Birds of Estuaries Enquiry (BoEE)/WeBS. The first presumption should be that refuges should be placed in areas where there are existing wader roosts, in regular use, although this need not mean every high tide.
2. Those roosts which regularly hold at least 1% of the relevant population threshold for any one species should be automatically considered as potential refuges.
3. In addition, inter-refuge distances should be agreed, on the basis of the results presented in the detailed analysis. Refuges need to be spaced 3km apart, on average, to cater for 50% of the population of a sedentary species such as Grey Plover. The table shows the inter-refuge distances necessary to enable 25%, 50%, 75%, 90% and 95%, respectively, of the populations of wintering adult Dunlin and Grey Plover to reach a roost refuge. This process will yield the ideal spacing of refuges.

Population percentage availability %	Inter-refuge distance <i>km</i>	
	Grey Plover	Dunlin
25	9	15
50	3	6
75	1	2
90	0.5	0.5
95	<0.5	<0.5

4. Wader roosts are not necessarily random assemblages of birds. It is important that roost refuges should encompass sites used by different parts of the estuary's wader population, since they may display different roosting distributions. Some species, such as Knot, often roost in large, single species aggregations whereas other species, such as Redshank, tend to roost in small numbers, in mixed species flocks. There is also an indication that birds from different breeding areas will overwinter in different parts of an estuary. Similarly, juvenile and immature birds may display different patterns of roost site use from adult birds. For these reasons, it is inappropriate to confine refuges to one part of an estuary, rather than to distribute them more evenly around it, if the biodiversity of wader populations is to be maintained.
5. Additionally, the results of the detailed analysis demonstrate that with increasing distance to a refuge a decreasing proportion of the population will be catered for. This x% of the

population may represent a discrete part of the population and not be biologically representative of the whole. Thus the guiding principles for the provision of refuges need to be based on the average inter-refuge distance and regular distance intervals to provide for a random cross-section of the population wintering on any one estuary.

6. In practice, the inter-refuge distance will need to vary within any one site to reflect a range of controlling factors, such as the suitability of habitat for roosting birds. Factors affecting suitability may be permanent, semi-permanent or temporary. Whilst permanent or semi-permanent features can be taken into account when planning refuges, temporary ones tend to be outside the control of those responsible for designating refuges.
7. Permanent/semi-permanent features which will affect the suitability of a refuge include proximity to human habitation, hedges etc. Thus, recognition of the fact that waders prefer to roost where they have an unimpeded view will, in practice, be translated to locating a refuge away from human habitation. Inevitably, the presence of such features will modify the actual inter-refuge distances.
8. Temporary features include height of vegetation, prevailing wind direction, cultivation of agricultural land. Waders prefer short vegetation or smoothly cultivated fields for roosting sites. Thus, within a mosaic of cultivation types, roosts may move fields in response to cropping regimes. Roosts also change location as a result of inclement weather conditions. So a change of wind direction may lead to a favoured roost location being temporarily abandoned in favour of a site which affords shelter from that particular direction.
9. Refuge size is an important aspect of provision. A refuge needs to be large enough for birds within to be unaffected by sources of disturbance outside the refuge. The refuge network needs to provide roosts at different heights of tide and so will need to encompass intertidal habitats, coastal fringe and hinterland - saltmarshes, fields etc. Thus a refuge may extend from the inland strip behind the sea wall or saltmarsh, seawards to mid-tide level.
10. The refuge also needs to allow for, for example, cropping regimes in a group of fields around which the roost may move. Therefore the refuge should encompass the group of fields most favoured by the birds and take into account the documented approach distance tolerated by waders.
11. The purpose of refuges is to provide undisturbed roost sites for waders, particularly at times of metabolic stress. Cold winters are one such special case. Some roosts may only achieve the threshold for importance in severe winters, but do so regularly in such conditions. Therefore, these roost locations need to be included in a programme of refuge provision.
12. Refuges should be established and monitored closely for a trial period, ideally including a range of winter weather conditions. The relationship between wader use of refuges and disturbance should be determined. This procedure will permit fine tuning of the guidelines.
13. Experimental manipulation and management of refuges should be introduced, as appropriate, to fine tune designation. It is important that refuges are monitored for several years, since it may take this long to test their effectiveness. The monitoring

programme should be in place prior to selected areas becoming refuges, to provide baseline information against which to test the effectiveness of these refuges. The co-operation of all interested parties is a prerequisite for success and close consultation is necessary at all stages.

