Goodyer,L.R., Symonds,F.L. and Evans,P.R. 1979. Leg flags: temporary colour rings. WSG Bull. 25: 12.
Prater,A.J. 1981. Estuary Birds of Britain and Ireland. Poyser, Calton.
Symonds,F.L., Langslow,D.R. and Pienkowski,M.W. 1983. Movements of wintering shorebirds within the Firth of Forth: species differences in usage of an intertidal complex. Biol. Conserv. in press.

Mike Moser, British Trust for Ornithology, Beech Grove, Tring, Herts.
Mike Carrier, 35 Lowry Hill Road, Carlisle, Cumbria.

ABSTRACTS OF PAPERS GIVEN AT THE 6TH INTERNATIONAL WORKSHOP ON THE ECOLOGY OF SHOREBIRDS, CARDIFF, 12 - 16 SEPTEMBER 1983

Seasonal changes in the spacing pattern of feeding Dunlins

D.H. Worrall, Department of Zoology, University College, Cardiff

Dunlins were studied at two sites on the northern shores of the Severn Estuary, South Wales. Flocks of Dunlins feeding away from the tide's edge were found to be smaller during the mid-winter months than during spring or autumn. The average within-flock density of these flocks also decreased significantly during this period. This decrease in the average density of birds feeding within the winter flocks was not a result of the decrease in flock size but was found to be consistent within all sizes of flock throughout the season.

Dunlins fed farther from their nearest neighbour in the middle of winter, and the area available for each bird to search unhindered by its nearest neighbour was also at a maximum. Within-flock aggression did not increase during those periods, but it was felt that the decrease in flock density was a direct response to the decreased availability or detectability of prey.

Why are waders like Topsy?

P.N. Ferns, C.J. Thomas & P.C. Hack, Department of Zoology, University College, Cardiff

The eggs of Golden Plovers *Pluvialis apricaria* and Dunlins *Calidris alpina* nesting in exactly the same sites in the central uplands of Wales have increased significantly in size in the period between 1900-1926 and 1982/83. During these 70 or so years, Golden Plover egg lengths have increased by 1.5% and breadths by 0.9%, whilst Dunlin egg breadths have increased by 1.3%. These increases are of the same order and size as those recorded by Vaiasanen (1969) for Ringed Plovers in Scandinavia over roughly the same period. Vaiasanen interpreted the latter changes as being due to climatic amelioration which allowed a northward spread of larger Ringed Plovers (which laid larger eggs) from breeding areas further south. A similar increase has occurred in the wing lengths of Scandinavian Redshanks, possibly for the same reason (Hale 1971). However, this explanation is unlikely to hold for Welsh Golden Plovers and Dunlins since both species are close to the southernmost limits of their breeding ranges in this area.

It seems rather curious that all four species of waders which have been investigated seem to be increasing in size (like Topsy). More work is clearly required to determine if this is a general trend amongst European species and, in particular, to discover what has happened in other regions during the same period.

Hale,W.G. 1971. A revision of the taxonomy of the Redshank *Tringa totanus*. Zool. J. Linn. Soc. 50: 199-268.
Vaiasanen,R.O. 1969. Evolution of the Ringed Plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. Ann. Acad. Sci. Fenn. (A), IV, 149: 1-90.

Habitat selection in breeding waders

P.N. Ferns, Department of Zoology, University College, Cardiff

On the basis of studies of Ringed Plovers *Charadrius hiaticula*, Turnstones *Arenaria interpres*, Dunlins *Calidris alpina*, Sanderlings *Calidris alba* and Knots *Calidris canutus* in the high arctic (see WSG Bulletin, 26:24), it is argued that wading birds establish breeding territories in order to provide females with the food resources necessary to form eggs within the territorial boundaries. Territoriality minimizes the expenditure of energy in commuting between a nesting area and a feeding site at a time when the total energy demand is at its peak. The habitats selected for nesting by these five species are different because of differences in their morphology and feeding methods.

Before the breeding territories are established, these waders may feed communally in the few snow free areas which are available. By the time incubation has commenced, further snow free areas may have become available, outside the defended territories, and these too may be exploited communally. Once the eggs hatch, territoriality breaks down completely and the chicks are escorted to the best feeding areas which are usually in low lying, well vegetated, marshy ground and are the last to emerge from the snow. One consequence of all this is that there are marked differences in the nesting habitats of these species but rather little difference in the habitats in which chicks feed.

This could be interpreted as a consequnce of the late snow melt and short summer season in the high arctic, but the idea that breeding territories provide females with the resources necessary for egg formation may have wider applicability. However, it cannot apply to several polygamous species, nor to individuals which nest near the coast and forage intertidally during the early part of the breeding season.

A Hemispheric Perspective on Shorebird Migration in the New World

R.I.G. Morrison, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario, Canada K1A 0E7; present address Scott Polar Research Institute, Cambridge CB2 1ER, UK.

