Energy Balance and Optimal Foraging Strategies in Shorebirds: Some Implications for Their Distributions and Movements in the Non-Breeding Season

Author: Evans, P. R.

Source: Ardea, 55(1–2) : 117-139

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v64.p117

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Ardea on 01 Mar 2025
Terms of Use: https://bioone.org/terms-of-use

ENERGY BALANCE AND OPTIMAL FORAGING STRATEGIES IN SHOREBIRDS: SOME IMPLICATIONS FOR THEIR DISTRIBUTIONS AND MOVEMENTS IN THE NON-BREEDING SEASON

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

CONTENTS

1. INTRODUCTION

This paper is an attempt to relate the studies and results of four discrete groups of research workers: those recording the distribution of shorebirds (chiefly Charadriidae and Scolopacidae), particularly in western Europe; those studying the foraging behaviour of chosen species; those modelling optimal foraging behaviour and testing their predictions in laboratory situations; and those measuring energy budgets and fat reserves of birds, both in the laboratory and in the field. Any attempt to cover so many topics in one paper is bound to lead to superficial treatment of any one subject. The reader is warned, therefore, not to expect a comprehensive review, but rather a descriptive framework within which detail can be fitted later. In many cases, detailed observations or measurements are unavailable, and parts of the framework sketched in this paper remain theoretical and speculative. To illustrate general principles, I have drawn heavily on the studies (many as yet unpublished) of my past and present research students; their contributions are acknowledged in the text. Most of our fieldwork has been undertaken at two sites in northeast England: the Lindisfarne National Nature Reserve in Northumberland (approximately 55° 40′ N, 1° 50′ W) and the estuary of the River Tees (approximately 54° 35′ N, 1° 35′ W). Nine species of waders occur there in winter in sufficient numbers to permit detailed studies. They are Oystercatcher *Haematopus ostralegus*, Grey Plover *Squatarola squatarola*, Ringed Plover *Charadrius hiaticula*, Curlew *Numenius arquata*, Bar-tailed Godwit *Limosa lapponica*, Redshank *Tringa totanus*, Knot *Calidris canutus*, Dunlin *Calidris alpina* and Sanderling *Crocethia alba*. Hence, most of the examples discussed in this paper refer to these nine species.

In the last decade, there has been increasing awareness of the need to find out the geographical distribution and migration patterns of those bird species which spend their non-breeding seasons on coasts and estuaries, since these habitats are relatively restricted in area and are particularly vulnerable to various forms of development and industrialization. As a result of the initiative of the International Waterfowl Research Bureau, counts of shorebirds have been made recently in many parts of Europe and north Africa, and several countries have developed their own schemes, involving counts at regular intervals throughout the year. From these, in conjunction with the results of extensive ringing of shorebirds, patterns of distribution and movement are beginning to emerge for several species, and even for discrete breeding populations within a species. What is not clear, however, is the extent to which the geographical distributions, being mapped now, follow the outer limits within which different species could survive during the non-breeding seasons. Migrant species probably will not fly further from their breeding areas than they must to reach suitable "wintering" sites, but are all suitable sites occupied at present? If so, the implications of further loss of estuarine habitat for the conservation of shorebird populations are clear, unless methods can be found to increase the "carrying capacity" of the areas that remain. Discussion of the ways in which numbers of birds might be adjusted to their resources in a particular site will not be included here; the problem is discussed elsewhere (Zwarts, this volume).

In this paper, I shall explore the role of environmental, chiefly climatic, factors in limiting the geographical distributions of different shorebird species. To survive in an area, an animal must be able to balance its energy income (from food) against its energy expenditure over a certain time-period. For shorebirds, as discussed later, this period is of the order of days. I shall be concerned, therefore, with the ways in which some physical factors of the environment reduce a bird's chances of achieving a daily energy balance, either by reducing its feeding time or rate of energy intake, or by increasing its energy expenditure, or by all three routes. These physical factors may directly affect the bird's foraging behaviour and/or physiology, and they may also act indirectly on the invertebrate prey species, to make them more or less available to their shorebird predators. I shall also speculate on adaptations which birds might use to reduce their daily energy expenditure under conditions of food shortage. Throughout this paper, the overriding importance of availability of prey, rather than total numbers or density of prey, will become apparent.

Most shorebirds carry measurable energy reserves in the non-breeding season, in the form of fat. These reserves may be used either to make up a deficit in the daily energy budget, or for movement. It will be obvious that, if a bird is faced by bad feeding conditions, the longer it stays in one site awaiting improved conditions, the less far it will be able to fly to search for better conditions elsewhere. Another aim of this paper is to identify those situations in which different species of shorebirds move from one estuary to another within their potential "wintering" range, on the assumption that they may do so in response to failures to balance their daily energy budgets. The proximate factors stimulating such movements need not be the same as those which time their autumn departures from the northern breeding grounds. As in many passerines, which leave their Palaearctic breeding grounds in autumn before their foods become scarce, the main migration periods for waders may be timed endogenously, by circannual rhythms (for passerines, see Gwinner 1972). Arguments based on failure to balance daily energy budgets will not, of course, reveal the reasons for local shifts in feeding areas, arising from changes in relative availability of prey in, and hence relative profitability *(sensu* Royama 1970) of, such areas. However, for an understanding of more extensive movements, a discussion of factors affecting energy balance seems as good a starting point as any.

2. FACTORS WHICH INCREASE THE DAILY ENERGY REQUIREMENTS

In the non-breeding season, a shorebird needs energy for three main purposes (1) to maintain its body temperature and normal metabolic processes, including digestion, (2) to fly, to and from its feeding grounds, and possibly to escape predators, and (3) to cover the costs of food gathering. Its energy requirements might increase beyond its capacity to satisfy them from food gathered on the same day, by an increase in any or all of the three components of its daily energy expenditure.

(1) A bird may require more energy to maintain its normal body temperature if the rate of heat loss from its body surface increases. In the thermoneutral zone, muscular adjustments of feather positions allow the insulative capacity of the plumage to be altered to balance changes in the rate of heat loss at different air temperatures. However, when the air temperature drops below the lower critical temperature, metabolic rate, and therefore energy requirements, increase. The contribution of this factor to the energy budgets of wintering shorebirds has not been measured. In the Yellowhammer *Emberiza citrinella,* a passerine which winters inland throughout northwest Europe, metabolic rate increases by almost one-third for every 10°C decrease in ambient temperature below the lower critical temperature of 25°C (Wallgren 1954). The lower critical temperatures of different shorebird species are not known, but it seems likely that most waders wintering in Europe north of the Mediterranean will experience midwinter temperatures which lie below their thermoneutral zones.

Heat loss is also accelerated by forced convection caused by wind. Again, nothing is known of the magnitude of such heat losses from shorebirds exposed to different wind speeds, but they could be considerable, since flying birds rely chiefly on forced convection to remove the heat produced by the pectoral muscles. Indeed, the rate of heat loss through skin and feathers, tested in a wind tunnel, could be almost doubled by wind speeds approximating to normal flight speeds (Hart & Berger 1972). Similarly, metabolic rates of living Snowy Owls almost doubled when wind speed rose from calm to 9 m/sec at temperatures of —20° and —30°C (Gessamann 1973).