RECOMMENDATIONS FOR FURTHER WORK

1. The instigation of a programme of experimental manipulation and monitoring of test refuges is strongly recommended. This would enable the adequacy of the number, size, distribution, buffer zone etc. to be determined. Detailed analysis of the results of the experimental work would allow fine tuning of the guidelines for the provision of refuges for roosting waders.
2. Redshank is either one of the least or the least mobile of the common wader species on the Wash and it would be useful to determine the proportion of their numbers catered for by varying inter-refuge distances. It might be possible to encourage the Wash Wader Ringing Group to concentrate on this species for a few years to try and increase the sample size which presently is too small.
3. To test the model and investigate how roosts relate to feeding areas, radio-tracking of a sample of Dunlin, Grey Plover and Redshank is recommended.

ACKNOWLEDGEMENTS

We are indebted to members of the Wash Wader Ringing Group for their unstinting efforts in collecting and coding wader ringing data. The early data was computerised as part of a Wader Study Group (WSG) project. More recently, the Wash Wader Ringing Group has computerised all its data which enabled this project to be undertaken.

The authors would like to thank Sue Warbrick and Dr Peter Lack for work on the WSG data archive and Gilbert Roberts, of Durham University, who has worked hard to extract the archive from the Durham system, the new version of which has complicated this process.

Dr Jeremy Greenwood was invaluable in helping model the dispersal data and Graham Appleton gave some very clear advice. Soph Foulger, Stephen Browne and Dr Ian Henderson helped with the figures and tables.

Ian Paterson, our English Nature project officer, was particularly incisive and helpful in the coordinating discussions.

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	Retrap location <i>Size of catch</i>
Initial catch location <i>Size of catch</i>	Retrap index Number retrapped Distance travelled

Table 6.2.1 The format of the tables in Section 6.3.

Species	Age	Time interval	Model	<i>n</i>	<i>a</i>
Grey Plover	Adult	Overall	$P = e^{ax}$	25	-0.8217**
Dunlin	Adult	Within-year	$P = e^{ax}$	6	-0.5002**
	Juvenile	Within-year	-		
	Adult	Between-year	$P = e^{ax}$	8	-0.4698**
Redshank	Adult	Within-year	-		
	Adult	Between-year	-		

**** P<0.001 *** P<0.01 ** P<0.05 * P<0.10 N.S. Not significant

Table 6.3.1 The regression coefficients and coefficients of determination adjusted for the degrees of freedom (R^2 adj.) of the models used to describe the cumulative probability distribution of waders at Terrington with distance.

	15248001 8	15247001 9	15247001 9	15248001 9	15248001 4	15248001 8	15248001 8	15248001 4	15248001 9	15249001 4	15249001 7	15247001 9	15249001 8	15
	32	27	14	10	71	23	11	35	35	106	24	19	130	
152470017	3.09 2 1.95	0 0 1.68	0 0 1.68	4.94 1 2.15	0.70 1 4.13	2.15 1 1.95	0 0 1.95	0 0 4.13	0 0 2.15	0.47 1 4.10	4.12 2 2.20	0 0 1.68	0.38 1 1.08	
152480018		0 0 1.80	0 0 1.80	0 0 1.10	0 0 4.75	0 0 0	0 0 0	0 0 4.75	0 0 1.10	0 0 4.55	0 0 1.80	0 0 1.80	0 0 0.88	
152470019			0 0 0	0 0 1.10	0 0 5.65	0 0 1.80	0 0 1.80	0 0 5.65	7.00 1 1.10	0 0 5.60	0 0 2.60	0 0 0	0 0 1.40	
152470019				0 0 1.10	0 0 5.65	0 0 1.80	0 0 1.80	0 0 5.65	0 0 1.10	0 0 5.60	0 0 2.60	0 0 0	0 0 1.40	
152480019					0 0 5.68	0 0 1.10	0 0 1.10	0 0 5.68	0 0 0	0 0 5.50	0 0 2.03	0 0 1.10	0 0 1.33	
152480014						0 0 4.75	0 0 4.75	0 0 0	0 0 5.68	0 0 0.53	0 0 3.95	0 0 5.65	0 0 4.40	
152480018							0 0 0	0 0 4.75	8.27 1 1.10	0 0 4.55	12.07 1 0.90	0 0 1.80	2.23 1 0.88	
152480018								0 0 4.75	0 0 1.10	0 0 4.55	0 0 0.90	0 0 1.80	0 0 0.88	
152480014									0 0 5.68	0 0 0.53	0 0 3.95	0 0 5.65	0 0 4.40	
152480019										0 0 5.50	0 0 2.03	0 0 1.10	0 0 1.33	
152490014											2.62 1 3.68	0 0 5.60	0.97 2 4.25	
152490017												0 0 2.60	2.14 1 1.35	
152470019													5.40 2 1.40	

Table 6.3.2a Within-year and between-year (all years) recapture matrices of adult Grey Plover caught at Terrington since the 1980/81 winter (only catches of 10 or more adults included). For cell content description see previous page. Shaded boxes in the body of the table are within-year catches (table continued next page).

