Verhandlungen

der

Ornithologischen Gesellschaft in Bayern

Band 23

Heft 2/3 (1978/79)

Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour

Michael W. Pienkowski

Department of Zoology, University of Durham,
South Road, Durham DH1 3LE, England.

Introduction

As is now well known, very large numbers of waders from breeding grounds across much of the Palaearctic and Eastern Nearctic moult and overwinter on the tidal lands of the East Atlantic from Scotland and Denmark southwards. It is also becoming clear, thanks to the counts organised by IWRB and others, that the specific composition of the wintering flocks varies greatly between sites separated by tens as well as hundreds of kilometres. This has implications for conservation policy in at least two general ways. Firstly, there is a need to ensure protection for an adequate range of sites to safeguard the variety of species. Secondly, some knowledge of the causes of these distributional differences would be useful for management plans for protected sites, in assessing the impact of losses of various sites or parts of sites, and in considering whether alternative surviving sites are likely to provide suitable habitats for displaced birds.

To detail the distribution and habitat requirements of each species would be tedious and, in many cases, difficult because of lack of data. Instead, this paper will consider, in general terms, the differences between the two most important families of waders, the Scolopacidae, including sandpipers, godwits and their allies, and the Charadriidae or plovers.
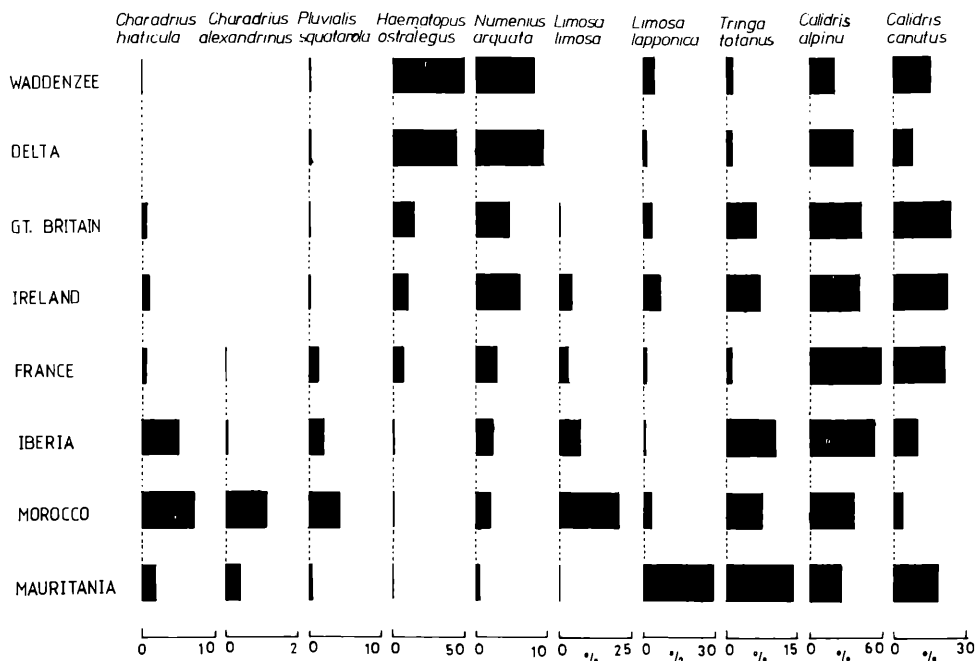
Figure 1.
Percentage composition of wintering wader populations on the coasts of the West Palaearctic.
Data from PRATER (1976).

Although some species of both families breed abundantly as far north as the highest arctic, the main wintering ranges of intertidal plovers do not extend as far north as those of sandpipers (Fig. 1). Even the northern-most wintering coastal species, the Ringed Plover *Charadrius hiaticula* and the Grey Plover *Pluvialis squatarola,* form a very small proportion of the wader population north of Iberia, whereas the coasts of the southern North Sea, the Irish Sea and the Bay of Biscay are, of course, of prime importance for many species of arctic and temperate breeding Scolopacidae. (Thesecoasts may, of course, be of importance also to restricted populations of some plover species, e. g. the British breeding Ringed Plovers, but this paper will not be concerned with distributional patterns below the species level.) In winter, sandpipers outnumber plovers by nearly 100:1 in the southern North Sea and by about 10:1 in north-west Africa. However, the proportion of plovers apparently continues to increase further south for, on a 50 km stretch of coastal lagoons in Ghana in December 1976, TAYLOR (1977) found that Ringed Plovers comprised 33 % of the wader population and Grey Plovers 8 %. As there can be no direct benefit in increasing the lenght of the migration between breeding and wintering areas, there must be a greater disadvantage to plovers than to at least some sandpipers in wintering farther north.

Differences in distribution between the families also occur on a smaller scale, within estuaries, and studies in several areas have shown these to be consistent (Fig. 2). Plovers generally feed at high tidal levels, Kentish or Snowy Plovers *Charadrius alexan-*
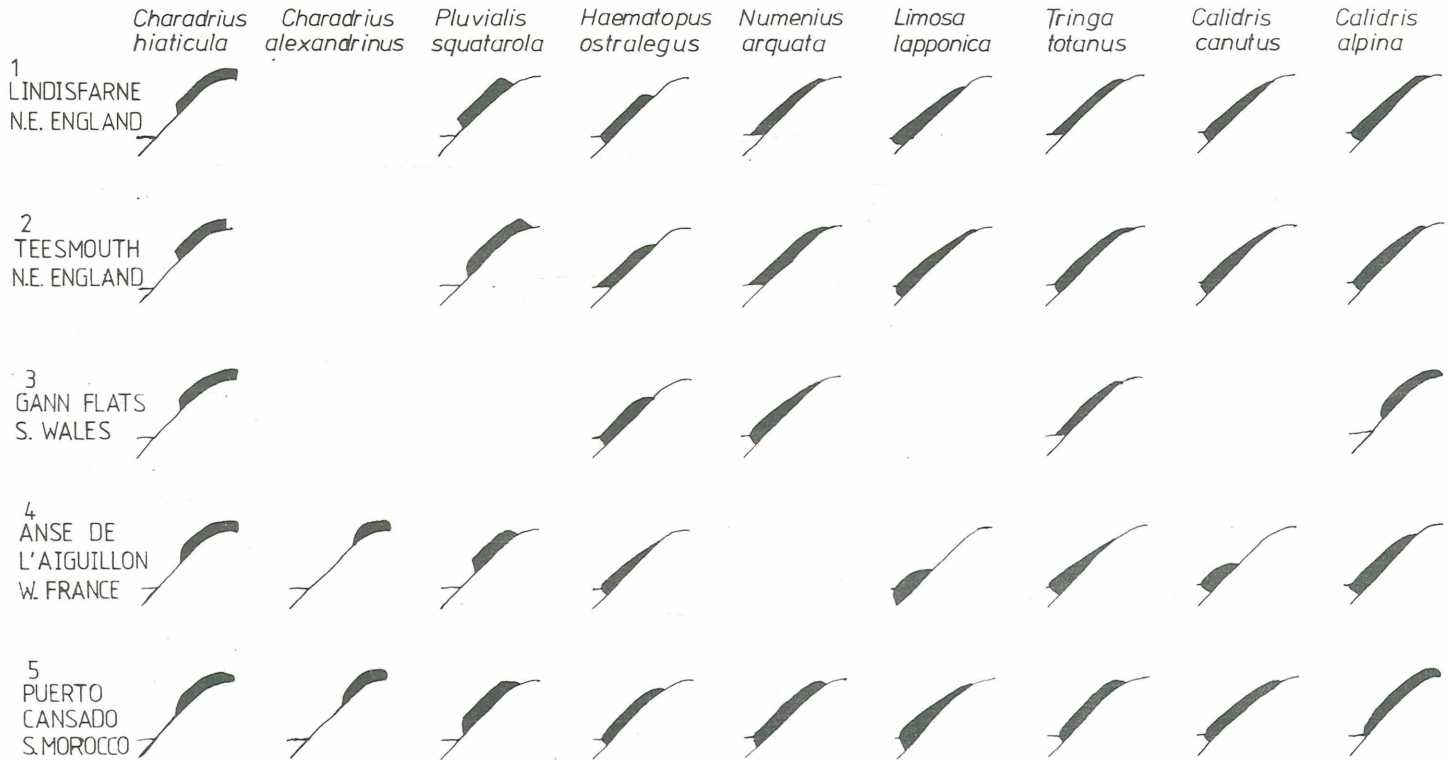
Figure 2.
Low water feeding distributions in relation to tidal level reported by various authors (1. PIEN-KOWSKI unpublished; 2. PIENKOWSKI 1973; 3. EDINGTON et al. 1973; 4. SPITZ 1964; 5. JOYES 1975 & PIENKOWSKI unpublished).
On each diagram, low water tidal level is indicated by the horizontal line and the top of the beach by the curve at the top of the sloping line.