(2) Large day-to-day changes in energy needed for flight seem much less likely than daily changes in energy expenditure to counteract heat loss. In the longer term, during the course of a winter, shorebirds may be forced to fly further from their roost sites to feeding grounds, if they deplete the food resources close to the roost. Hamilton *et al.* (1967) provided a model for radial dispersal from a roost to feeding areas, in which they suggest that the disadvantage of a long flight to a distant feeding site, in terms of time lost for feeding and extra energy expended in getting there, is balanced by the advantage of a reduction in intraspecific competition at the distant site. This allows a higher feeding rate. Zwarts (1974) has applied similar arguments to waders in the Netherlands, but he does not discuss why those waders feeding on the flats furthest from the roost did not form another roost, nearer to their feeding areas. Are good roost sites for waders in short supply? Or would birds which formed a breakaway roost be at a disadvantage with respect to any information-transfer function of the roost (Ward & Zahavi 1973)? Whatever the answers to these questions, it seems unlikely that shorebirds allocate markedly different amounts of energy to flight between roost and feeding grounds on successive days.

(3) In contrast, the energy costs of food gathering may increase considerably and suddenly for a variety of reasons. (a) If prey become scarce, either because their density has been reduced by predation, or because they become less available (for reasons discussed below), a bird will take longer to find a given quantity of food, and will therefore expend more energy in finding it. (b) Waders which feed at the tide edge may have to spend more energy in foraging when wave action is more severe. This will be true if they follow each wave as it advances and retreats up and down the beach, so that they may feed in a particular depth of water. Species affected by wave action include Bar-tailed Godwits, which often feed in water up to 15 cm deep, and Sanderling, which feed in very shallow water, particularly on the ebbing tide. (c) Strong winds may also increase the energy costs of foraging. Under such conditions, many waders feed with their heads pointing partly into the wind, but if they need to feed along the tide edge, they may well have to compensate for a cross-wind component. Even away from the tide-edge, strong winds can interfere with the typical "run-stop-peck" feeding movements of plovers by restricting the directions or speeds of their runs. Strong winds may also increase the energy needed by a bird to maintain its orientation and position relative to other birds feeding in a flock. Finally, (d) the energy costs of food gathering may be affected by the type of substrate in which the bird is searching. To maintain the same rate of

progress through fine mud as over sand must surely require increased energetic costs. Whether this situation is made worse at low temperatures is not known. Although the viscosity of mud might then increase, a bird walking over it might not sink in so far, as is obvious when the extreme condition of frozen mud is considered. Information relevant to the effects of temperature on walking rate, as mediated by substrate, is limited. At Teesmouth, in both the spring and autumn of 1973, Dunlin increased significantly the number of paces they made each minute as mud temperatures decreased (Pienkowski 1973, Knights 1974). It is unlikely, therefore, that the energy costs of walking through the mud were higher at lower temperatures. The effects of higher temperatures, which might make mud less viscous but promote drying of the surface-layer, are likewise uncertain.

Many of the processes which contribute to increased daily energy requirements are affected simultaneously by changes in a particular physical factor in the environment, e.g. lowering of temperature. The combined effects of changes in such physical factors will be summarized later, together with a consideration of the time-scale on which they operate.

3. FACTORS WHICH REDUCE THE RATE OF FOOD INTAKE

Birds may fail to achieve a neutral daily energy balance because, under certain circumstances, they cannot collect as much food as normal, and not only because their food requirements are sometimes raised. Reduced daily food intake may arise through a reduction in prey availability, or through a reduction in the capacity of the predator to hunt effectively, even though prey availability remains unchanged.

Predators hunting by sight are less effective at night. Indeed, most passerines do not try to forage at night, but roost during the hours of darkness. Feeding opportunities for waders, however, are governed largely by the tidal cycle, and many species feed by night as well as by day. At night, they may be able to feed by sight in areas where phosphorescent prey of suitable size are available. For example, Redshank have been recorded to take opossum shrimps (Mysids) at night (Goss-Custard 1969). But most waders change their feeding behaviour by night and appear to hunt by touch. This may not be as effective as hunting by sight, for reasons discussed later. For example, Grey Plover feeding chiefly on the ragworm *Nereis diversicolor* at Teesmouth made on average only 3.5 pecks/minute at night, compared to 5.5 to 5.8 pecks/minute by day on the same mudflat. Also at Teesmouth, wintering populations of five species, Grey Plover, Curlew, Bar-tailed Godwit, Redshank and Dunlin, fed less extensively by night than by day: fewer birds were present by night in each preferred daytime feeding site, and those present at night usually fed for a shorter portion of the tidal cycle than by day (Goss-Custard, Evans *et al.* in press). These instances suggest that most waders feeding in the intertidal zone feed more effectively by day and will therefore find it more difficult to obtain a given quantity of food in December, when hours of daylight are shortest, than at other times of year. They will also have more difficulty in feeding effectively when high tides cover the feeding grounds in the middle of the day rather than in the morning and evening. This second constraint will not apply to those species which can feed even at high water e.g. along the strand line. However, at night this habitat would seem less suitable than the intertidal zone for a bird hunting by touch, since many of the potential prey, e.g. Diptera and amphipods, are mobile. One of the chief species to exploit the strand line is the Turnstone *Arenaria interpres.* Unlike most waders, Turnstone always roost at night (M. Becuwe, D. Brearey, W. Marshall pers. comms.), even in mid-winter, but whether this implies that they are unable to feed by night, or have no need to, is not clear.

Even by day, circumstances may arise which reduce the efficiency of a predator hunting by sight. Bar-tailed Godwits feed on lugworms *Arenicola marina* in several of their major wintering areas. They detect these when the lugworms back up their L-shaped burrows to defaecate; cast formation is obvious and takes several seconds. Godwits become progressively less successful at detecting the formation of new casts in an area, the longer the time after the area has been uncovered by the ebbing tide, since the sands become more thickly covered with casts, and the background "noise" against which the cue must be detected is thereby raised (Smith 1975).

Shorebirds feeding in water face two additional difficulties if they search for visual cues to the presence of prey. Firstly, strong wave action stirs up sediments which may obscure signs of, e.g., prey emerging from a burrow in the substrate, or swimming. Secondly, birds which feed with their heads above the water surface have to overcome the problem of the change in refractive index between air and water, which leads to distortion of the location of a potential prey, unless it is viewed from directly overhead. This problem is augmented by wind action, which makes the surface of the water choppy.

Predators hunting by touch avoid these restrictions on hunting efficiency, but the area they can search thoroughly is much smaller than can be searched by sight in the same time. Also, they cannot both search and handle prey at the same time, whereas this is possible for predators hunting by sight. Hunting by touch will therefore be effective only if prey are fairly uniformly dispersed and the density of available prey is high. Its effectiveness would be improved if birds were able to detect a prey item not only by hitting it with the bill, but also by feeling the position of, for example, a burrow, by changes in the resistance provided by the substrate to bill movement in different directions. However, Oystercatchers detect cockles *Cerastoderma edule* only by direct contact between bill and bivalve (Hulscher, this volume).

Little has been written of the possibility that waders could detect prey by sound. Perry (1945) claimed that the feeding movements of Grey Plover ("run-stop-peck") allowed the birds to listen for worms near the mud surface. But if this method of hunting is used, it is limited probably to foraging away from the tide edge. Even then, the sounds of strong winds, or breaking waves even several hundred metres away, would probably be sufficient to mask the sound of invertebrate activity. On calm nights, movements of sandhoppers (*Talitrus* and *Orchestia* spp.) are certainly audible and could provide cues for feeding shorebirds. Laboratory experiments convinced Lange (1968) that plovers use acoustic cues to localize prey.