	15248001	15247001	15247001	15248001	15248001	15248001	15248001	15248001	15248001	15249001	15249001	15247001	15249001	15249001	
	8	9	9	9	9	8	8	4	9	4	7	9	8	8	
	32	27	14	10	71	23	11	35	35	106	24	19	130	46	
152490018															0
130															0
152490018															0
46															
152490016															
21															
152490017															
10															
152480014															
21															
152480014															
14															

Table 6.3.2b Within-year and between-year (all years) recapture matrices of adult Grey Plover caught at Terrington since the 1980/81 winter (only catches of 10 or more adults included). Shaded boxes in the body of the table are within-year catches (table continued from previous page).

1981/82	152480019 <i>358</i>	152490018 <i>189</i>
152480019 <i>631</i>	0.44 1 0	7.55 9 1.33
152480019 <i>358</i>		11.82 8 1.33

1982/83	152480019 <i>294</i>	152490016 <i>231</i>
152490018 <i>337</i>	3.03 3 1.33	10.28 8 2.30
152480019 <i>294</i>		7.36 5 3.60

Table 6.3.3.1a Within-year recapture matrices of adult Dunlin caught at Terrington during the 1981/82 and 1982/83 winters (only catches of 150 or more adults included).

1988/89	152480019 <i>504</i>	152490017 <i>219</i>	152480019 <i>513</i>	152480019 <i>551</i>	152480019 <i>945</i>	152480014 <i>582</i>	152480019 <i>201</i>
152490017 <i>377</i>	1.05 2 2.03	1.21 1 0	3.10 6 2.03	0.48 1 2.03	1.12 4 2.03	0.46 1 3.95	1.32 1 2.03
152480019 <i>504</i>		0 0 2.03	1.16 3 0	2.52 7 0	3.15 15 0	0.34 1 5.68	0 0 0
152490017 <i>219</i>			5.34 6 2.03	1.66 2 2.03	3.38 7 2.03	0.78 1 3.95	0 0 2.03
152480019 <i>513</i>				0.71 2 0	1.24 6 0	1 3 5.68	2.91 3 0
152480019 <i>551</i>					0.38 2 0	0.94 3 5.68	2.71 3 0
152480019 <i>945</i>						0.55 3 5.68	5.79 11 0
152480014 <i>582</i>							0 0 5.68

Table 6.3.3.1b Within-year recapture matrices of adult Dunlin caught at Terrington during the 1988/89 winter (only catches of 150 or more adults included).

1989/90	152490018 <i>197</i>	152490014 <i>235</i>	152490014 <i>276</i>	152490014 <i>328</i>
152490017 <i>276</i>	0 0 1.35	3.08 2 3.68	3.94 3 3.68	4.42 4 3.68
152490018 <i>197</i>		4.32 2 4.25	0 0 4.25	1.55 1 4.25
152490014 <i>235</i>			27.75 18 0	9.08 7 0
152490014 <i>276</i>				4.42 4 0

1990/91	152490018 <i>658</i>	152480019 <i>166</i>	152490018 <i>151</i>
152490017 <i>180</i>	2.53 3 1.35	0 0 2.03	0 0 4.25
152490018 <i>658</i>		0.92 1 1.33	0 0 0
152480019 <i>166</i>			7.98 2 1.33

Table 6.3.3.1c Within-year recapture matrices of adult Dunlin caught at Terrington during the 1989/90 and 1990/91 winters (only catches of 150 or more adults included).

1980/81	152480019 <i>306</i>	152480019 <i>325</i>	152480019 <i>109</i>
152480019 <i>200</i>	13.07 12 0	9.23 9 0	0 0 0
152480019 <i>306</i>		8.71 13 0	4.00 2 0
152480019 <i>325</i>			5.65 3 0

1988/89	152480019 <i>120</i>	152480019 <i>101</i>
152480014 <i>127</i>	0 0 5.48	0 0 5.48
152480019 <i>120</i>		0 0 0

1989/90	152490014 <i>120</i>	152490014 <i>189</i>
152490017 <i>118</i>	14.13 3 3.68	11.96 4 3.68
152490014 <i>120</i>		2.94 1 0

Table 6.3.3.2 Within-year recapture matrices of juvenile Dunlin caught at Terrington during the 1980/81, the 1988/89 and the 1989/90 winters (only catches of 100 or more juveniles included).