drinus mainly at the top of the beach, Ringed Plovers above mid-tidal level, and Grey Plovers mainly at mid-tidal levels. In contrast, the sandpipers and the Oystercatcher *Haematopus ostralegus* range widely in the intertidal zone, but tend to be concentrated near the tide edge where prey animals are usually near the mud surface (e. g. VADER 1964).

This paper attempts to account for the more southerly wintering distribution of plovers and their use of feeding areas at higher tidal levels by examining their feeding ecology and behaviour.

Foraging behaviour and food

The feeding behaviours of the two families differ markedly. Plovers forage, probably visually, by waiting for prey to reveal itself, either by coming to the surface of the ground, or if already on the surface, by moving. The birds run rapidly to catch and swallow the prey before resuming a waiting position. They also run rapidly to new waiting positions if no prey are detected. Plovers have fairly short bills and do not normally probe into the substratum. In contrast, sandpipers frequently use an apparently tactile foraging method (although the initial positioning of the bill may be aided by visual cues), placing the bill tip on the surface or slightly into the substratum to detect prey, and probing deeper to catch animals detected. This searching method is usually accompanied by continual walking over the area searched. Although plovers very rarely use any technique other than the one described above, sandpipers show more varied feeding behaviour but usually include at least some element of tactile foraging. In the rest of this paper I shall use the terms 'plover strategy' and 'sandpiper strategy' to refer to the two techniques, although it should be noted that the methods are not exclusive to the two families.

One obvious explanation could be that these differences in foraging methods are adaptations to feeding on different types of prey. Indeed, GOSS-CUSTARD (1977) suggested that Redshanks *Tringa totanus* preferred some prey species to others, and a few studies (e. g. GOSS-CUSTARD 1970, GOSS-CUSTARD et al. 1977) have correlated densities of overwintering Curlews *Numenius arquata* and Redshanks their main prey species. However, Table 1 summarizes several studies in which the foods of a range of wader species have been investigated in each of several areas. Two points are clear: (i) the main prey of each species varied greatly amongst areas according to what was present, and (ii) at any one site, a variety of bird species, both plovers and sandpipers, tended to take the same prey species. These general conclusions would not be altered if subsidiary prey were also included in the comparisons. Clearly, therefore, it is unlikely that the two shorebird feeding strategies are adaptations to the capture of particular prey species.

Most intertidal invertebrates tend to spend a large part of the period of tidal emergence hidden in the substrate, in many cases beyond the reach of waders' bills. From time to time, they make themselves temporarily available to predators. The two shorebird foraging behaviours represent alternative ways of exploiting the behaviour of their prey, as will now be shown.

	LEDSKÄR[1]	HUSUM[2]	HOHWACHT[2]	HELGOLAND[2]	ESSEX[3]	TEESMOUTH[4]	LINDISFARNE[5]
CHARADRIIDAE							
Charadrius hiaticula	Coleoptera	*Nereis*	Coleoptera Diptera	*Littorina*	—	*Nereis* ? *Corophium*	*Scoloplos* small Crustacea
Pluvialis squatarola	—	*Nereis*	—	—	*Hydrobia*	*Nereis*	*Scoloplos Nereis Arenicola*
SCOLOPACIDAE							
Numenius arquata	—	*Nereis*	—	—	*Carcinus*	*Nereis*	—
Limosa lapponica	—	*Nereis*	—	—	—	*Nereis*	*Arenicola Scoloplos Nereis*
Tringa totanus	Coleoptera	*Nereis*	—	—	*Hydrobia*	*Nereis*	—
Calidris canutus	—	*Hydrobia Littorina*	—	—	—	*Mytilus Hydrobia*	—
Calidris alpina	Coleoptera	*Nereis*	Diptera	—	*Hydrobia*	Oligochaeta *Nereis Hydrobia*	*Scoloplos* small Polychaeta and Oligochaeta

Table 1. Main prey taken by various species of waders at sites where a range of species have been studied. Sources: 1. NORLIN (1965) in autumn; 2. HOFMANN & HOERSCHELMANN (1969), mainly in autumn; 3. BURTON (1968, 1974 & *in litt.*) mainly in winter; 4. D. M. HERDSON (unpublished), PIENKOWSKI (1973), in winter; 5. EVANS & SMITH (1975), SMITH (1975), PIENKOWSKI (1978) in winter.

Foraging strategy and prey behaviour

In examining the behavioural interactions between waders and their prey it is necessary to study a limited area intensively, and the following sections are based mainly on work at Lindisfarne National Nature Reserve, N. E. England by SMITH (1975) on the Bar-tailed Godwit *Limosa lapponica* and PIENKOWSKI (1978) on other species, particularly the plovers *Charadrius hiaticula* and *Pluvialis squatarola*.

Although, as shown above, different prey are taken at different sites, at least some of the conclusions reached at Lindisfarne concerning the interactions of the predators' and the prey's behaviour should have wider applicability, because: (i) several sandpiper species have been studied elsewhere with compatible results and, although relatively little investigated elsewhere, feeding of plovers is highly stereotyped; (ii) despite the wide variety of prey species which may be taken, many of these are affected in a rather similar way by physical conditions, e. g. substrate temperature. However, the particular conditions which lead to, e. g., a cessation of activity probably vary from one invertebrate species to another (e. g. VADER 1964, GOSS-CUSTARD 1969, SMITH 1975, PIENKOWSKI 1978); and (iii) personal observations at various other sites tended to agree with those at Lindisfarne.

When using the 'sandpiper strategy', the area searched by a bird per unit time is the distance it walks in this time multiplied by the combined distance on either side of its path that it searches with its bill, the 'path width'

The prey taken per minute = area searched per minute = prey density = proportion of prey within depth reach of predator = the probability of detecting, selecting and catching the prey ....equation (1).