4. FACTORS WHICH REDUCE THE AVAILABILITY OF PREY

Even though the sensory pathways used by a shorebird to hunt its prey may be able to work at their maximum effectiveness, the bird may well not be able to maintain its normal rate of prey capture if the prey become less available. As a result of predation itself, the number of potential prey present in a given area will be reduced progressively, and this will lead eventually to a fall in the rate of prey capture. But even if prey density in the substratum could be held constant, the availability of prey to a bird could be altered by external conditions, in the following ways.

Many intertidal organisms living in sand or mud move or burrow to greater depths within the sediment as its temperature falls. Some potential prey species normally live beyond the reach of the beaks of short-billed waders such as plovers, even at moderate substrate temperatures of 10-15°C. At lower temperatures, a few degrees above freezing point, many annelids and bivalves stay out of range of even a Curlew's bill, i.e. at a depth of more than 15 cm. Low temperatures may decrease the availability of such prey in another way. Although several species, e.g. *Arenicola* and *Nereis diversicolor,* normally live at depths beyond the reach of shorebirds' bills, nevertheless they are regular items of the diet of several species. The birds can obtain the worms only when they come to the surface to feed, irrigate or defaecate. At low substrate temperatures, they become less active and thus less often available to the predator. Thus the density of available prey at any moment in time is reduced.

High temperatures may also reduce prey availability. Intertidal invertebrates living in soft sediments may again move to greater depths, in this instance to avoid dessication; some of those living on rocky shores seek shelter or deep pools when the tide ebbs. Animals living in sandy substrata may become less active during the low water period on windy than on calm days, as the sand then dries out more rapidly. Lugworms have been shown to defaecate less often on windy days (Smith 1975), thereby presenting cues less frequently to foraging Bar-tailed Godwits.

Shorebird prey may also become less available in response to the presence of their predators. The crustacean *Corophium volutator* emerges less often from the top of its burrow when Redshank are walking over the mud surface nearby (Goss-Custard 1970). This cause of a reduction in prey availability will be particularly important to shorebirds feeding by sight.

On the other hand, the predator may force the prey to show themselves. This may be the function of foot-paddling in plovers; such behaviour can disturb small crustacea in the upper layers of sandy sediments (M. W. Pienkowski, pers. comm.).

The position and activity of intertidal invertebrates is also governed endogenously in some species, in relation to the tidal cycle. For example, the crustacean *Bathyporeia pilosa* is most active on the ebbing tide (Preece 1971) and may then form an important food of the Sanderling *Crocethia alba* which often feeds in shallow water at the tide edge, pursuing the retreating waves.

Thus the availability of prey can have major influences on the rate of food intake; but how far particle size of the substrate from which a prey has to be extracted may modify this rate is not known.

5. FACTORS WHICH REDUCE POTENTIAL FEEDING TIME

Feeding time may be limited by the extent of the tidal range interacting with the intertidal distribution of suitable prey. Many invertebrate species are common only below the mid-tide level, and may therefore be exposed for relatively short periods in each tidal cycle. In those species which reach their highest densities subtidally, lower densities are exposed to predation on neap than on spring tides. Indeed, some preferred prey, such as the sand-mason worm *Lanice conchilega* taken by Curlew and Bar-tailed Godwit, may be exposed only at low water on spring tides. There is also a possibility that some intertidal animals normally living at fairly high tidal levels may move to lower intertidal or even sub-tidal levels during neap tides. Evidence for movements of this type in *Arenicola* has been provided by Darby (1975). Movements to lower tidal levels, associated with cold weather, are known for many marine invertebrates.

6. THE INFLUENCE OF PHYSICAL FACTORS ON ENERGY BALANCE

From the previous sections, it is clear that four major features of the environment affect the chances of a bird achieving a neutral energy balance if it feeds in the intertidal zone. These are wind, tide, daylength and temperature.

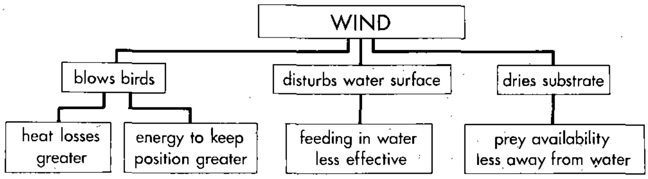

Fig. 1. Effects of wind on feeding and energy requirements of shorebirds.

Some direct consequences of wind action are summarized in Fig. 1. Although little is known of the magnitude of the effects caused by different wind speeds, one would predict that to avoid negative energy balance on windy days, shorebirds should feed in sheltered areas even though these may not hold the highest densities of their preferred prey. In so far as particular prey species become less active in a dry substrate, their shorebird predators would be expected to feed closer to the tide edge on windy days. Such behaviour has been recorded in Bar-tailed Godwits feeding on *Arenicola marina* (Smith 1975). However, an upper limit may be set to the closeness of packing of birds along the tide-line, not only because one bird may reduce the availability of prey to another (by removing prey or causing them to cease activity temporarily) but also through an increase in aggressive interactions which reduce potential feeding time. In plovers, which usually feed away from the tide edge and further apart from each other than sandpipers, the reduction in food intake in windy conditions can be considerable. For example, a colour-marked Grey Plover was watched at Teesmouth on two days of similar temperature in early April; on one, the wind was blowing at about 8m/sec, on the second at about 13m/sec, gusting to 20m/sec. This bird fed on the same site on both days, and observations were made at the same stage of tide, about two hours before low water. On the less windy day, the bird made an average of 3.9 attempts to take prey each minute, and 47% were successful; on the more windy day, it managed only 1.9 pecks at the mud each minute, and only 39% were successful. The reduction in biomass intake was not as severe as these figures suggest, as the plover took a higher proportion of large prey *(Nereis diversicolor)* on the windier day, namely 70%, as opposed to 35% on the less windy day (D. J. Townshend pers. comm.).

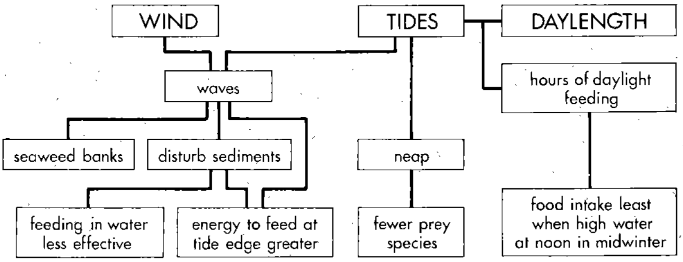

Fig. 2. Combined effects of daylength, tides and waves on feeding of shorebirds.

Some interactions of wind, tide and daylength which affect a shorebird's chances of achieving neutral energy balance are shown in Fig. 2. As mentioned earlier, the alternation of spring and neap tides alone may determine the range of prey species and the time for which they are available to a bird. Because of movements of some prey species, particularly in association with seasonal changes in temperature, the variety of potential prey may alter seasonally. On a much shorter time scale, strong onshore winds may delay the rate of ebb of a particular tide, and even prevent exposure of the lower intertidal zones on a particular day, thereby restricting to sub-optimal feeding areas, temporarily, those birds whose prey is most abundant in the lower zones.