Data from a series of internationally-coordinated survey schemes are now being used to provide information on the distribution and migration of shorebirds throughout their ranges in the New World. In North America, these schemes include aerial and ground surveys by the Canadian Wildlife Service in James Bay, Hudson Bay and along the St. Lawrence River, and the Maritime Shorebird Survey and International Shorebird Survey schemes, consisting of a network of volunteer participants, in eastern and central Canada and the U.S.A. In South America, extensive aerial surveys carried out under the Shorebird Atlas Project of the Canadian Wildlife Service Latin American Program have provided information from the northern and Atlantic coasts of South America.

For the Semipalmated Sandpiper Calidris pusilla, the upper Bay of Fundy is the most important migration area, and the principal wintering grounds are in Suriname and French Guiana, where 70% and 20%,respectively, of an estimated 1.9 million "peeps" were located on winter surveys in January/February 1982. Morphometric analyses at migration and wintering areas may be used to trace movements of eastern and western populations. Important autumn migration areas for Red Knot Calidris canutus were found in James/Hudson Bays, Massachusetts, New Jersey and Suriname, with the principal wintering areas occurring in Patagonia and Tierra del Fuego, Argentina. Largest concentrations found to date occurred on spring migration in Delaware Bay, New Jersey (95,500). Hudsonian Godwits Limosa haemastica appear to make a direct flight from James Bay to South America, where an undiscovered stopover area is used before movement to the principal wintering areas in Argentina: large wintering concentrations were found in Tierra del Fuego. In James/Hudson Bays, the birds' distributions were related to food abudance at both local and regional levels.

The importance of birds in controlling the structure of rocky intertidal communities: a southern African perspective.

Philip A.R. Hockey, Percy Fitzpatrick Institute for African Ornithology, University of Cape Town, Rondebosch, 7700, South Africa.

Birds affect intertidal plant and animal communities in two basic ways. Through guano deposition they enhance the nutrient status of the intertidal and nearshore ecosystems, resulting in increased primary and secondary production; and, as predators, they remove appreciable numbers of invertebrates from the shore.

The effects of guano deposition are most radical around seabird breeding islands. Enhanced algal growth rates at these sites leads to rapid growth of grazing gastropods, primarily limpets, which are important prey species for the African Black Oystercatcher Haematopus moquini. African Black Oystercatchers are abundant at offshore islands and remove large numbers of limpets (up to one million per km of shore per year). The reduction in limpet density caused by oystercatcher predation leads to the formation of large beds of macroalgae in the mid- and upper intertidal regions, as the remaining limpet populations are not sufficient to control algal growth at the sporeling stage. These beds of macroalgae support a rich infauna, comprising chiefly crustacea, gastropods and insect larvae, which provide a food source for smaller shorebirds such as Turnstones Arenaria interpres, Sanderlings Calidris alba, and Cape Wagtails Motacilla capensis. Limpet populations at islands are able to withstand the heavy predation pressure from oystercatchers by virtue of their rapid growth rate. An appreciable proportion of limpets at islands grow too large to be preyed on by oystercatchers, and it is the gamete production by these individuals which guarantees recruitment to the population regardless of predation pressure on smaller individuals.

On the mainland, nutrient levels are much lower and algal production consequently is less. Oystercatchers are much scarcer on the mainland and limpet populations are controlled by food supply rather than by predation. Macroalgal beds rarely develop in the mid and high shore regions and there is consequently no feeding facilitation by oystercatchers for smaller shorebirds.

By studying intertidal predatory processes under natural conditions of varying predation pressure, and isolating the mechanisms for invertebrate population maintenance, suggestions can be made for effective management of the intertidal zone. In many parts of southern Africa, intertidal invertebrates are heavily preyed on by man for food and bait. Such heavily exploited communities are almost invariably degraded, and, in the absence of active management, will continue to degrade. This leads to a depauperate environment for shorebirds, and the loss of a valuable economic resource.

The feeding economy and growth of Common Snipe chicks

R.E. Green, The Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK.

Nesting phenology and the diet, growth and survival of Snipe chicks were studied in four areas of the seasonally flooded Cambridgeshire washlands. Nesting started in mid April or up to two months later if flooding prevented it. Egg laying ceased earlier at sites with good drainage, where the ground became difficult for Snipe to probe with their bills, than at poorly drained sites. Some egg-laying occurred up to mid July. Snipe feed by probing soft soil for earthworms and dipteran larvae. At hatching broods are divided between the parents into two sub-broods of two chicks each which are cared for independently. Chicks are fed by the adults on worms and larvae. Mean weight gain rates of sub-broods of Snipe chicks were not related to egg size but to the density of soil invertebrates (mainly earthworms). Within sub-broods the two chicks often grew at markedly different rates and one chick usually died in the first week of life. The chick which was heavier at hatching tended to grow faster than its sibling and was more likely to survive. Hatching order and bill size at hatching had no effect.