(We cannot, with the data available, distinguish between the components of the probability arising from each of these three factors.) This strategy is used at Lindisfarne by waders as different in size as the small Dunlin *Calidris alpina* feeding on small worms and various other small prey, and the large Bar-tailed Godwit feeding on the medium-sized polychaete *Scoloplos armiger*.

When using the 'plover strategy' a bird stands still, apparently scanning on area, until it either moves rapidly a short distance and then repeats the process or runs to peck at prey. Thus, unlike the sandpiper strategy in which an area is searched by fairly steady movement over a certain time period, plovers watch a potential catching area (assuming that searching is visual) until a cue is detected. The location of the area searched may be changed but the factor limiting the rate of prey capture is the rate of appearance of prey.

Thus the prey taken per minute = area 'watched' × prey density × probability of individual prey animal appearing per minute × probability of detecting, selecting and catching prey ....equation (2).

This probability is, of course, different from that of the sandpiper strategy. It is likely to be higher as it refers to prey which has revealed itself in some way rather than

that hidden in the mud. However, the proportion of all prey which are both active and at the surface will be somewhat lower than the proportion hidden but within range of the birds' bills.

The 'plover strategy' is used at Lindisfarne by both plover species feeding on small surface-living crustacea (which probably reveal themselves by swimming movements), on *Scoloplos* and on the large polychaete *Arenicola marina*. Bar-tailed Godwits also use a form of 'plover strategy' when feeding on *Arenicola* although they may simultaneously employ a form of 'sandpiper strategy' to feed on *Scoloplos*.

There is little doubt that the appearance of casts produced by *Arenicola* backing up their burrows to defaecate at the surface is the cue to which plovers and godwits respond, as the birds can be seen running to casts as they are being formed and taking worms from them. In contrast, *Scoloplos* produce small outflows of water from their holes (which have diameters of up to about 1 mm) when near the surface. Although it is not certain that plovers respond to the outflows from the holes of *Scoloplos,* it seems likely because (i) the outflows from the holes are good predictors of the presence of worms near the surface; (ii) no other cues are apparent; and (iii) factors affecting visibility of outflows, at least to human eyes, also affect the feeding behaviour of the plovers. These include wetness of the substratum, occurrence of rain, wind strength and light intensity.

Factors affecting prey availability and feeding rate of waders

The behaviour of prey animals and therefore their availability to predators is affected by physical conditions, such as light intensity, wind strength and temperature, which may also affect the birds' food requirements and the ease with which birds can detect cues.

Generally waders appear to avoid feeding at night unless they are unable to gain sufficient food in daylight (e. g. GOSS-CUSTARD 1969, HEPPLESTON 1971). Observations at Lindisfarne using night-viewing apparatus (an image-intensifier) showed that even plovers are able to feed during cloudy or moonless nights, either by utilizing the very low light intensities or by detecting their prey by sound. (Evidence for acoustic detection of prey by plovers has been presented by FALLET (1962) and LANGE (1968), but see also HEPPNER (1965) for an analysis of problems in acoustic detection of earthworms by the thrush *Turdus migratorius* which forages in a manner similar to that of plovers.) However, feeding rate was depressed even in twilight: the mean pecking rate of a flock of Ringed Plovers at Lindisfarne fell significantly ($P < 0.01$) from 16.7 pecks/min. in the period before sunset to 7.3 shortly after sunset. One would expect the feeding rates of 'plover strategists' to be depressed at night more than those of 'sandpiper strategists' (cf. HULSCHER 1976). Since in winter the daylight period becomes progressively shorter further north, this alone might be sufficient to explain the more southerly distribution of the 'plover strategists'

High winds increase waders' food requirements by chilling birds, reduce feeding efficiency by impeding movement, reduce prey availability by drying the substrate surface above the tide edge (thereby causing prey to move deeper or become inactive) and reduce visibility by creating waves over water covered areas (EVANS & SMITH 1975). In
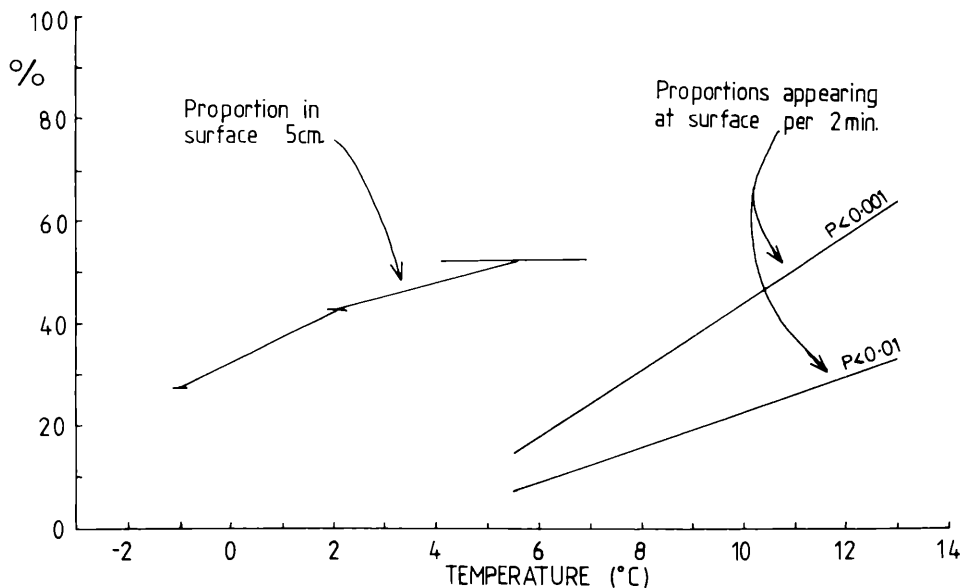
Figure 3.
Effect of temperature on depth and activity of *Scoloplos armiger* at Lindisfarne. The proportions of *Scoloplos* present in the surface 5 cm (from SMITH 1975) are shown as horizontal lines indicating the temperature range for each measurement. The numbers of outflows of water on the surface from *Scoloplos* holes per 2 minute period, expressed as a percentage of those present, are given as regression lines for two sample areas (PIENKOWSKI 1978). Both slopes are significantly different from zero.

very high winds waders move to more sheltered feeding and roosting areas such as lee shores or creeks (SPITZ 1964, SMITH 1975, PIENKOWSKI 1978, D. J. TOWNSHEND pers. comm.) or may cease feeding altogether (SMITH 1975, EVANS 1976).