The interaction of wind and tide to produce waves also leads to less favourable feeding conditions. Wave action is most severe with onshore winds, and increases with the time for which the wind blows from a particular direction, and with the fetch, the distance of open water over which the waves travel to the coast (see, for example, Darbyshire & Draper 1963). The extent of movement of the water's edge, when waves break, will depend partly on their height and partly on the time between successive waves. The gradient of the beach is also of importance. In places where wave action is often severe, beaches tend to shelve steeply and to comprise either rocks or coarse-grained sands. The surface layers of any such sediments are shifted regularly, and sedentary invertebrates living in them bury deeply. Those living on the rocks attach themselves firmly or live deep in fissures in the rocks. The variety of prey species available to shorebirds in these sites is therefore more limited than in normally sheltered bays or estuaries. Wave action often persists for hours or even days after the winds which generated the waves have moderated. In these cases, the severity of wave action in different possible feeding sites within an area would be expected to determine the day-to-day distribution of those shorebird species which feed at the tide edge or in the water. The effects of waves on foraging success may override the effects of variations in the density of preferred prey amongst the sites.

The importance of daylength in affecting the chances of a bird achieving a neutral energy balance depends on the relative success of foraging by day and by night. This in turn depends on the range of feeding methods available to the bird, the suitability of such methods for catching the range of prey present in an area, and on any differences in behaviour (and therefore availability) of the prey by day and by night (Vader 1964). Many species of shorebirds are remarkably plastic in the range of feeding methods they are able to employ, and hence in the variety of habitats they can utilize. Bar-tailed Godwits, for example, can pick food from hard surfaces such as coral reefs, probe into sand to obtain polychaetes and bivalves, or swish their bills from side to side through soft mud or water to seive out annelids (Evans 1975). At Teesmouth, even Grey Plover have been found to modify their normal feeding method, and to pick up a succession of small food items (probably *Hydrobia ulvae)* at each stop, rather than just a single item as is their normal practice (Evans *et al.* in press). However, the range of feeding methods used by night is usually less than by day, as would be expected if visual searching is not effective at night. Little is known of the behaviour by night of those prey species which are favoured foods by day of different shorebird species. Many crustacea, tested under laboratory conditions, are more active by night; for example, the shore crab *Carcinus maenas* (Naylor 1965). However, activity patterns in the field may bear little resemblance to those seen in the laboratory, as shown by Smith (1975) for *Arenicola marina*. Very few measurements have yet been made of shorebird foraging behaviour by night for comparison with those made by day for the same species in the same feeding areas. Not until these are available will it be possible to quantify the importance of the reduction in daylength during the autumn to the ability of birds to balance their daily energy budgets. However, it is of relevance that the energy (fat) reserves of Bar-tailed Godwits in mild winters are highest in December, when days are shortest, rather than in January when temperatures tend to be lowest (Evans & Smith 1975). This suggests that if weather conditions deteriorate, birds may be least able to meet increased energy demands when daylight foraging times are least (other things being equal), and then need to draw most heavily on their fat reserves.

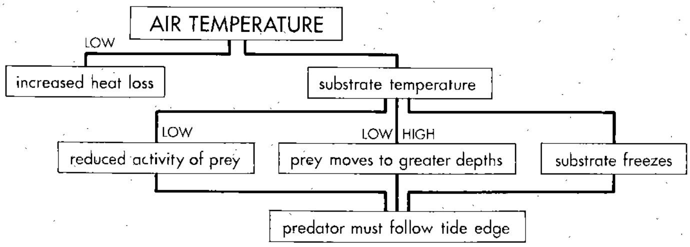

Fig. 3. Effects of temperature on feeding and energy requirements of shorebirds.

The routes by which temperature affects a shorebird's energy balance are summarized in Fig. 3. Energy requirements will increase most rapidly on cold, windy days; prey availability on sandy or muddy intertidal areas will be least when the surface of the exposed substrate freezes. At such times, sea temperature will normally remain above the substrate temperature and feeding will be possible chiefly at the tide edge, or in areas recently uncovered by the retreating tide. Birds will also do best to feed in these locations whenever the sea temperature exceeds the air temperature, even if the sediments do not freeze when uncovered by the tide, for prey activity and availability will be greater in areas of higher substrate temperature, namely those covered by seawater.

As air temperatures increase well above freezing point, up to a shorebird's lower critical temperature, energy requirements for maintenance will decrease, but again the bird may have to spend more energy in foraging unless it restricts its activities to the tide edge. In these cases, sea temperature is less than air temperature and prey are more available in situations in which they do not face the danger of dessication. On Heron

Island, at the southern end of the Great Barrier Reef, off the Australian coast, seawater temperatures are regularly above 20°C and air temperatures even higher during most of each day. Oystercatchers feeding on the bivalve *Atactodea striata,* which is found just below the sand surface, like the European cockle, closely followed the retreating tide when foraging (Evans 1975). At no time did they feed on open sandflats, as Oystercatchers sometimes do in winter in Britain and the Netherlands when hunting cockles. Presumably the coral sands on Heron Island dried very quickly and caused the bivalves to close their shells or burrow more deeply, thereby becoming unavailable to the Oystercatchers.

7. OPTIMAL FORAGING STRATEGIES IN SHOREBIRDS — SOME ENERGETIC CONSIDERATIONS

So far, the discussion has considered those circumstances in which energy balance in shorebirds is put in jeopardy by processes over which a bird has no control. It has, however, the opportunity to choose between different methods of foraging under each set of environmental conditions — or to choose not to forage at all. Many discussions of optimal foraging strategies have not made explicit whether the predator is meant to be maximizing the rate of food intake or the rate of net energy gain. The two are not synonomous, for (i) only part of the food eaten is assimilated, and this proportion may vary according to the rate of food intake, and (ii) the energetic costs of foraging by different methods can differ considerably. In the section which follows, I shall consider only rates of gain of net energy, that is energy assimilated from food less energy used to gather that food.

Figure 4 presents a graphical model of the rates of energy assimilated and energy available for maintenance, under two conditions of prey availability (plentiful and scarce), resulting from two possible feeding methods, A and B. A is an energetically costly method of collecting food, B less so. When prey are plentiful, method A is more effective than method B in terms of the rate of net energy gain, and the feeding time required to provide an energy gain equal to the daily maintenace energy is less than by method B. When prey are scarce, however, the relative effectiveness of the two methods are reversed. Note that the energy costs per unit time of gathering food by a particular method are considered to be independent of the level of prey availability. All that is required to make method B more effective as prey become scarcer is that the rate of prey capture by method A should decrease more rapidly than that by method B.