Breeding Dunlins *Calidris alpina schinzii* in S W Sweden: some results from a population study

Paul E. Jonsson, Dept. of Animal Ecology, University of Lund, S-223 62 Lund, Sweden.

The *schinzii* race of the Dunlin has decreased markedly in the Baltic/North Sea area during the last 50 years, mainly due to habitat destruction. A total of about 2200 pairs are estimated still to breed on grazed shore-meadows and salt-marshes in this region. The population in south Sweden holds about 250 pairs.

In the Foteviken area in SW Scania, a smaller population was studied during 1981-1983. Most of the breeding birds (21-23 pairs) were individually colour-marked. In the study area, a 60 hectare shore-meadow, the mean density of breeding birds was 6.2 pairs/10 ha. The Dunlins arrive to the area in mid-March, males about a week before the females. Egg-laying starts in mid-late April and replacement clutches have been found in mid-June. Most of the birds leave the area in late June, females earlier than males.

Adult return-rates were on average 82.9% for males and 70.5% for females. Of the ringed chicks, 12.9% came back after one year and 25.8% after two years. Mate-faithfulness was on average 45% after one year.

Males displayed intensively during most of the breeding season, but they did not seem to defend any territories. Most of the aggression observed occurred on the shore where most of the feeding took place at communal sites. Small brackish water-pools became important feeding sites when sea-shore was unavailable during high water level periods. Birds with chicks fed mostly among the meadow vegetation and family parties were seen to wander far away from the nest site (up to 400-500 m).

During the three years 83 nests were found and 73.5% of these were lost due to egg predation. Potential predators were stoat, fox, badger, mink and crows. Hatching rates for the three years were 0.87, 0.41 and 0.10 young/breeding adult, respectively.

The observed reproductive rate is insufficient in maintaining a stable population, so immigration from other areas might occur.

The mating system of Kentish Plovers *Charadrius alexandrinus* : some observations and experiments

C.M. Lessells, Imperial College, Silwood Park, Ascot, Berks. SL5 7PY, UK.

Kentish Plovers *Charadrius alexandrinus* have a mating system in which one parent, usually the female, deserts the brood about a week after hatching. Observations of colour-ringed birds show that the bird which deserts is able to remate and produce another clutch that season (Lessells in press).

During 1981 and 1982 experiments were carried out in the salt-pans of the Carmargue, southern France to investigate the selection pressures influencing the evolution of the mating system.

(A) *Mate removal experiment*. One of the pair were removed early in incubation (held in captivity and later released) to determine whether one adult could successfully incubate the clutch. These experiments showed that; (i) females were more likely to desert than males, (ii) among males the heavier birds deserted, and (iii) birds were more likely to desert early in the season. If the adult stayed; (i) birds whose mates had been removed spent a greater proportion of each day incubating than birds of the same sex did when incubating in a pair, (ii) despite this the eggs were left unattended for a greater proportion of each day, (iii) more trips were made to and from the nest, and (iv) four birds (two males and two females) who were caught at least five days after mate removal showed no consistent loss of weight, pectoral muscle size or fat reserves. The effect on the clutch was; (i) an increase in the incubation period, (ii) 100% hatching success of the 15 eggs which survived predation, and (iii) a lower (though not significantly so) predation rate.

(B) *Mate + clutch removal*. Both mate and clutch were removed simultaneously to determine the length of time taken to remate. (Adults were again held in captivity and subsequently released). This experiment showed; (i) females took no longer to remate and produce a clutch than a pair would normally take to replace a lost clutch, and (ii) males took significantly longer to remate and for their new mate to produce a clutch than a pair would normally take to replace a lost clutch.

Reference

Lessells,C.M. In press. The mating system of Kentish Plovers. *Ibis*.

Breeding efforts and survivorship of breeding Oystercatchers on Skokholm.

Harris,M.P. & Safriel,U.N., ITE, Hill of Brathens, Banchory, Kincardineshire, AB3 4BY, UK.

The annual survival was followed between 1963 and 1977, during which the breeding population remained stable. The mean annual survival was 0.906 and the reasons for the small annual differences were not obvious. Most mortality occurred away from the breeding area. Age had no effect on survival. Breeding had no adverse effects on the chances of a bird returning the next season. The reverse occurred: birds which did not lay had a reduced chance of surviving, probably because they were already stressed or sick, and so could not get a territory. A pool of mature non-breeders buffered the population against fluctuations in survival rates.

Mortality, feeding and fighting in young Oystercatchers

J.D. Goss-Custard, ITE, Furzebrook Research Station, Wareham, Dorset BH20 5AS, UK.