The effect of temperature on prey availability is possibly the easiest to study and it may well be the most important factor in many situations. As temperatures fall, most prey species become less active and tend to move deeper into the substrate. This is exemplified by S*coloplos* at Lindisfarne in Fig. 3 which illustrates the variation with substrate temperature of (i) the proportion at any one moment of worms in the top 5 cm of the substrate (i. e. those most liable to predation by Bar-tailed Godwits–SMITH 1975), and (ii) the activity of the worms as revealed by the number of outflows of water from their holes per two minute period (expressed as a percentage of the number of worms present in the area watched). The positions of these lines are not directly comparable on the vertical axis as one involves a time function and the other does not, but their general shapes and their positions relative to the horizontal axis are comparable. The frequency of outflows from holes of *Scoloplos* decreases rapidly and significantly ($P < 0.001$ in one sample area, $P < 0.01$ in another), as temperature falls, and the decrease is apparent even at temperatures above $10°C$. However, the same proportion of *Scoloplos* remains in the upper sand layers until temperatures as low as $4°C$ and, even when reduction of the proportion on the surface layer does occur, there is still such wide variation that the change in proportion was not significant in the samples.
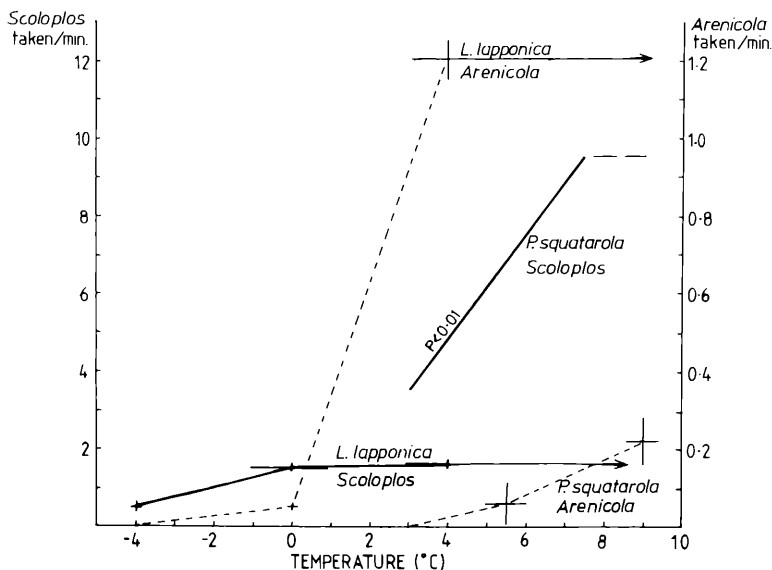
Figure 4.

Feeding rates of Bar-tailed Godwit, *Limosa lapponica* (from SMITH 1975) and Grey Plover *Pluvialis squatarola* (PIENKOWSKI 1978) on *Arenicola marina* (dashed lines) and other prey, almost entirely *Scoloplos armiger,* (solid lines) at Lindisfarne. The feeding rate of *Pluvialis* on *Scoloplos* is given as a regression line (P < 0.01) based on data between 2°C and 8°C. Other rates are shown as horizontal lines indicating the temperature range for each measurement and vertical lines indicating ± 1 standard error.

As godwits appear to use the tactile 'sandpiper strategy' and plovers visual searching when feeding on *Scoloplos,* one would expect the feeding rate of plovers to decrease, as temperature falls, before that of godwits. The godwits' feeding rate should also remain independent of temperature above about 4°C. This is, in fact, what happens (Fig. 4); the feeding rate of Grey Plover falls rapidly between 8°C and 2°C but that of Godwit remains constant down to 0°C and falls slowly below. At higher temperatures, *Arenicola,* which spend most of the time beyond the reach even of long-billed Godwits, become active and available, and both species use 'plover-strategies' to catch them. As the effects of temperature on the activity and depth distribution of *Scoloplos* appear to be typical of intertidal invertebrates (although the particular temperature levels at which they operate may, of course, differ), the resulting difference in the effects of temperature on plover and sandpiper feeding strategies may be fairly general.

Possible mechanisms to compensate reductions in feeding rates

Probably because of the greater depression of feeding rates of plovers than of sandpipers resulting from low temperatures, in winter in Britain plovers often feed for longer per tidal cycle than do sandpipers of similar size. Figure 5 shows that, at Teesmouth in N. E. England, within groups of birds using the same general feeding method,
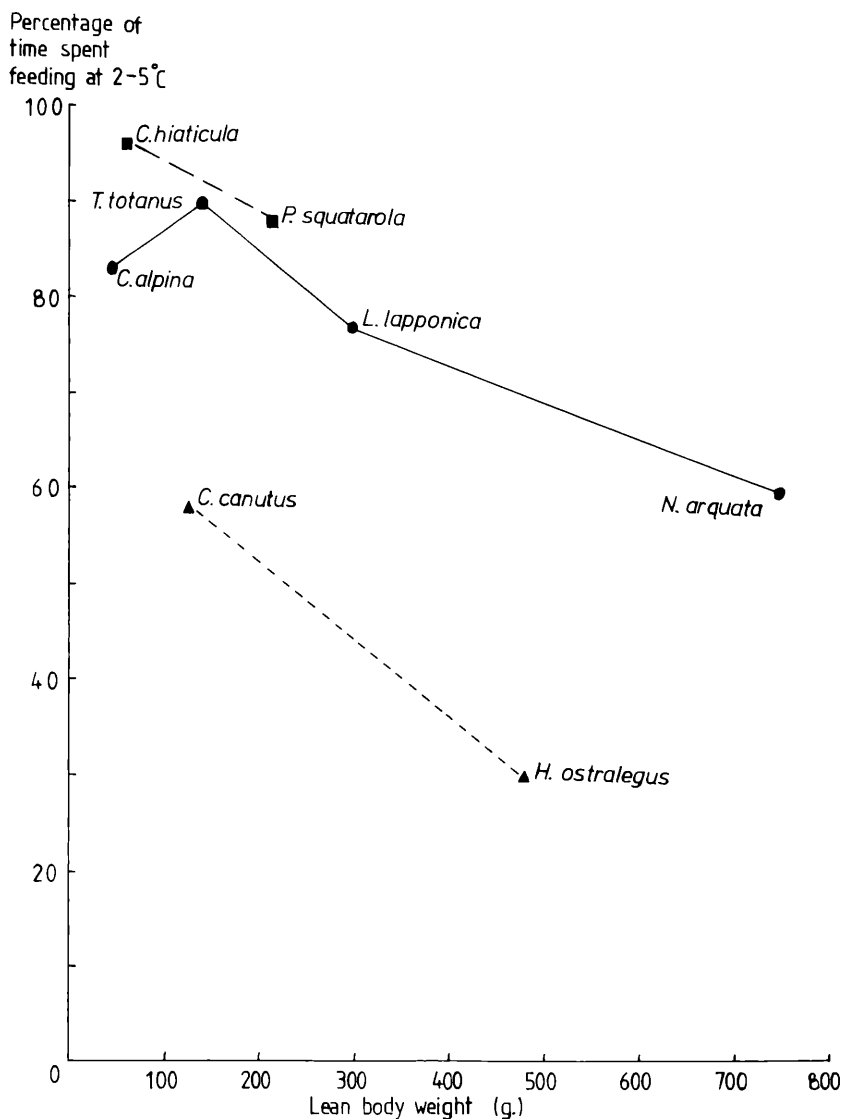
Figure 5.
The percentages of the daylight period spent feeding at Teesmouth in January and February 1973 by various species. (At this time, some intertidal area was available somewhere in the estuary at all states of tide.) ▲------▲ Mussel bed feeders, ●———● sandpiper strategists, ■ — — ■ plovers (source: PIENKOWSKI 1973 and unpublished).

large species tended to feed for shorter times than smaller ones. (This relationship appears to be fairly general and may arise because the energy requirements of birds are related to the three quarter power of body weight (see EBBINGE et al. 1975) and also because, at low temperatures, small birds may have increased food requirements due to the higher rates of heat loss per unit weight from small bodies than large ones.) Between groups, those feeding on exposed beds of mussels *Mytilus edulis* (where little searching is required) fed for the shortest time, sandpiper-strategists for longer, and plovers the longest. Because of the calculations involved in obtaining these values it is not possible to give confidence limits but the pattern was consistent at Teesmouth and in various other sites, such as the Wash (J. D. GOSS-CUSTARD, pers. comm.) and Lindisfarne (pers. obs.).