It seems probable that a change in foraging behaviour from an energetically more costly to a less costly method of food gathering occurs in the Bar-tailed Godwit when feeding conditions become difficult. At substrate temperatures above 3°C, their prey at Lindisfarne comprises chiefly *Arenicola marina,* whose availability is unaffected by temperature in the

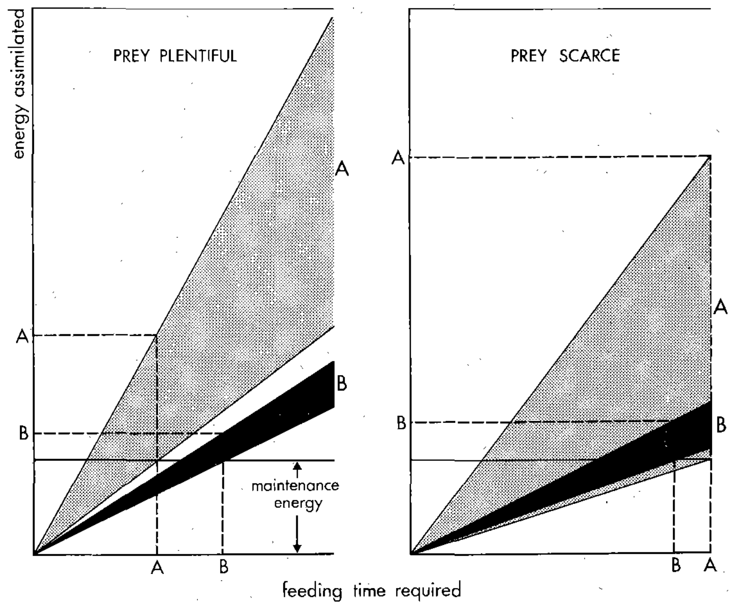

Fig. 4. Models of energy partitioning for two foraging methods, A and B, under two conditions of prey availability, plentiful and scarce. For each method, the steeper boundary line indicates the rate at which energy is assimilated from food gathered, and the flatter boundary line the rate at which energy is available for maintenance. The vertical distance between the two boundary lines represents the energy expended in foraging by that method. A much higher proportion of the energy intake is used to cover the costs of the energetically expensive foraging method A than to cover the costs of method B. When prey availability declines, the rate of intake (and assimilation) of energy decreases by both foraging methods, but more severely by method A. The rate of use of energy for foraging is unchanged. Letters on the horizontal and vertical axes of both diagrams indicate, respectively, the feeding times and energy intakes required to satisfy the maintenance energy requirements by the two foraging methods.

range 3-10°C (Smith 1975). In the wild, under such conditions, Godwits eat a biomass of worms each day equivalent to between 5 and 6 times their daily basal metabolic rate. In captivity at similar temperatures, each of two Godwits ate a biomass of *Calliphora* larvae equivalent to only 3 times their daily basal metabolic rate. Hence, birds in natural conditions expend almost as much energy in gathering food as in staying alive. To do this, they search an area of between 9 and 10 m^2/min for those *Arenicola* forming casts at the sand surface. As temperatures fall below 3°C, *Arenicola* become progressively less active, and therefore less available to Godwits, yet the birds search progressively smaller areas (Smith 1975). The most plausible explanation is that the Godwits are reducing foraging costs by walking more slowly, and Smith's data show that they are in fact taking a much higher proportion of small prey, the polychaete *Scoloplos armiger,* in their diet at low substrate temperatures.

The model presented in Figure 4 predicts that the switch in feeding method from A to B, to maximize the rate of net energy gain, should occur at a prey density at which the rate of assimilation of energy, and therefore of biomass intake, by method A is still considerably higher than by method B. At first sight, this is a surprising prediction; so also is the prediction that, under some conditions, it might be energetically more favourable for a shorebird not to forage at all, even though it could manage to obtain prey at a measurable rate. If a species was restricted to a single feeding method (A in Fig. 4), halving the maximum rate of prey capture, as a result of adverse feeding conditions, would provide insufficient energy to cover the costs of foraging, and the rate of net energy gain would become negative. Instances of shorebirds staying on the roost throughout potential feeding periods have been recorded in very cold weather (Oystercatchers in the Netherlands — J. B. Hulscher, pers. comm.) and during gales (Bar-tailed Godwits at Lindisfarne — Evans & Smith 1975).

There may be other energetic advantages in not feeding if the rate of food energy intake would be only slightly greater than the costs of feeding. Energy is needed for food processing, and Westerterp (1976) has shown that in laboratory rats kept at temperatures within their thermoneutral zone, and fed *ad libitum,* this energy cost makes up 11-15% of the total metabolic rate. Such energy costs could be saved if animals switched to use of energy reserves, but the percentage saved would presumably be less at temperatures below the thermoneutral zone, since maintenance energy requirements, and therefore total metabolic rate, will increase under such conditions.

Westerterp (1976) also found a decrease in core (deep body) temperature in rats kept at temperatures within their thermoneutral zone but deprived of food for a few days. He estimated that this drop in temperature might have saved 25% of the normal maintenance energy requirements. Whether shorebirds can use a similar energy-sparing adaptation if they are unable to feed effectively for several days, e.g. during prolonged gales or cold weather, is not known.

Maximizing the rate of net energy gain is only one possible optimal foraging strategy. It is based on the assumption that there is an overriding selective advantage in minimizing the time taken to collect the food necessary to achieve neutral energy balance each day. Such an assumption may be valid if predation is more important as a cause of death than starvation. In California, avian predators are an important source of shorebird mortality in winter (Page & Whiteacre 1975), but, at least in recent years, it is rare to see birds of prey taking estuarine shorebirds in Europe. Here, starvation may be the greater source of mortality in winter.

In some shorebird species, individuals maintain large nearest-neighbour distances while feeding, and may drive off conspecifics which encroach on their feeding sites. Such behaviour has been recorded for Grey Plover at Teesmouth. Colour-marked individuals have usually been found on the same feeding sites at the same stage of the tidal cycle on different days. An individual may move its feeding site several times as the tide uncovers and then covers suitable feeding areas, but the temporal pattern of use of the different sites in relation to the tidal cycle seems reasonably consistent on consecutive days. For species which maintain this type of dispersion pattern and feeding routine, it could be of advantage to individuals to conserve the food stocks in each feeding site to ensure that prey density does not fall to critically low levels during a winter, as might result from the high food demands of an energetically costly feeding method. Referring again to Fig. 4, it may be seen that the time required to achieve neutral energy balance by feeding by method B is about 50% greater than by method A if prey is plentiful — but the food intake required by method A is almost double that by method B. When prey is scarce, not only is the time taken to achieve neutral energy balance slightly greater by method A than by method B, but the food intake required is three times as great. Thus, provided that the time taken to satisfy daily energy requirements by a less costly foraging method is less than the time available each day for obtaining food (determined by the times of exposure and submersion of suitable feeding areas), it may be of selective advantage to a shorebird to use a foraging method which does not maximize the rate of net energy gain, but rather minimizes the rate at which food stocks are depleted. This argument cannot, of course, be applied to those shorebird species which feed in closely packed flocks, or those which change their feeding sites from day to day. It also assumes that if different species feed in the same site, they take different prey; this may be an unrealistic assumption for shorebirds, at least in areas where the range of prey is restricted, for example in polluted estuaries.

8. THE DISTRIBUTION OF SHOREBIRDS IN THE NON-BREEDING SEASON

The outer limits to the geographical distribution of waders in the non-breeding season must be set by the ability of different species to achieve, on average, a neutral daily energy balance. It is uncertain for how long the fat reserves carried by shorebirds in mid-winter could supply the daily energy demands of a bird if it cannot or does not feed. Thus the time-period over which energy gain and expenditure must balance is not known, though it is of the order of days rather than weeks. Bar-tailed Godwits store fat amounting to at most about 12% of their total body weight in mild winters (Evans & Smith 1975). This would be sufficient to provide about 3 days' subsistence energy if used at the rate of about five times the daily basal metabolic rate, as estimated under field conditions by Smith (1975). However, possible energy-sparing adaptations during starvation, discussed earlier, were not considered in making this calculation, nor was the effect of an increase in the rate of heat loss arising from high winds at low temperatures.