Compared with adult Oystercatchers wintering on the Exe estuary, first and second winter birds have a higher mortality and eat fewer mussels. Instead, most eat ragworms *Nereis diversicolor*, clams *Scrobicularia plana*, and earthworms in the fields. We are studying the possibility that the change in mortality with age is linked to the change in diet. Since many first-year birds try mussels when they arrive on the Exe in August but turn to *Nereis* by October, we are testing two hypotheses. The first is that competition with dominant adults forces the young birds off the mussel beds so that they are obliged to eat other prey. Though competition on the beds is intense and young birds subdominant, this is unlikely to be the case since first-year birds leave beds even where adults are scarce. the second hypothesis is that young birds are less efficient at feeding on mussels than on other foods until they learn the necessary skills. The available evidence favours this hypothesis for birds in their first autumn because they feed very slowly on mussels in the absence of adults, and have a much higher intake rate when feeding on Nereis. However, they learn fast how to feed on mussels, so competition may play an important part in determining where, and on what, birds feed in their second and third winters. This is now being tested.

Diet-related breeding success, inland breeding and population increase of British Oystercatchers

Uriel L. Safriel, The Hebrew University of Jerusalem, Jerusalem 91904, Israel.

Of the ca. 50 Oystercatcher pairs breeding on Skokholm in 1965 and 1966, 15% bred near the shore and 85% bred 'inland'. 28% fed their young on limpets and 72% on terrestrial arthropods and earthworms. 'Terrestrial-feeders' were three times more successful than 'limpet-feeders' in fledging young, irrespective of variation in initial brood size and of hatching date, but depending on differential losses to predation by gulls. This is because vigilance by parents is relatively low in limpet-feeders' territories, and limpet-fed young are, on average, relatively undernourished and behave more 'carelessly'. Since the 1930s, populations of both Oystercatchers and shore-breeding gulls have increased on Skokholm. The increase of the Oystercatcher seems associated with a shift 'inland', until the island became saturated in the late 1940s.

Norton-Griffith's (1968) observations and fostering experiments suggest that limpet-feeders always produce limpet-feeding young, and that an earthworm-feeding type cannot arise through imitation since food-specialisation is transmitted culturally. However, Feldman & Cavalli-Sforza (1976) proposed a model showing how a genetically determined 'ineducability' may persist in spite of being disadvantageous. The rare 'ineducables' remain unskilled generalists that can easily switch to terrestrial food. It is proposed that the increase in gull density along the shores selected for an increase in numbers of 'inland' breeders. This increased the likelihood of an inland breeder also being an 'ineducable' that had switched easily to feeding on earthworms. This produced a new combination of an inland-breeding terrestrial feeder that was highly successful under conditions of intense gull predation on the shore.

Thus, the increase in shore-breeding gulls could have triggered a genetically-based behavioural change in Skokholm Oystercatchers, which might have been responsible for the shift to 'inland' habitats and terrestrial food, and promoted population increase. This interpretation of events on Skokholm may be equally applicable for the general trend of habitat shift and population increase of other British populations.

Feldman,M.W. & L.L.Cavalli-Sforza. 1976. Cultural and biological evolutionary processes, selection for a trait under complex transmission. Theor. Pop. Biol, 9: 238-259.

Norton-Griffiths,M. 1969. The feeding behaviour of the Oystercatcher (Haematopus ostralegus). D.Phil. Thesis, University of Oxford.

Prey detection by intertidally-feeding Lapwings

Neil Metcalfe, Department of Zoology, University of Glasgow, Glasgow G12 8QQ, UK.

Observations on adult Lapwings Vanellus vanellus foraging on the mudflats of the Clyde estuary showed that they detected prey during stationary scanning pauses. The majority of prey were taken within three paces of the scanning position. Nereis diversicolor was taken at greater distances than Corophium volutator. The proportionate incidence of pecks that proved abortive increased with distance from the pause position. It was argued that these were due to prey cue misidentification rather than escape of the prey. After failing to detect prey from one position, birds 'gave up' and moved to a fresh one, the median distance moved corresponding to the radius of an area within which 99% of prey items were located. The distance moved to take prey (including steps taken after capture but before the next scanning position) rarely took birds beyond the boundary of the previously-scanned area. Birds that chose to remain in the same scanning position had higher subsequent probabilities of taking prey than those that moved to scan a fresh area. There was a negative correlation between success rate and rate of movement, caused by increased distances moved between pauses in low quality foraging areas, and not by handling times interfering with searching.

Annual survival rates of shorebirds at Teesmouth, N.E. England

P.R. Evans, Department of Zoology, University of Durham, South Road, Durham DH1 3LE, UK.

Since 1975, minimum survival rates have been measured for five species of shorebird (Numenius arquata, Limosa lapponica, Pluvialis squatarola, Arenaria interpres, Calidris alba) by observations of the return of individually colour-marked birds to Teesmouth each winter. For adult wintering birds, no evidence has been found for return of surviving birds to estuaries other than Teesmouth, though other adults may pass through Teesmouth only in autumn and/or spring, and stay for such short periods that they are not observed each year. Return rates provide minimum survival rates because (i) colour-marking might lower survival (tests suggest this is not so), (ii) catching may affect survival or site-fidelity (particularly during the moult period), and (iii) birds caught may not be representative of the population (e.g. they may be 'poor quality' birds pushed to the edge of a flock and hence more easily caught).