		1981/82		
		152480019	152480019	152490018
		<i>631</i>	<i>358</i>	<i>189</i>
1980/81	152480019	0.74 3 0	4.35 10 0	2.47 3 1.33
	<i>642</i>			
1980/81	152480019	6.13 6 0	0 0 0	3.41 1 1.33
	<i>155</i>			

		1982/83		
		152490018	152480019	152490016
		<i>337</i>	<i>294</i>	<i>231</i>
1981/82	152480019	1.88 4 1.33	3.23 6 0	9.60 14 3.60
	<i>631</i>			
1981/82	152480019	0.83 1 1.33	3.80 4 0	7.26 6 3.60
	<i>358</i>			
1981/82	152490018	0 0 0	0 0 0	9.16 4 2.30
	<i>189</i>			

Table 6.3.3a Between-year recapture matrices of adult Dunlin caught at Terrington between the 1980/81 and 1981/82 winters and the 1981/82 and 1982/83 winters (only catches of 150 or more adults included).

		1986/87
		152490014
		<i>354</i>
1985/86	152480014	1.87
	<i>151</i>	1
		0.53

		1989/90				
		152490017	152490018	152490014	152490014	152490014
		<i>276</i>	<i>197</i>	<i>235</i>	<i>276</i>	<i>328</i>
1988/89	152490017	0.96	5.39	0	0.96	1.62
		1	4	0	1	2
	<i>377</i>	0	1.35	3.68	3.68	3.68
	152480019	1.44	3.02	1.69	0	1.81
		2	3	2	0	3
	<i>504</i>	2.03	1.33	5.50	5.50	5.50
	152490017	4.96	2.32	1.94	1.65	0
		3	1	1	1	0
<i>219</i>	0	1.35	3.68	3.68	3.68	
152480019	1.41	0	0.83	0.71	0	
	2	0	1	1	0	
<i>513</i>	2.03	1.33	5.50	5.50	5.50	
152480019	0.66	4.61	0.77	0	1.11	
	1	5	1	0	2	
<i>551</i>	2.03	1.33	5.50	5.50	5.50	
152480019	2.30	1.07	0.90	0	1.29	
	6	2	2	0	4	
<i>945</i>	2.03	1.33	5.50	5.50	5.50	
152480014	0	0	1.46	0.62	1.05	
	0	0	2	1	2	
<i>582</i>	3.95	4.40	0.53	0.53	0.53	

	152480019	0	0	0	0	1.52
	<i>201</i>	0	0	0	0	1
		2.03	1.33	5.50	5.50	5.50

Table 6.3.3b Between-year recapture matrices of adult Dunlin caught at Terrington between the 1985/86 and 1986/87 winters and the 1988/89 and 1989/90 winters (only catches of 150 or more adults included).

		1990/91			
		152490017	152490018	152480019	152490018
		<i>180</i>	<i>658</i>	<i>166</i>	<i>151</i>
1989/90	152490017	0	3.30	0	2.40
		0	6	0	1
	<i>276</i>	0	1.35	2.03	1.35
	152490018	0	3.09	0	3.36
		0	4	0	1
	<i>197</i>	1.35	0	1.33	0
	152490014	0	0	0	0
		0	0	0	0
	<i>235</i>	3.68	4.25	5.50	4.25
	152490014	0	0.55	0	0
		0	1	0	0
	<i>276</i>	3.68	4.25	5.50	4.25
	152490014	5.08	1.39	3.67	2.02
		3	3	2	1
	<i>328</i>	3.68	4.25	5.50	4.25

Table 6.3.3.3c Between-year recapture matrices of adult Dunlin caught at Terrington between the 1989/90 and 1990/91 winters (only catches of 150 or more adults included).