For birds wintering in the northern hemisphere, daylength and average temperature would be expected to be major determinants of the northern limits of distribution in December and January. It is unlikely that wind speeds and patterns at high latitudes are sufficiently consistent to act as ultimate factors restricting shorebird distribution. Daylength is likely to be more important in restricting those species which hunt their prey visually, and temperature more important to those which employ a variety of senses while foraging. Although both low temperature and high wind speeds increase the rate of heat loss from a bird and decrease prey availability, in the short term birds can alter their foraging behaviour and feeding sites more easily to avoid high winds than to avoid low temperatures. As energy requirements increase and/or prey availability decreases, birds need to feed for a higher proportion of each day. Under such conditions, many shorebird species augment the time for which they can feed in the intertidal zone by feeding in coastal marshes over the periods of high water. This can be done in windy weather; however at low temperatures such feeding areas become unavailable when frozen. Hence, in freezing conditions birds are restricted to feeding in the intertidal zone and therefore for only a limited part of each 24 hours. They are also restricted to feeding chiefly at the tide edge, where both intra- and interspecific competition for food may occur. In such situations, the larger species in an encounter usually wins, but as heavier individuals require more food to achieve their daily energy balance, it is not possible to argue straightforwardly that larger species should be found wintering at higher latitudes than smaller species.

One of the striking features of shorebird migrations after the breeding season is that some populations of many species cross the equator to winter in the southern hemisphere. Here they encounter lengthening days and increasing temperatures and so avoid some of the problems which befall those populations which remain to the north of the equator. However, many otherwise suitable intertidal feeding areas in the tropics, and even further south, are fringed by mangroves, which extend downshore to mid-tide level or beyond. Only one species of wader, the Common Sandpiper *Tringa hypoleucos* has been recorded feeding on exposed mud within mangroves (see, for example, Nisbet 1968), although several species perch on these trees to roost at high water. Species which do not feed within mangroves are restricted to less than 6 hours' feeding in each tidal cycle. This may be insufficient to allow them to achieve an energy balance, particularly in regions of high temperature, where invertebrate activity and availability may be reduced. Thus in tropical regions, coral reefs and those islands which are free from mangroves may be the only important areas in which shorebirds can spend the non-breeding season.

Although the northern limits of distributions may be set by climatic factors, and equatorial limits by the presence of mangroves, shorebirds are not uniformly dispersed within the belts of latitudes suitable for "wintering". Some of the reasons for this are associated with the distributions of the preferred prey of each wader species, as documented in the Netherlands by Wolff (1969). Absence of waders from those shores of western Europe and northwest Africa which face the Atlantic, and which are not sheltered from the direct action of waves and swell, is understandable. So too is the concentration of wintering shorebirds in the estuaries entering the Irish and North Seas, since these areas are relatively sheltered from severe wave action.

It has become clear recently that the distribution of many wader species in winter is not static, but that movements into and out of major geographical areas are continually taking place. Since the beginning of this decade, monthly counts of shorebirds have been made in most British estuaries that are important feeding grounds for shorebirds in the non-breeding season. Counts for 1971/72, 1972/73 and 1973/74 have been summarized by Prater (1973, 1974, 1975). The number of estuaries in which counts have been made regularly has increased slightly over these three years, and this should be borne in mind assessing the data presented in Fig. 5. This shows the monthly

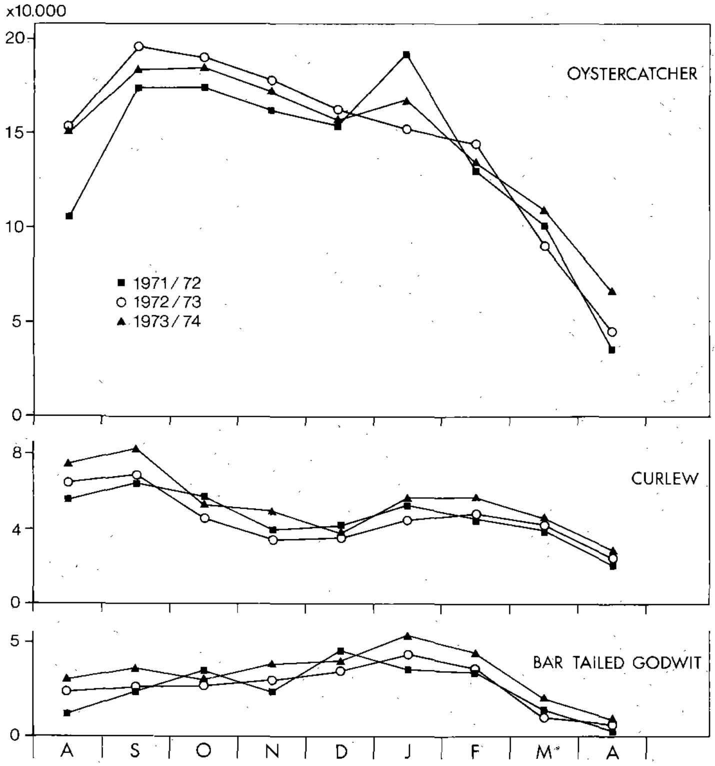

Fig. 5. Monthly counts of three species of shorebirds, *Haematopus ostralegus* (top), *Numenius arquata* (centre) and *Limosa lapponica* (bottom) in the British Isles in three winters. Data from Prater (1973, 1974, 1975).

totals for the whole of Britain for three species, Oystercatcher, Curlew and Bar-tailed Godwit, in successive winters. As may be seen, the pattern of seasonal change in numbers was very similar for any one species in all three years. However, whereas numbers of Oystercatchers declined only slightly from September to February, numbers of Curlew fell to their lowest levels in December but then rose again in the New Year, while numbers of Godwits rose steadily throughout the autumn and winter to reach a peak in February. Of these three extreme types of seasonal pattern, only that of the Oystercatcher could conceivably be explained by mortality, rather than by movement.

For any one species, the pattern of seasonal change in numbers considered on a more local level, for example within one estuary, is often similar to the pattern for the whole of Britain. Fig. 6 presents the counts of Curlew and Bar-tailed Godwits using the Tees estuary in recent winters. The seasonal trends in the numbers of birds roosting in the estuary closely parallel those for the whole of Britain shown in Fig. 5. However, the number of Godwits feeding on Seal Sands (140 ha), the largest intertidal feeding site within the Tees estuary, remained remarkably constant from November to February, even though the number of roosting birds increased (Fig. 6). Trends in numbers of Grey Plover roosting in the Tees estuary and feeding on Seal Sands were closely similar to the respective patterns for Godwits. For both species, the birds which arrived on the estuary during the winter must have

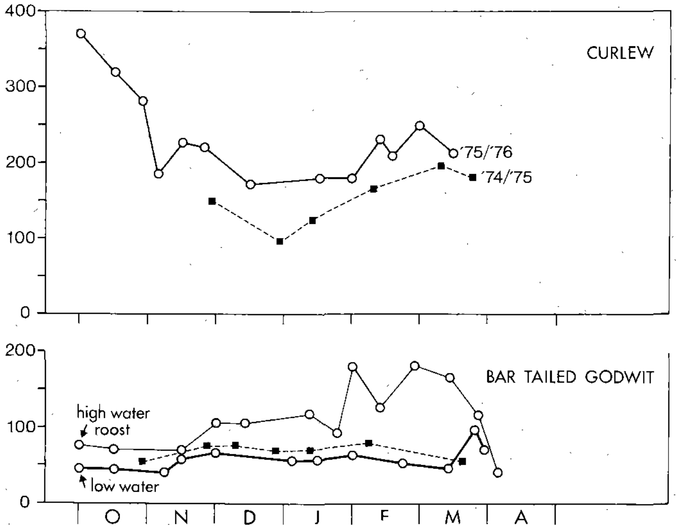

Fig. 6. Counts of *Numenius arquata* (top) and *Limosa lapponica* (bottom) on the Tees estuary in the winters of 1974/75 (filled squares, dashed lines) and 1975/76 (open circles, solid lines). The 1975/76 counts of Bar-tailed Godwits comprise birds at roosts (upper line) and birds feeding at low tide on Seal Sands (lower line).