In spite of these possible biases, annual survival of adult Sanderling has averaged 83% (6 years), of Turnstone 85% (6 years) and of Curlew 77% (5 years). If birds fail to return between one autumn and the next, their time of death may be allocated to winter (if a bird is last seen before the normal date of spring departure of the population) or during migration and breeding. On this basis, most deaths of these three shorebird species occur in winter, but only in Sanderling was mortality appreciably higher in the very cold winter 1978/79. Curlew mortality is higher than expected for such a large bird, perhaps the result of hunting pressures.

The functional response of an optimally foraging Oystercatcher

Jan Wanink, Zoological Laboratory, University of Groningen, Postbox 14, 9750 AA Haren, Netherlands
Leo Zwarts, RIJP, Postbox 21040, 8900 JA Leeuwarden, Netherlands

A predator which is maximizing its intake rate has to decide how to search and whether it should take or reject a located prey. We performed an experiment to analyze the foraging decisions of an Oystercatcher preying on the bivalve Scrobicularia plana (35 - 36 mm long) which we buried in the substrate at eight different depth classes.

Handling time was measured and appeared to increase for deeper-lying shells. Therefore the profitability of the prey (having a constant energy content) was negatively correlated with burying depth.

Nine different prey densities (4 - 437 m^{-2}) were offered. Since we were able to calculate the bird's encounter rate with the different depth classes, and we knew the relationship between prey depth and handling time, we could predict the intake rate for all prey densities if depth classes 0 cm, 0+1 cm, till 0+1.....+7 cm were selected.

Optimal foraging theory predicts that the bird should select depth classes by which the intake rate is maximized. In our experiment the Oystercatcher should take all classes at the lower prey densities and select only prey depth 0 cm (thus reject 1 - 7 cm) if density was high. The observed depth selection and intake rate were as predicted for the four lower prey densities only. At high densities the Oystercatcher was able to obtain an intake rate above the predicted value, though the bird also took prey from depth classes which it should ignore. It turned out that the bird started to select prey having unexpectedly low handling times; probably shells with their valves not completely closed and thus easy to prise.

The observed relationship between prey density and intake rate could not be described by Holling's type-2 functional response, because the instantaneous rate of discovery, as well as the handling time, were not density-independent as is assumed in Holling's disc equation.

Behaviour of the Killdeer Charadrius vociferus toward intruders in the breeding season

Munir K. Bunni, Iraq Natural History Museum, University of Baghdad, Baghdad, Iraq.

The reactions of Killdeers in the breeding season toward intruders of their own and other species, including man, result from drives to escape, attack, or, more frequently, a combination of both. Different combinations bring about different behaviours, since the escape drive urges the bird to flee and protect itself, whilst the aggressive drive, which becomes prominent in the breeding season, motivates the bird to stay and defend its territory, eggs or young. Intraspecific encounters produced many behaviours. Behaviour towards other birds, and man, was similar to that in intraspecific encounters, but crouch-runs, mobbing flights and injury-feigning were caused mainly by the presence of human intruders. Males were more aggressive than females in intraspecific encounters, but in the presence of a human intruder females were more aggressive, more vociferus, and kept closer to the intruder. Aggressiveness reached a peak in the middle of the breeding season. Crouching as a reaction to intruders was not displacement-brooding, but contained a strong escape element that may be related to the habit of "freezing" by young Killdeers.

Injury-feigning, like many other intruder reactions, can be best explained as a conflict between escape and aggression, resulting in a mixture of the intention-movements of both drives. Variations in injury-feigning resulted from differences in the degree of conflict between the drives. At its simplest, a bird merely crouched in a depression, or behind an object, with its back towards the intruder. Weak displays of injury-feigning occurred before egg-laying and the strongest were usually at hatching. Injury-feigning largely ceased soon after hatching, but catching the young, even when they were well developed, sometimes evoked injury-feigning by parents which had otherwise ceased to display. When eggs were lost, the intensity of injury-feigning declined immediately.

During the first nesting of each pair, the male performed injury-feigning more often than the female. However with second nests and broods the aggressive drive of males had declined, and they injury-feigned only occasionally. At this time the strong aggressive drive of females had declined to a level at which it no longer dominated the escape drive, so that females frequently performed injury-feigning. Injury-feigning may have originated from the locomotory intention-movements of escape and attack. These have become ritualised and adapted to elicit hunting by predators, or to startle or threaten them.

The breeding ecology of the Oystercatcher Haematopus ostralegus L. in the Evros Delta, Greece

Vasilis Goutner, Department of Zoology, University of Thessaloniki, Thessaloniki, Greece

Oystercatchers occurred in the Delta throughout the year. Outside the breeding season they gathered in coastal regions, and dispersed to the inland parts of the Delta at the end of March. These movements were caused by changes in the sea water level, the human activities in the area, interactions with other birds, and searching for breeding territories. Territories were established earlier in the coastal region because of high levels of disturbance in other areas. The population increased after mid-June because birds arrived in the Delta from elsewhere.