On cold days in mid-winter, plovers suffer reduced feeding rates (requiring long feeding times) added to long nights (which also lead to reduced feeding rates). There is then a greater chance that a bird using 'plover strategy' will become unable to balance its energy budget (net income minus requirement) on a cold day than will one using a 'sandpiper strategy' Elsewhere it has been shown that, within one species, the peak amount of winter fat reserves increases with increasing latitudes, and decreasing mean temperature. This suggests that fat is an adaptive "insurance" against the increased chance of meeting days on which it is not possible to balance the energy budget (LLOYD et al. in prep.). One might expect, by similar argument, that in a given situation in northern Europe plovers should carry more fat in winter than sandpipers of similar size. Data from the Wash (MINTON 1975) and Lindisfarne (EVANS & SMITH 1975) do indeed show that the two wintering plovers increase in weight by 30 % or more above the autumn and spring levels, whereas the increase in other species ('sandpiper-strategists') range from 10 % to 23 % (Table 2). In smaller samples, P. R. EVANS (unpublished) has confirmed that most of the increase in weight is due to fat.

	Estimated lean weight (g)	Midwinter weight addition (%)
Charadrius hiaticula	60	30 +
Pluvialis squatarola	210	31
Calidris alpina	47	21
Calidris alba	51	16
Arenaria interpres	105	17
Calidris canutus	130	22
Tringa totanus	140	16
Limosa lapponica	♂ 270 ♀ 330	10
Haematopus ostralegus	480	23

Table 2.

Mean midwinter weight increases in waders in eastern England (data from EVANS & SMITH 1975, MINTON 1975). Lean weights have been measured by body composition analysis for some species (EVANS & SMITH 1975, LLOYD et al. in prep., EVANS unpublished) and for other species are taken as the lowest monthly mean weight reached during the year. (This approximation is justified by comparison with those species for which analyses of body composition are available.)

A further possible method of preventing negative daily energy balance is to reduce requirements. This may be the reason why some Grey Plovers at the Wash (BRANSON & MINTON 1976) and the Waddenzee (BOERE 1976) arrest moult of their flight feathers in late autumn and complete the moult in spring. Most other species complete moult before mid-winter.

Clearly, despite all these possible compensatory adaptations, the northern limit of wintering of 'plover-strategists' is likely to be farther south than that of 'sandpiper-strategists'

A further factor may affect feeding opportunities. There is evidence that plovers may avoid feeding in areas of high densities of other feeding waders. This comes from three sources: (i) At Lindisfarne a negative correlation was found (P < 0.05) between the numbers of plovers and the numbers of other waders feeding in a study area. (ii) At Teesmouth Grey Plovers left the main feeding banks about 1 hour, and significantly (P < 0.001 on all occasions), before Bar-tailed Godwits and Curlews, long before the tide covered the area but just at the time that these other species moved into the area (PIENKOWSKI 1973 and unpublished). (iii) At Lindisfarne, after most Bar-tailed Godwits left in April, Grey Plovers, many of which remain until May, continued feeding on their main feeding banks until these were reached by the tide whereas earlier in the season they left these areas as Bar-tailed Godwits and even Dunlins moved into the area ahead of the advancing tide edge.

The reason for this avoidance, if real, is uncertain but it is possible that the presence of large numbers of other birds prevents full use being made of the plovers' potential catching area (area "watched"). This avoidance behaviour may be the reason that plovers tend to feed at higher tidal levels than sandpipers, which tend to concentrate at the tide edge where prey is generally nearer the surface (e. g. VADER 1964). This use of higher tidal levels may exacerbate the problems of plovers in cold weather as such areas are more liable to freezing and a covering of ice than lower ones.

Comparison of 'plover' and 'sandpiper' strategies

Most of the above considerations tend to favour the 'sandpiper strategy' rather than the 'plover strategy' What then is the advantage of being a plover?

The feeding of Grey Plovers and Bar-tailed Godwits on *Scoloplos* at various temperatures can be compared using values measured in the field (SMITH 1975, PIENKOWSKI 1978) and inserted in the two equations (1) and (2) given earlier. The feeding rates were measured by direct observation of feeding birds, as were the search and 'watch' areas, aided by the use of cine-photography. Prey density and the depth distribution were determined by sampling the substrate, and numbers of outflows per unit time measured by direct observation of the substrate. Taking, for example, the situation of 6°C at an area of 600 *Scoloplos*/m², the equations are:

Godwit: 1.6 *Scoloplos*/min
= 9 m² searched/min × 600 worms/m² × 0.52 in depth range × probability A
. . probability A of detection, selection and capture = 0.0006
Grey Plover: 7.5 *Scoloplos*/min
= 1.4 m² "watched" × 600 worms/m² × 0.14 appearing/min × probability B
. probability B of detection, selection and capture = 0.06

(The absolute values for numbers of prey taken per minute by the two species are not directly comparable as the *Scoloplos* taken are not necessarily of the same size.)

It could be argued that this difference of 1:100 between probabilities A and B was due solely to a preference by Godwits for *Arenicola* (which were being hunted concurrently), so that detected *Scoloplos* were not fully exploited. One would expect the component of probability A due to any such selection to increase (towards unity) as temperatures fell causing prey to become less available, and indeed, at 0°C, probability A had risen to 0.0016. However, this also applied to the 'plover strategy' as, at 3°C, the Grey Plover probability B had increased to 0.4 (also presumably due to increased probability of the birds' selecting detected prey). Further, although the Godwit probability A had risen as temperature fell, and this maintained *Scoloplos* intake at 1.5/min at 0°C (compared with 1.6/min above 3°C), it did not compensate for a reduction in *Arenicola* intake from 1.2/min to 0.05/min. In such a situation one might expect any further scope for increasing intake rate to be utilized. At the lower temperature of –4°C, *Arenicola* intake fell to zero and *Scoloplos* to 0.5/min but probability B probably did not reach 0.01 (although data on depth distribution of *Scoloplos* are not available for this temperature). Thus, although probabilities A and B both vary to some extent with temperature, the ratio between them appears to be maintained at the order of magnitude of 1:100. This also appears to apply to a comparison between two smaller species, Dunlin and Ringed Plover.