1980/81	152490017 <i>30</i>	152480015 <i>103</i>
152480019 <i>29</i>	0 0 2.03	0 0 3.65
152490017 <i>30</i>		0 0 2.50

1981/82	152480020 <i>27</i>	152480019 <i>228</i>	152490017 <i>183</i>	152490017 <i>132</i>
152480020 <i>153</i>	0 0 0	0 0 1.58	5.95 10 3.60	3.30 4 3.60
152480020 <i>27</i>		0 0 1.58	0 0 3.60	4.68 1 3.60
152480019 <i>228</i>			6.79 17 2.03	3.32 6 2.03
152490017 <i>183</i>				2.07 3 0

1982/83	152480019 <i>58</i>
152480019 <i>161</i>	1.79 1 0

Table 6.3.4.1a Within-year recapture matrices of adult Redshank caught at Terrington during the 1980/81, the 1981/82 and the 1982/83 winters (only catches of 25 or more adults included).

1987/88	152480020 <i>81</i>	152480019 <i>225</i>
152480019 <i>63</i>	0 0 1.58	0 0 0
152480020 <i>81</i>		3.66 4 1.58

1988/89	152480020 <i>33</i>
152480020 <i>641</i>	1.58 2 0

Table 6.3.4.1b Within-year recapture matrices of adult Redshank caught at Terrington during the 1987/88 and the 1988/89 winters (only catches of 25 or more adults included).

		1981/82				
		152480020	152480020	152480019	152490017	152490017
		<i>153</i>	<i>27</i>	<i>228</i>	<i>183</i>	<i>132</i>
1980/81	152480019	0	0	0	6.28	0
	<i>29</i>	0	0	0	2	0
		1.58	1.58	0	2.03	2.03
1980/81	152490017	0	0	0	0	12.63
	<i>30</i>	0	0	0	0	3
		3.60	3.60	2.03	0	0
1980/81	152480015	0	0	0	2.65	0
	<i>103</i>	0	0	0	3	0
		0	0	0	2.50	0

		1982/83	
		152480019	152480019
		<i>161</i>	<i>58</i>
1981/82	152480020	2.03	5.64
	<i>153</i>	3	3
		1.58	1.58
	152480020	0	0
	<i>27</i>	0	0
		1.58	1.58
1981/82	152480019	2.73	0
	<i>228</i>	6	0
		0	0
1981/82	152490017	4.53	1.57
	<i>183</i>	8	1
		2.03	2.03
1981/82	152490017	2.35	0
	<i>132</i>	3	0
		2.03	2.03

Table 6.3.4.2a Between-year recapture matrices of adult Redshank caught at Terrington between the 1980/81 and the 1981/82 winters and the 1981/82 and the 1982/83 winters (only catches of 25 or more adults included).

		1986/87
		152490014
		<i>51</i>
1985/86	152470019	0
		0
	<i>57</i>	0

		1987/88		
		152480019	152480020	152480019
		<i>63</i>	<i>81</i>	<i>225</i>
1986/87	152490014	0	0	0
		0	0	0
	<i>51</i>	5.50	6.85	5.50

		1988/89	
		152480020	152480020
		<i>641</i>	<i>33</i>
1987/88	152480019	4.95	0
		12	0
	<i>63</i>	1.58	1.58
	152480020	0.64	0
		2	0
	<i>81</i>	0	0
	152490019	3.70	8.98
		32	4
	<i>225</i>	1.58	1.58

Table 6.3.4.2b Between-year recapture matrices of adult Redshank caught at Terrington between the 1985/86 and the 1986/87 winters, the 1986/87 and the 1987/88 winters and the 1987/88 and the 1988/89 winters (only catches of 25 or more adults included).

Species	Time interval	Distance <i>km</i>	Proportion of Grey Plover within reach of the refuge %
Grey Plover	Within-year and between-all-years	100	2.43
		50	4.87
		45	5.41
		40	6.09
		35	6.95
		30	8.11
		25	9.74
		20	12.17
		18	13.51
		16	15.19
		14	17.33
		12	20.14
		10	23.94
		9	26.37
		8	29.29
		7	32.81
		6	37.12
		5	42.44
		4	49.06
		3	57.48
2	68.19		
1	82.00		
0.5	90.40		
0	100.0		

Table 6.4.1 Variation in the proportion of Grey Plover within reach of a refuge according to inter-refuge distance: based on the overall dispersal model (Table 6.3.1).

Species	Time interval	Distance <i>km</i>	Proportion of waders within reach of the refuge %
Dunlin	Within-year	100	4.00
		50	8.00
		45	8.89
		40	10.00
		35	11.42
		30	13.32
		25	15.96
		20	19.86
		18	21.97
		16	24.53
		14	27.70
		12	31.66
		10	36.71
		9	39.75
		8	43.22
		7	47.20
		6	51.78
		5	57.07
		4	63.20
		3	70.34
2	78.69		
1	88.48		
0.5	94.00		
0	100.0		

Table 6.4.2 Variation in the proportion of Dunlin within reach of a refuge according to inter-refuge distance: based on the within-year dispersal model (Table 6.3.1).