The preferred nesting substrate was "loose", consisting of sand, sandy-clay and bivalve shells, rarely with grass. Significant preference for nest sites was found for areas with shallow water (feeding areas) nearby, with lack of disturbance, and with the presence of a "look-out" position within the territory. Oystercatchers nested frequently close to other aggressive bird species. These often gave alarm calls to warn off intruders.

Egg-laying began soon after mid-April and occurred mainly in April and May. Egg-laying was interrupted when feeding grounds were covered by high water levels. High levels restricted the areas available for feeding, and hence the available nutrients for egg production. The incubation period was 25 - 27 days. Hatching started about mid-May. The most important reasons for failure were predation by corvids, and egg collection by people. Predation was the main cause of the observed chick losses. Deformities were rare. Chicks fledged when 32 - 34 days old, and during the fledging period were fed by their parents. Food was mainly annelid worms and crabs, and also bivalves, crustaceans, decapods and insects. Hatching success increased when the corvid nests were destroyed. This resulted in reduced levels of nest predation.

Growth and mortality in chicks of meadow birds

A.J. Beintema, Rijksinstituut voor Natuurbeheer, Postbus 46, 3956 ZR, Leersum, The Netherlands

In 1976 a scheme was started to estimate the age of chicks of meadow birds (Oystercatcher, Lapwing, Black-tailed Godwit, Redshank, Ruff) at the day of capture, by bird ringers. Age estimates are based on bill-length. Bill-length was chosen after studying growth patterns in captivity. Calibration was first based on chicks reared in captivity, and later on capture-recapture data in the field. Since 1976, over 20,000 bill measurements of Lapwing chicks (and several thousands of chicks of other species) have been collected, with enthusiastic help of many individual bird ringers. The numbers of chicks caught are tabulated as in the simplified example in Figure 1. In Figure 1, column totals give the daily ringing totals (all age classes combined), and row totals give annual ringing totals for each age class separately. Diagonal totals give the distribution of hatching dates (Bird curve). Row totals decline with age, as a result of chick mortality. With certain restrictions, mortality rates during the chick stage can be estimated from these row totals, or in more detail, from each diagonal row. Analysis is complicated because of bias, resulting from variations in ringing effort, and age dependent capture chances.

Some preliminary observations are a) the daily survival rate in larger Lapwing chicks (10-35 days old) is approximately 0.96. This value is remarkably constant over the years; b) The daily survival rate in small Lapwing chicks (1-10 days) is much lower, at c.0.82. This value varies considerably between years; and c) clear within-year trends have not yet been found.

It is postulated that problems in temperature regulation, and the effects of this on time budgets (feeding versus being brooded) of chicks, play an important role in early chick mortality.

age						
2			3	9	6	3
1		5	15	10	5	
0	10	30	20	10		
	1	2	3	4	5	6 date

Figure 1. Simplified age-date table of chicks, hatching during four days, and fledging after 2 days, with a daily survival of 0.5 during the first day, and 0.6 during the second day. Total chick survival is 0.3.

Do Forvie Eiders rear enough ducklings to maintain their numbers?

Stephen R. Baillie, BTO, Beech Grove, Tring, Herts., HP23 5NR, UK.
Henry Milne, Culterty Field Station, Newburgh, Ellon, Aberdeenshire, AB4 0AA, UK.

The Sands of Forvie National Nature Reserve, Aberdeenshire holds the largest Eider *Somateria mellissima* colony in Britain, with a summer population of about 5000 adults, of which about 2000 pairs breed. About 80% of the population migrates south to winter on the Tay and Forth estuaries, while the rest remains at Forvie throughout the year. Between 1961 and 1981 the summer population was stable or increasing slowly. Winter numbers at Forvie increased by about 4% per year.

Survival of ducklings between hatching and fledging was very low, averaging 7%. This resulted in less than 500 ducklings fledging in 16 of the 21 years studied. In the remaining 5 years, survival was relatively high, with between 800 and 1500 ducklings fledging per year. Duckling survival was negatively correlated with wet and windy weather during the duckling period, and results largely from gull predation (Mendenhall 1975).

First year and adult survival rates were estimated from ringing recoveries (Brownie *et al* 1978, North and Morgan 1979). First year survival averaged 67%. Using all recoveries of birds ringed as adults, adult survival was estimated as 93%. This figure is probably too low as many of these adult birds were poor quality individuals caught in traps. As estimate of 96%, based on recoveries of birds ringed as adult females, many of which were caught on nests, is likely to be more reliable.Re-sightings of birds colour-ringed as ducklings indicated that most females reared at Forvie return there to breed, but only about half the males do so.