It would be desirable to compare the profitabilities of the two strategies at high tidal levels with low density but active prey. In such situations, however, sandpipers generally use at least some component of a 'plover strategy' so that direct comparisons are not easily achieved. An indication of the situation may be obtained by using values of search area and 'watch' areas-which seem to change little-from lower areas, and the ratio of probabilities of 1:100. We can then consider an area of low prey density of 50 surface-living prey per m² at high temperature so that all are surface active and, therefore, both within reach of sandpipers and available to plovers. In such a situation, the equations become:

Godwits:
9 m² searched/min × 50 prey/m² × 1 in depth range × probability of 0.001
= 0.45 prey/min
Grey Plover:
1.4 m² "watched" × 50 prey/m² × 1 appearing/min × probability of 0.1
= 7.2 prey/min

Thus 'plover strategy' is most effective when temperatures are high so that prey animals are active, causing a high proportion of those within the depth range of 'sandpiper strategy' to be also surface active and therefore available to a 'plover strategy' If this occurs where prey density is low, the 'plover strategy' is likely to be advantageous over the 'sandpiper strategy' The average densities at Lindisfarne of surface-living crustacea at high tidal levels approximate to the density of 50 animals/m² used above, and here Ringed Plovers are the commonest feeding waders while those Dunlins also present tend to use elements of 'plover strategy' Densities of *Arenicola* in the intertidal flats are rather lower than this and few are within reach of godwits at any one time, so that the effective density within bill-reach rarely exceeds 1 animal/m² However, a
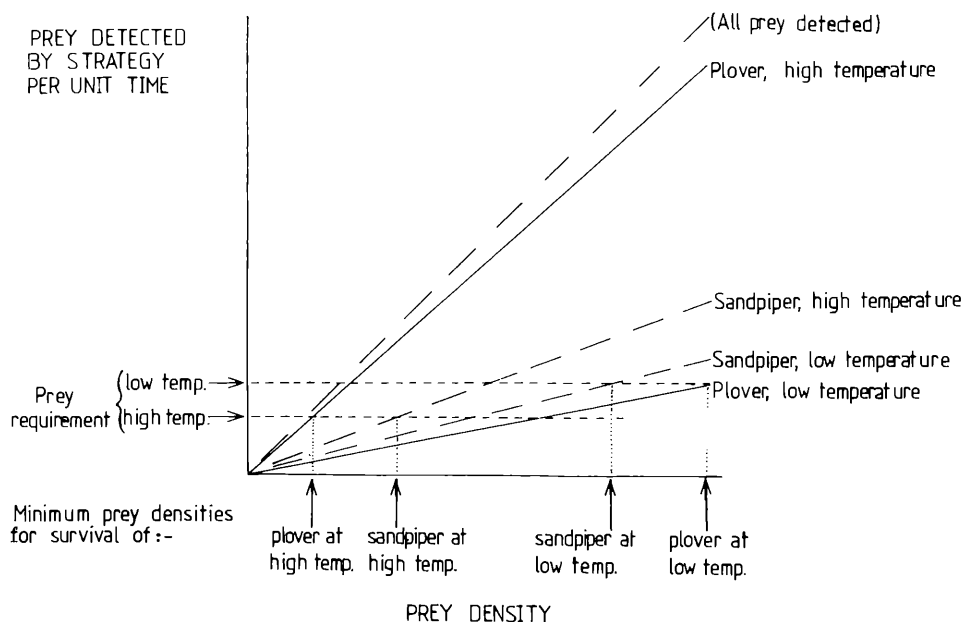
Figure 6.
Simplified schematic general comparison between plover and sandpiper feeding strategists. Prey detected takes into account both the numbers of prey within range of the various techniques and that proportion detected. For explanation of figure, see text.

high proportion of those within bill-reach probably also appear at the surface to defaecate, and both godwit and Grey Plover use a 'plover strategy' here.

The suggested system is generalized diagrammatically in Figure 6, where the numbers of prey detected at different temperatures by the two strategies are plotted against density of prey. If all prey are detected the line has a slope of 45°, and in some warm conditions the detectability to 'plover strategy' may approach this line. At lower temperatures, however, the numbers detected fall rapidly because of much reduced prey activity. The proportion detected by the 'sandpiper strategy' never reaches such high levels as that by the plovers because of the relatively low chance of detection by short-range tactile means, but the decrease in the proportion detectable with falling temperature is less rapid, as prey depth generally increases more slowly and at lower temperatures than prey activity decreases. Also shown in Figure 6 are two notional levels of the minimum number of detected prey required to fulfil energy requirements at two temperatures if all prey detected are taken. Where these levels are intersected by the lines of numbers detected gives, in this simplistic model, the minimum density of prey at which a particular strategy can operate for a bird in a particular temperature regime.

When further information on feeding rates, prey sizes and energetic values is available, it is hoped to develop this simple model so that approximate numerical values may be attached to some of the limiting densities. However, even from Figure 6, it can be seen that, provided that temperatures are high, 'plover strategies' can utilize lower

prey densities than 'sandpiper strategies' on, for example, sandy beaches (where the prey tend to be at low density, but near the surface and active) and the higher flats at low-water, as described above. In northern latitudes, however, these beaches and high flats tend to be deserted in mid-winter, when 'sandpiper strategists' can still utilize prey buried in the mud provided that this is at a fairly high density. In conditions of high density and high activity, both strategies should be effective, and this may be the situation on the breeding grounds of many species when insects are abundant. At intermediate levels of prey activity, however, sandpipers may restrict the distribution of plovers by the possible interference mechanisms discussed above.

'Plover strategists' are probably also at an advantage in areas of more compacted substrate where probing for prey becomes limited to those species with reinforced bills, such as Oystercatcher and Curlew (cf. Burton 1974). On the most compacted substrates feeding is possibly only on prey at the surface and the 'plover strategy' dominates, as used by, e. g., Golden Plover *Pluvialis apricaria* and Lapwing *Vanellus vanellus* on agricultural land-which is probably nearer to the evolutionary ancestral plover habitat. Of course, such terrestrial habitats in north temperate wintering areas are liable to freezing, and additional use of shore-feeding and cold weather movements are well known in these species (e. g. Dobinson & Richards 1964).

Plovers have also evolved techniques of increasing the availability of prey by foot-vibration. This appears to increase prey activity and/or stimulate movement from depth to the surface by a variety of mechanisms in different prey species (Simmons 1961, Sparks 1961, Pienkowski 1978).

Some implications for conservation

There are, of course, more specific habitat requirements and such factors as substrate particle size, salinity, wave-action, cover, prey distribution and distance from roosting site have been discussed by, e. g., Wolff (1969), Zwarts (1974) and Pienkowski & Knight (1977). Within the general framework of this paper we can, however, consider some of the conservation implications of distribution and habitat requirements apparently arising from feeding strategy, which has hitherto received little attention in this regard, apart from the recent paper by Evans (1976).

1. A first point, already obvious, is the need for a wide latitudinal spread in protected areas to allow for the different patterns in different species. The plovers, as a family, are heavily dependent on areas generally less closely watched by ornithologists and conservationists.