Species	Time interval	Distance <i>km</i>	Proportion of waders within reach of the refuge %
Dunlin	Between-year	100	4.26
		50	8.51
		45	9.46
		40	10.64
		35	12.16
		30	14.18
		25	16.98
		20	21.09
		18	23.31
		16	25.99
		14	29.27
		12	33.36
		10	38.51
		9	41.59
		8	45.09
		7	49.07
		6	53.62
		5	58.84
		4	64.84
		3	71.77
2	79.79		
1	89.12		
0.5	94.35		
0	100.0		

Table 6.4.3 Variation in the proportion of Dunlin within reach of a refuge according to inter-refuge distance: based on the between-year dispersal model (Table 6.3.1).

Lots of Figures

APPENDICES

Justification of R (recapture rate) as a measure useful in this study.

Let the two populations have the same constant sizes N_1 and N_2 (as approximations the principles work if the population sizes are not constant).

Let m birds move from one site to the other.

Let the first capture be of c_1 birds and the second capture, at the second site, be of c_2 birds.

Let the number of recaptures be r .

The proportion of marked (ringed) birds at the first site immediately after the first capture = $\frac{c_1}{N_1}$

Number of marked birds moving from sites 1 to 2 = $\frac{c_1 m}{N_1}$

The proportion of the population caught in the second catch = $\frac{c_2}{N_2}$

Number of marked birds caught, $r = \frac{c_1 m}{N_1 N_2} \cdot \frac{c_2}{N_2} = \frac{c_1 c_2 m}{N_1 N_2}$

The recapture rate, R , as measured, is = $\frac{r}{c_1 c_2}$

therefore $R = \frac{m}{N_1 N_2}$

Let p be the probability that a bird emigrates from site 1.

Let G be the global population. The relative likelihood of a bird that has emigrated from somewhere settling in site 2 is then $\alpha N_2 / G$, where α is a constant (which may be specific to site 2).

Then the probability that a bird moves from site 1 to site 2 = $\frac{p \alpha N_2}{G}$

The number of birds moving, m , is thus $p \alpha N_1 N_2 / G$.

Hence $\frac{m}{N_1 N_2} = \frac{p \alpha}{G}$

Since $R = \frac{m}{N_1 N_2}$, $R = \frac{p \alpha}{G}$

$N_1 N_2 G$

Since G can be regarded as constant, R measures the probability of a bird moving between sites 1 and 2, compounded of the probabilities of leaving site 1 (p) and the site-specific constant that relates to probability of it then moving into site 2.

II What is the probability of a bird reaching a refuge?

The probability distribution of the birds being able to move a certain distance approximates to the cumulative retrap rate.

The probability distribution was assumed to be a logarithmic function:

$$P = e^{-ax}$$

$$(\ln P = -ax)$$

If refuges are D apart, then all birds are within $D/2$ of the nearest refuge.

The birds are assumed to be totally randomly distributed over the whole length of the Wash before flying in to roost.

Refuges will recruit birds from either side of themselves according to the probability distribution (Figure 6.2.3).

At large inter-refuge distances none of the randomly distributed birds beyond the tail of the probability distribution will be able to reach a refuge but a gradually increasing proportion of the birds nearer a refuge will be able to reach it (Figure 6.2.3a).

As the inter-refuge distance shortens a greater proportion of the population of birds will be able to reach a refuge and some birds towards the tail-end of the probability distribution (the birds that can fly further) will be able to reach two or more refuges (Figure 6.2.3c).

According to the model used for the probability distribution there will always be some birds that cannot reach a refuge unless the inter-refuge distance is zero and these birds are represented in Figure 6.2.3c by the area bounded by the dotted lines.

The total population between a refuge and $D/2$ can be taken to be the area $D/2$ (distance \times 100% probability (1) of getting all the birds).

The proportion of birds that can reach a refuge $D/2$ distant is the area under the probability distribution from the refuge to $D/2$ divided by the total population over that distance.

Hence, the proportion of birds that can reach the nearest refuge is:

$$\frac{D/2}{2} \int_0^{D/2} e^{-ax} dx = \left[\frac{-1}{a} e^{-ax} \right]_0^{D/2}$$