fed in sites other than Seal Sands, unless they displaced birds from Seal Sands, to (presumably) sub-optimal feeding grounds. By marking several Grey Plover and Curlew with individually identifiable coloured leg-bands, we have established that some individuals stay throughout the winter months on Seal Sands and return there in the following autumn. Fidelity of some individuals of other wader species to "wintering" areas has been shown by ringing in other British estuaries, for example, The Wash (Minton 1975). However, little is known of the immediate origins or destinations of the variable numbers of birds which move into or out of such estuaries during a winter. To understand the dynamic distribution patterns of birds within their non-breeding ranges, therefore, we must not only provide reasons for the movements of most species, but also explain why some individuals of those same species remain in one site throughout the period between their autumn and spring migrations.

Other problems are raised by the results of the British wader counts. Although the seasonal changes in numbers of Grey Plover were fairly similar in different years (Fig. 7), numbers were about 50% higher in 1973/74 than in the previous winter. This cannot be attributed solely to the larger number of estuaries counted in the later year, as the increase was recorded at individual estuaries also. In contrast, numbers of Oystercatchers varied very little between years (Fig. 5). How should these data be interpreted? If a similar

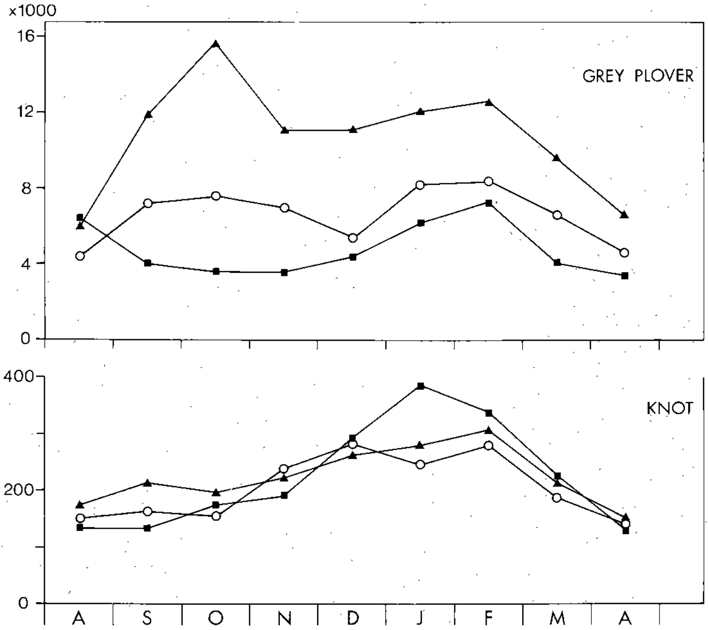

Fig. 7. Monthly counts of *Squatarola squatarola* (top) and *Calidris canutus* (bottom) in the British Isles in three winters. Key as in Fig. 5. Figures on the vertical axes are thousands. Data from Prater (1973, 1974, 1975).

proportion of the populations of each species come to Britain each autumn, annual variations in numbers settling reflect annual variations in breeding performance. However, it is possible that similar numbers of Grey Plover attempt to settle in Britain each autumn, but a varying proportion succeeds in doing so. This would occur if the "carrying capacity" of the British estuaries was filled each year, but the capacity itself varied. (Note that the "carrying capacity" might well vary seasonally also.) Finally, the counts of Knot (Fig. 7) are unusual in that the seasonal patterns of numbers in Britain were not similar in the three years studied. Although numbers reached their peak in mid-winter in all three years, the large influx of Knot in January 1972, amounting to about 100,000 birds, was not recorded in later Januaries. From where did they come, and why? and why were other species, with the possible exception of the Oystercatcher (Fig. 5), not affected?

The counts for Britain and Teesmouth also raise the question: which environmental factors (if any) time the movements of the different species. Only two species, Curlew and Redshank (data from Prater 1973, 1974, 1975 and Evans *et al.* in press), show changes in numbers which parallel first the decreases and then the increases in daylength and average temperature during a winter. If temperature acts as a proximate factor, stimulating "hard-weather movements", these should have been detected particularly easily at the start of the long cold spell in the winter of 1962/63. Redshank mortality was particularly high at that time, and although several British-ringed birds were recovered in France in that winter, most recoveries came from localities close to the ringing sites within Britain. This was true also of Curlew, which did not suffer such heavy mortality (Spencer 1964, Pilcher 1964). It seems, therefore, that most of those birds present in mid-winter attempted to survive the period of adverse weather without attempting to find better feeding conditions elsewhere. Thus temperature was probably not the stimulus for movements earlier in the autumn.

Seasonal changes in the numbers of Bar-tailed Godwits (Fig. 5) and Grey Plover (Fig. 7) run contrary to changes in those environmental factors which might have been expected to make it difficult for them to achieve a daily balance between energy intake and expenditure. Possibly the British Isles is at the end of the migration routes of these two species; if so, until the points of departure, from which birds move to Britain throughout the autumn and early winter, are known, it will not be possible to identify which environmental factors stimulate their movements. Alternatively, birds of these two species may have moved further south than Britain in early autumn, and then have gradually returned northwards during the winter. Large numbers of Godwits are known to reach the Banc d'Arguin in Mauritania, West Africa, by early autumn (Knight and Dick 1974) but it is not known how long they stay there.

Numbers of Knot (Fig. 7) and Dunlin (data from Prater 1973, 1974, 1975) show seasonal changes rather similar to those of the Godwit. Although

Dunlin suffered considerable mortality during the cold winter of 1962/63 (Pilcher 1964), no evidence of "hard-weather movements" was obtained from ringing (Spencer 1964). Thus it cannot be concluded that Dunlin numbers in Britain increase in autumn and early winter in response to decreasing temperatures elsewhere in Europe. On the other hand, Knot have been counted in larger numbers in Britain during hard weather, for example in January 1972. Thus their pattern of seasonal change in numbers may well be related to temperature, though whether they move in response to negative energy balance, or before it occurs, remains an open question.

With a possible exception in the case of the Knot, therefore, it seems that environmental variables may not be important proximate factors for the timing of movements of shorebirds within their non-breeding ranges. If endogenous timers are involved, the question of the evolutionary advantage of movement from one area to another, as opposed to fidelity to a wintering site, still remains. To answer this, it will be necessary to examine the availability of potential invertebrate prey at different places within the non-breeding range of each species and at different times during the year. Differences in timing of reproduction and growth in different geographical areas occur in prey species such as *Nereis diversicolor,* perhaps in response to sea temperature, and these may affect markedly the biomass and availability of prey. So, too, may the impact of predation by the birds themselves, during the course of a winter. Further understanding of the distribution and movements of shorebirds is most likely to come from detailed studies of feeding behaviour and prey availability in the field. On the other hand, the role of laboratory physiological studies on heat loss and energy utilization, is likely to be of most importance in predicting for how long birds can survive when they are unable to feed, and hence the extent of mortality to be expected under different adverse weather conditions, for it seems clear that most shorebirds do not move away when faced with an energy crisis.