2. There are considerable differences in species composition between apparently fairly similar sites in the same general area. This is exemplified by the percentage composition by species of waders at the three main sites on the coast of Morocco, as reported by Blondel (1964). (Although later, less complete surveys have differed somewhat in totals counted, the general pattern remains the same.) Lapwing and Golden Plover were clearly restricted to the north where wet meadow habitat is present. The three shore plovers formed nearly half of the wader population at Sidi Moussa/Oualidia where the salt-pan and lagoon habitat may be equivalent to the

		MERJA ZERGA	SIDI MOUSSA/ OUALIDIA	PUERTO CANSADO
	Total population	322,000	11,500	105,000
		%	%	%
Charadriidae	Vanellus vanellus	14	0	0
	Charadrius hiaticula	3	22	7
	Charadrius alexandrinus	0.03	4	2
	Pluvialis apricaria	3	0	0
	Pluvialis squatarola	3	22	7
	Total Charadriidae	22	48	15
Seolopacidae	Numenius arquata	0.02	3	3
	Limosa limosa	31	0	0
	Limosa lapponica	0.02	0	6
	Tringa totanus	2	22	22
	Calidris canutus	0.02	0.9	10
	Calidris minuta	0.03	22	8
	Calidris alpina	43	5	30

Table 3.
Species composition of waders wintering at the three main sites in Morocco in January 1964 (data from BLONDEL 1964).

higher tidal levels of more natural wetlands. The next highest contribution of these species is at the predominantly sandy Puerto Cansado and least at the muddy Merja Zerga. As might be expected, the sandpiper species show a wide variety of distributional patterns but most nearly approaching those of the shore plovers is that of the Little Stint *Calidris minuta*. This species and the Sanderling *Calidris alba* appear to use a plover-type visual strategy, although much speeded and often involving continual motion, darting after small, active prey in and deposited by waves on the shore (see EHLERT 1964, BENGTSON & SVENSSON 1968).

There is, therefore, a need to conserve a range of sites within an area and the loss of one site is not necessarily compensated adequately by retention of others. This may have implications for the Ramsar Convention. It is also important to note the possibility that areas of relatively low wader numbers and densities may be particularly important to some species, notably plovers, which usually occur at lower densities than sandpipers.

3. The different feeding distributions within estuaries may also be relevant to conservation as, for example, higher tidal levels tend to be more liable to disturbance and reclamation. P. R. EVANS describes the partial reclamation of Teesmouth elsewhere in this volume. The species most badly affected by this was the Ringed Plover the wintering numbers of which were reduced to less than 10 % of former levels whereas corresponding values for other species ranged between 25 % and 100 %. Whether the greater reduction in numbers of Ringed Plovers was due to loss of the higher tidal levels, the reduction in potential feeding time, or increased density of other species is uncertain. That there were great differences between species is, however, clear.

	Peak Count 1971	Peak Count 1972 (as % of 1971)
Charadrius hiaticula	400	25 %
Pluvialis squatarola	75	16 %
Tringa totanus	250	14 %
Recurvirostra avosetta	245	13 %
Haematopus ostralegus	300	10 %
Calidris alba	400	8 %
Calidris canutus	100	5 %
Calidris alpina	1,000	5 %
Charadrius alexandrinus	250	5 %

Table 4.
Changes in autumn wader populations following the blocking of Oued Chebeika estuary (data from JOYES et al. 1977).

There can also be situations where plovers are least affected. The estuary of Oued Chebeika in south Morocco was blocked for about a year by the building of a bank carrying a road across the mouth (JOYES et al. 1977). While the estuary was effectively a lake the only remaining habitats suitable for waders were the water's edge on fairly low productivity sand, the shallow water and marsh. Those species least (but still heavily) reduced in numbers (Table 4) were Ringed and Grey Plovers which had utilized these higher areas before the road was built; more heavily affected were the marsh species, Redshank and Avocet *Recurvirostra avosetta*. Those decreasing most were the species of the lower intertidal flats, and also the Kentish Plover, the latter possibly because of the reduction in area, due to raised water level, of the zone not reached by most tides where it had previously fed.

4. Finally, it is worth noting that recent studies on the feeding of waders have taken place during a series of mild winters. As discussed above, reduction in temperature may make areas untenable for both families of shore waders, and in Europe in late autumn this may lead to onward movement to the south and west (though this does not seem to occur in response to a sudden onset of cold weather in mid-winter [EVANS 1976]). Some species may, indeed, require a sequence of sites in the non-breeding season. These could include autumn and spring moulting areas and migrational staging posts where birds could not spend the winter because the density of available prey falls too low each year; and wintering areas of milder climate. Here, even if prey density is lower-and possibly inadequate for fattening and moult of large populations-availability would remain higher. Comparable situations could apply on a local scale for waders not normally restricted to intertidal habitats, e. g., Golden Plovers and Lapwings, if food in some areas becomes temporarily unavailable. Such detailed movements of populations of waders are less easy to study than those of geese, mentioned elsewhere in this volume by R. DRENT, as more wader species and populations are involved and the flocks are not as discrete. Thus, information relevant to these final speculations cannot be obtained from observations alone and will require ringing studies on the occurrence and timing of short duration and short distance movements, and also studies on prey densities and availabilities to waders in different areas.

Summary

Although some species of both main families of waders breed abundantly at high latitudes, the main intertidal wintering ranges of the Charadriidae (plovers) do not extend as far north as do those of the Scolopacidae (sandpipers, curlews, snipes and their allies). Habitat differences also occur on a smaller scale, e. g. plovers tend to feed at higher tidal levels than sandpipers. This paper tries to account for these differences from the viewpoint of feeding ecology.

Plovers forage almost exclusively by using an apparently visual searching method. This involves long pauses and rapid runs to catch prey. Most sandpipers use at least some element of tactile searching. This difference arises not because they take different types of prey, since they frequently do not, but because they exploit in different ways the behaviours of the prey animals which make them temporarily available to the birds. The ways in which various factors, particularly temperature and prey density, may affect the feeding strategies and, through these, the birds' distribution patterns is explored, using in particular material from detailed studies at Lindisfarne National Nature Reserve in N. E. England.

Finally, some of the implications for conservation, resulting from the distribution patterns and general habitat requirements associated with these feeding strategies, are considered.

Zusammenfassung

Obwohl einige Arten der beiden wichtigsten Limikolenfamilien in großer Zahl im hohen Norden brüten, erstrecken sich die in der Gezeitenzone liegenden Überwinterungsgebiete der Charadriidae (Regenpfeifer) nicht so weit nordwärts wie jene der Scolopacidae (Schnepfen). Daneben gibt es auch kleinräumige Unterschiede: die Charadriidae z. B. haben die Tendenz, die Nahrung näher bei der Hochwasserlinie zu suchen, als die Scolopacidae. Die vorliegende Arbeit versucht, diese Unterschiede aus der Ernährungsökologie zu erklären.

Regenpfeifer suchen die Nehrung beinahe ausschließlich visuell (stehen, schauen und rennen, fangen), während die meisten Schnepfen die Nahrung wenigstens teilweise mit Hilfe des Tastsinnes suchen. Dieser Unterschied scheint weniger damit zu erklären, daß die beiden Familien sich auf verschiedene Beutetiere spezialisiert hätten, als vielmehr damit, daß sie sich verschiedene Verhaltensweisen der Beutetiere zu Nutzen machen. Es wird untersucht, in welcher Weise verschiedene Faktoren, vor allem Temperatur und Dichte der Beutetiere, die Methode der Nahrungssuche und damit indirekt auch das Verbreitungsmuster der Limikolen bestimmen. Dieser Teil der Arbeit stützt sich hauptsächlich auf eingehende Untersuchungen in Lindisfarne, einem nationalen Naturschutzgebiet in Nordostengland.

Zum Schluß wird diskutiert, welche Konsequenzen aus den verschiedenen Biotoppräferenzen, die offenbar weitgehend nahrungsökologisch bedingt sind, im Hinblick auf den Schutz von Limikolen und ihren Rastgebieten zu ziehen sind.