The population size at the start of the study, the numbers of ducklings fledged each year and the estimated survival rates, were used to predict changes in the size of the population. Comparison of these predicted values with actual counts of the population indicated that if adult survival is only 93%, some immigration must have taken place. If, however, it is 96%, duckling production has been sufficient to maintain the size of the population. The proportion of adult females in the population which had been ringed as ducklings provided an independent check that 96% adult survival was close to the true value. Thus high adult survival was sufficient for the low fledging success of the population.

References

Brownie,C., Anderson,D.R., Burnham,K.P. and Robson,D.S. (1978) Statistical inference from band recovery data - a handbook *United States Department of the Interior Fish and Wildlife Resource Publication* 131.

Mendenhall,V.M. (1975). *Growth and mortality factors of Eider ducklings (Somateria m. mollissima) in North-East Scotland*. Ph.d thesis, University of Aberdeen.

North,P.M. and Morgan,B.J.T. (1979). Modelling Heron survival using weather data. *Biometrics* 35, 667-681.

Mating system and breeding biology of the Little Stint Calidris minuta

Olavi Hildén, Department of Zoology, University of Helsinki, SF-00100 Helsinki 10, Finland.

During five summers between 1976-83, the mating system, breeding biology and behaviour of the Little Stint Calidris minuta was studied in Finnmark, northernmost Norway. The population is small, is scattered over extensive areas and fluctuates widely from year to year, which makes collection of sufficient data difficult. In total, 45 nests have been found and 41 adults ringed, measured and weighed.

The species has strict habitat requirements in Finnmark, at the periphery of its breeding range. All the nesting grounds found have included shallow freshwater areas (lakes, pools, river deltas) with flat, sparsely vegetated, shores and surrounded by low tundra heaths. At the best localities, Little Stints show a tendency to form semi-colonies.

Little Stints are completely opportunistic birds, settling to breed where conditions are favourable. Consequently, the numbers found at different localities have varied greatly from year to year, and none of the colour-ringed birds has been recovered. In this respect the Little Stint differs from Temminck's Stint, which shows a strong site tenacity.

The mating system seems to involve successive bigamy by both sexes, each female laying two clutches with different males and in different areas. The facts supporting this are: 1) each clutch is always incubated by a single bird, either a male or a female; 2) in "male nests", the female always disappears from the territory immediately after clutch-completion; 3) no pairs of nests with identical eggs have been found in the study areas; 4) in late June new birds may arrive and start nesting; and 5) the number of nests within an area under continuous observation may exceed the number of pairs. It is not clear, however, which males fertilize the second clutch.

Egg-laying takes place in mid- or late June. The nest lies almost exposed on the tundra, usually on dry ground and not far from the shore. Of 44 complete clutches, 5 had 3 eggs, 38 had 4 eggs and one had 7 eggs. The incubation period was in three cases 20 to 21 days. A newly-hatched chick weighs 3.9 g, on average.

Optimal foraging in mixed species wader groups

D.B.A. Thompson and C.J. Barnard, Department of Zoology, University of Nottingham, Nottingham, U.K.

Optimal foraging theory (OFT) makes precise predictions about how predators maximise their foraging efficiency. Prey size selection by several wader species, notably Oystercatcher Haematopus ostralegus and Redshank Tringa totanus, has been well studied in this respect. Three predictions of OFT have been upheld: (i) that predators select the most profitable prey type (in terms of energy intake per unit handling time); (ii) that predators increase selection for profitable prey as encounter rate with these increases; and (iii) predators take unprofitable prey only when their encounter rate with profitable prey is low.

We tested these same predictions in mixed species winter associations of Lapwings Vanellus vanellus, Golden Plovers Pluvialis apricaria and Black-headed Gulls Larus ridibundus foraging for earthworms on agricultural pasture. We assumed that birds selected worms on the basis of energy content and a number of time and probabilistic costs which we measured in the field. In the absence of gulls, both Lapings and Golden Plovers took mainly the most profitable size class of worm (16-32mm). They became more selective as the density of profitable worms increased in the turf. In the presence of gulls (which existed solely by stealing large worms from plovers), plovers took significantly smaller worms, again as predicted by our model which incorporated the additional costs of losing worms to gulls. However Lapwings did not increase selectivity for these worms, so the presence of gulls was associated with a failure by Lapwings to respond to prey density in the way predicted by OFT.

An optimal diet-breadth model predicted that birds should take the three most profitable size classes when their encounter rates with these was high. It turned out that these made up 85-90% of the birds diet, and that the probability of taking unprofitable worms was negatively correlated with the probability of taking profitable worms. However, birds did not ignore unprofitable worms completely when profitable worms were abundant. This appeared to be due to the problem of assessing the size of concealed worms and the likelihood of making mistakes.