9. SUMMARY

In an attempt to understand the geographical distribution and movements of shorebirds in the non-breeding season, circumstances are reviewed which make it difficult for a bird to obtain sufficient food to balance its daily energy requirements. The survey considers first the factors which lead to increased energy requirements, reduced hunting effectiveness of the bird, reduced prey availability and reduced time for feeding. The effects of wind, tide, daylength and temperature on energy balance are then summarized, with examples.

Alternative foraging strategies provide a possible means of reducing energy expenditure when food availability decreases. When prey availability is high, hunting methods which require a high rate of energy usage may provide higher rates of net gain of energy (to be used for maintenance) than energetically less costly methods, but the reverse may be true when prey are scarce. The optimal foraging method, considered as that which minimizes the time required for feeding, may then change with prey availability. However, if starvation, not predation, is the chief source of mortality, the optimal foraging method may be that by which the food needed to provide the daily maintenance energy is minimized. If the energetic costs of foraging exceed the energy gained as food in a given time, a bird does best not to forage. This has been observed in very cold and windy weather.

The northern geographical limits to shorebird distributions in the non-breeding season are probably set by average temperature and daylength. Many species may be unable to utilize intertidal feeding areas in tropical regions if these are fringed by mangroves. Within the "wintering" areas, some individuals of most species move from place to place, while others remain in a single site, to which they may return in subsequent autumns. Movements of most species cannot be related directly to adverse physical conditions in the environment, though Knot come to Britain in larger numbers in cold winters. Few species perform "hard-weather movements"; most stay in, and attempt to survive, adverse conditions. Laboratory measurements of heat loss may enable prediction of survival times, but field studies of feeding behaviour and prey availability in different geographical areas will be needed to understand further the patterns of distribution and movements of shorebirds in the non-breeding season.

10. ACKNOWLEDGEMENTS

The ideas developed in this paper have been tried out on various of my past and present research students at Durham University. Although they may not always approve of the uses to which I have put their comments and data, I wish particularly to thank M. W. Pienkowski, who read an earlier draft of this paper, and Dr. P. C. Smith; also D. M. Brearey, N. C. Davidson, D. M. Herdson, P. J. Knights, Dr. A. V. Millard, S. J. Moon and D. J. Townshend. At various times during the last few years, I have been stimulated by discussions with Dr. J. D. Goss-Custard, Drs. J. B. Hulscher and L. Zwarts on shorebird feeding behaviour; I thank them for the time and trouble they have taken to explain their ideas and work to me. I also thank the Nuffield Foundation for a travel grant which enabled me to visit Australia, and thereby to revise considerably my ideas about suitable feeding habitats for waders. Finally, I wish to acknowledge my debt to Dr. E. A. R. Ennion, whose enthusiasm for studying and catching shorebirds in northeast England, before even the introduction of mist-nets, infected me with a similar deep interest in this group of birds.

11. REFERENCES

Darby, J. 1975. Dispersion patterns of the lugworm *Arenicola marina*. Unpublished Hons. Thesis, Department of Zoology, University of Edinburgh.

Darbyshire, M. & L. Draper. 1963. Forecasting wind-generated sea waves. Engineering 195: 482—484.

Evans, P. R. 1975. Notes on the feeding of waders on Heron Island. Sunbird 6: 25—30.

Evans, P. R. & P. C. Smith. 1975. Studies of shorebirds at Lindisfarne, Northumberland. II. Fat and pectoral muscle as indicators of body condition in the Bar-tailed Godwit. Wildfowl 26: 64—76.

Evans, P. R., *et al.* (in press) Short-term effects of reclamation of Seal Sands, Teesmouth, on wintering shorebirds and Shelduck.

Gessamann, J. A. 1973. Chap. 9 in Ecological Energetics of Homeotherms Vol. 20 of Monograph series, Utah State University Press, Logan, Utah.

Goss-Custard, J. D. 1969. The winter feeding ecology of the Redshank *Tringa totanus*. Ibis III: 338—356.

Goss-Custard, J. D. 1970. Dispersion in some overwintering wading birds. In Social Behaviour in birds and mammals (Ed. J. H. Crook) Academic Press, London.

Gwinner, E. 1972. Adaptive functions of circannual rhythms in warblers. Proc. 15th Int. Ornith. Congress: 218—236.

Hamilton, W. J. III, W. M. Gilbert, F. H. Heppner & R. J. Planck. 1967. Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centres. Ecology 48: 825—833.

Hart, J. S. & M. Berger. 1972. Energetics, water economy and temperature regulation during flight. Proc. 15th Int. Ornith. Congress: 189—199.

Knight, P. & W. J. A. Dick. 1974. Wader counts in Mauritania. Bull. Int. Waterfowl Res. Bureau 37: 37—38.

Knights, P. J. 1974. The effect of recent reclamation of the Tees estuary on the numbers and feeding activities of overwintering waders and Shelducks. Unpublished report to Coastal Ecology Research Station, Institute of Terrestrial Ecology.

Lange, G. 1968. Über Nahrung, Nahrungsaufnahme und Verdauungstrakt mitteleuropäischer Limikolen. Beiträge zur Vogelkunde 13: 225—334.

Minton, C. D. T. 1975. The Waders of The Wash — ringing and biometric studies. Report to Wash Feasibility Study, Water Resources Board.

Naylor, E. 1958. Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas*. J. Exp. Biol. 35: 602—610.

Nisbet, I. C. T. 1968. The utilization of mangroves by Malayan birds. Ibis 110: 348—352.

Page, G. & D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77: 73—83.

Perry, R. 1945. A Naturalist on Lindisfarne. Country Life, London.

Pienkowski, M. 1973. Feeding activities of wading birds and Shelducks at Teesmouth and some possible effects of further loss of habitat. Unpublished report to Coastal Ecology Research Station, Institute of Terrestrial Ecology.

Pilcher, R. E. M. 1964. Effect of the cold weather of 1962-63 on birds of the north coast of the Wash. Wildfowl 15: 23—26.

Prater, A. J. 1973. BTO/RSPB Birds of Estuaries Enquiry. Report for 1971-72. Tring: British Trust for Ornithology.

Prater, A. J. 1974. Ditto, Report for 1972-73.

Prater, A. J. 1975. Ditto, Report for 1973-74.

Preece, G. S. 1971. The swimming rhythm of *Bathyporeia pilosa* (Crustacea: Amphipoda). J. mar. Biol. Assn. U.K. 51: 777—791.

Royama, T. 1970. Factors governing the hunting behaviour and food selection of the Great Tit *Parus major*. J. Animal Ecology 39: 619—668.

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

Spencer, R. 1964. Report on bird-ringing for 1963. British Birds 57: 525—582.

Vader, W. J. M. 1964. A preliminary investigation into the reaction of the infauna of tidal flats to tidal fluctuations in water level. Netherlands J. Sea Research 2: 189—222.

Wallgren, H. 1954. Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. Acta Zoologica Fennica 84: 1—110.

Ward, P. & A. Zahavi. 1973. The importance of certain assemblages of birds as "information centres" for foodfinding. Ibis 115: 517—534.

Westerterp, K. 1976. How rats economize; Energy loss in starvation. Doctoral dissertation, University of Groningen.

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. Amsterdam.