References

BENGTSON, S.-A. & SVENSSON, B. (1968): Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates.   Oikos 19: 152-157.

BLONDEL, J. & C. (1964): Remarques sur l'hivernage des limicoles et autres oiseaux aquatiques au Maroc (janvier 1964) Alauda 32: 250–279.

BOERE, G. C. (1976): The significance of the Dutch Waddenzee in the annual life cycle of arctic, subarctic and boreal waders.   Part 1. The functions as a moulting area.   Ardea 64: 210-291.

BRANSON, N. J. B. A. & MINTON, C. D. T. (1976): Moult, measurements and migrations of the Grey Plover.   Bird Study 23: 257-266.

BURTON, P. J. K. (1966): Food and feeding methods of Curlew, Golden Plover and Lapwing.   Ibis 108: 455.

BURTON, P. J. K. (1974): Feeding and the feeding apparatus in waders.   British Museum (Natural History), London.

DOBINSON, H. M. & RICHARDS, A. J. (1964): The effects of the severe winter of 1962/63 on birds in Britain.   Br. Birds 57: 373-434.

EBBINGE, B., CANTERS, K. & DRENT, R. (1975): Foraging routines and estimated daily food intake in Barnacle Geese in the northern Netherlands. Wildfowl 26: 5-19.

EDINGTON, J. M., MORGAN, P. J. & MORGAN, R. A. (1973): Feeding patterns of wading birds on the Gann Flat and river estuary at Dale.   Field Studies 3: 783-800.

EHLERT, W. (1964): Zur Ökologie und Biologie der Ernährung einiger Limikolen-Arten. J. Orn. 105: 1-53.

EVANS, P. R. (1976): Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season.   Ardea 64: 117-139.

EVANS, P. R. & SMITH, P. C. (1975): Studies of shorebirds at Lindisfarne, Northumberland. 2. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. Wildfowl 26: 64-76.

FALLET, M. (1962): Über Bodenvögel und ihre terricolen Beutetiere. Technik der Nahrungssuche und Populationsdynamik. Zool. Anz. 168: 187–212.

GOSS-CUSTARD, J. D. (1969): The winter feeding ecology of the Redshank *Tringa totanus*.   Ibis 111: 338-356.

GOSS-CUSTARD, J. D. (1970): The responses of Redshank *(Tringa totanus* [L.]) to spatial variations in the density of their prey.   J. Anim. Ecol. 39: 91-113.

GOSS-CUSTARD, J. D. (1977): The energetics of prey selection by Redshank, *Tringa totanus* (L.), in relation to prey density.   J. Anim. Ecol. 46: 1-19.

GOSS-CUSTARD, J. D., KAY, D. G. & BLINDELL, R. M. (1977): The density of migratory and overwintering Redshank, *Tringa totanus* (L.) and Curlew, *Numenius arquata* (L.) in relation to the density of their prey in south-east England.   Estuarine & Coastal Marine Science 5: 497-510.

HEPPLESTON, P. B. (1971): The feeding ecology of Oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland.   J. Anim. Ecol. 40: 651-672.

HEPPNER, F. (1965): Sensory mechanisms and environmental cues used by the American Robin in locating earthworms.   Condor 67: 247-256.

HOFMANN, H. & HOERSCHELMANN, H. (1969): Nahrungsuntersuchungen bei Limikolen durch Mageninhaltsanalysen. Corax 3: 7-22.

HULSCHER, J. B. (1976): Localisation of cockles *(Cardium edule* L.) by the Oystercatcher *(Haematopus ostralegus* L.) in darkness and daylight.   Ardea 64: 292-310.

JOYES, A. (1975): Puerto Cansado: Intertidal invertebrates and notes on the distribution and feeding of waders and Flamingoes.   pp 22-23 in PIENKOWSKI, M. W. (Ed.) Studies on coastal birds and wetlands in Morocco 1972.   Joint report of University of East Anglia Expedition to Tarfaya Province, Morocco 1972 and Cambridge Sidi Moussa Expedition 1972.   Norwich.

JOYES, A., KNIGHT, P. J., LEAH, R. T. & PIENKOWSKI, M. W. 1977.   The blockage of the Oued Chebeika estuary and its effects on the avifauna.   Bull. Inst. Scientifique Chérifien, Rabat (in press).

LANGE, G. 1968. Über Nahrung, Nahrungsaufnahme und Verdauungstrakt mitteleuropäischer Limikolen. Beitr. Vogelkde. 13: 225–334.

LLOYD, C. S., PIENKOWSKI, M. W. & MINTON, C. D. T. (in prep.): Seasonal and migrational weight changes in Dunlins *Calidris alpina.*

MINTON, C. D. T. (1975): The waders of the Wash-ringing and biometric studies.   Report of Scientific Study G of the Wash Water Storage Scheme Feasibility Study, to the Natural Environment Research Council.

NORLIN, Å. (1965): Zur Nahrungswahl von Limikolen in Schweden (Beobachtungsstation Ledskär). Vogelwarte 23: 97–101.

PIENKOWSKI, M. W. (1973): Feeding activities of wading birds and Shelducks at Teesmouth and some possible effects of further loss of habitat.   Report to Coastal Ecology Research Station, The Nature Conservancy.

PIENKOWSKI, M. W. (1978): Studies on aspects of the ecology and behaviour of Ringed Plover *Charadrius hiaticula* and Grey Plover *Pluvialis squatarola* (in prep.).

PIENKOWSKI, M. W. & KNIGHT, P. J. (1977): La migration postnuptiale des limicoles sur la côte atlantique du Maroc.   Alauda 45: 165-190.

PRATER, A. J. (1976): The distribution of coastal waders in Europe and North Africa. pp. 255-271 in SMART, M. (Ed.) Proc. 5th Int. Conf. Consrv. Wetland and Waterfowl, Heiligenhafen, 1974.

SIMMONS, K. E. L. (1961): Foot-movements in plovers and other birds.   Br. Birds 54: 34-39.

SMITH, P. C. (1975): A study of the winter feeding ecology and behaviour of the Bar-tailed Godwit *(Limosa lapponica).*   Ph. D. thesis, University of Durham.

SMITH, P. C. & EVANS, P. R. (1973): Studies of shorebirds at Lindisfarne, Northumberland.   1. Feeding ecology and behaviour of the Bar-tailed Godwit.   Wildfowl 24: 135-139.

SPARKS, J. H. (1961): The relationship between foot-movements and feeding in shorebirds.   Br. Birds 54: 337-340.

SPITZ, F. (1964): Repartition ecologique des Anatidés et Limicoles de la zone maritime du sud de la Vendée.   Terre et Vie 18: 452-488.

TAYLOR, I. (1977): Wader counts in coastal Ghana, December 1976.   Wader Study Group Bull. 21 (in press).

VADER, W. J. M. (1964): A preliminary investigation into the reaction of the infauna of tidal flats to tidal fluctuations in water level.   Neth. J. Sea Res. 2: 189-222.

WOLFF, W. J. (1969): Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms.   Ardea 57: 1-28.

ZWARTS, L. (1974): Vogels van het brakke getijgebied, ecologische onderzoekingen op de ventsagersplaten.   Amsterdam.