A more complex OFT model was applied to the kleptoparasitic feeding activities of gulls, where the main components were the energetic cost of an attack, the energy content of the worm attacked, and the probability of the gull being detected (and so having to chase the target plover) whilst making its attack. Between 85% and 92% of attacks made by gulls occurred over the range of distances (between gull and target plover) which maximised their net rate of energy intake, and 96% of the gulls diet was composed of the most profitable sizes of worm made available to plovers. Furthermore, there was a positive relationship between the rate at which gulls stole large worms and rate at which they were produced by plovers. Interestingly, gulls did not attack Lapwings and Golden Plovers at random, instead they biassed their attacks towards Lapwings against which they were more successful. Gulls foraged most efficiently when stealing worms from Lapwings in flocks without Golden Plovers. This was because mixed-species plover flocks tended to have higher gull:plover ratios, and higher rates of intraspecific aggression between gulls.

References

Thompson,D.B.A. 1983. Prey assessment by plovers (Charadriidae): net rate of energy intake and vulnerability to kleptoparasites. Animal Behaviour 31: 1226-1236.

Thompson,D.B.A. & Barnard,C.J. 1984. Prey selection by plovers: optimal foraging in mixed species groups. Animal Behaviour 32: in press.

Thompson,D.B.A. Kleptoparasitism and host choice: dynamic optimal foraging by gulls. Submitted.

The breeding wader population of the Western Isles and the Integrated Development Programme

N.E. Buxton, Nature Conservancy Council, 4 Sand Street, Coulregrein, Stornoway, Isle of Lewis, U.K.

Over the last decade, it has become apparent that considerable numbers of waders breed on the machair of the western seaboard of the Western Isles. In 1982, the Western Isles became the recipient of grant aid via an Integrated Development Programme (IDP), partly funded by the EEC. A proportion of the funds were available for land improvements. In order to assess accurately the implications of the IDP for wildlife, it was necessary to have a detailed knowledge of the numbers and distributions of the wader species.

A joint survey in 1983 by the Nature Conservancy Council and Wader Study Group showed that there was a total breeding wader population of some 12200 pairs on the machair of the Southern Isles (the Sound of Harris southwards). Lapwings *Vanellus vanellus* were most numerous (3450 pairs), but Oystercatchers *Haematopus ostralegus*, Ringed Plovers *Charadrius hiaticula*, Dunlins *Calidris alpina* and Redshanks *Tringa totanus* were also common (about 2000 pairs each). Detailed information on the distribution of each species was obtained.

Of the IDP land improvement projects so far submitted for grant aid, approximately 10% each involved drainage or reseeding, and 50% concerned fencing. These have involved largely reclamation of previously cultivated land, or replacement of existing fencing, so to date the grant-aided projects have had little effect on the natural environment. It is possible that this emphasis may change over the succeeding years of the IDP. However, the full international importance of the breeding wader populations is now appreciated, and their distribution - a vital basis for environmental advice to the IDP - is mapped.

The Feeding Ecology of Semipalmated Sandpipers in the Bay of Fundy

Peter W. Hicklin, Canadian Wildlife Service, Sackville, N.B., Canada EOA 3C0

The southward migration of Semipalmated Sandpipers in the Bay of Fundy begins around 18-20 July, and peak numbers of 100,000 or more are attained about 1-5 August at roost sites in Shepody Bay. Numbers decline soon after peak numbers are reached. While in Fundy, the birds store fat reserves in preparation for a non-stop flight to the northern coast of South America. The main prey taken by Semipalmated Sandpipers in Fundy is the burrowing amphipod *Corophium volutator*. The sandpipers forage on those mud flats with the greater densities of *Corophium volutator*, and on those flats they spend the greater proportion of the available foraging time in areas of higher *Corophium* densities.

Corophium reproduces over the summer months and production is greatest in May and July. Using McNeil and Cadieux's (1972 *Bird-Banding*) formula, the fat level required for Semipalmated Sandpipers to fly from Fundy to the Lesser Antilles and the coast of Surinam is 15-20 grams. Analysis of 68 specimens showed that 42% had attained those levels of fat stores 9 days after migration began. The mean fresh weights of adult sandpipers increased markedly during the first 10 days of migration and levelled out after 1 August. Between 20 July and 1 August, rates of fat deposition ranged between 0.9 and 2.5 grams fat bird^{-1} day^{-1}. The birds which first arrived in late July selectively preyed on the larger amphipods (the wintering and May cohorts). By mid-August, the mean size (length and biomass) of *Corophium* in the mud was significantly reduced. However, numerical densities increased owing to high reproductive rates. Because of the decreased size and therefore energy content of individual prey items, juvenile sandpipers need to ingest a larger number of prey each day or to stay in the area for longer periods in order to maintain rates of fat deposition similar to those of adults.

Redshanks in the breeding season

W.G. Hale, Department of Biology, Liverpool Polytechnic, Byrom Street, Liverpool L3 3AF, U.K.

In many waders, studies of the breeding biology are hampered by the lack of sexual dimorphism. In the Redshank there are significant overlaps in weight, wing-length and coloration. Behaviour is not a reliable method of sexing. In some cases males will attempt to copulate with other males. Cloacal size immediately after laying allows the sexing of some females, but in the long term the most reliable method is to construct a web of pairings over the season; data from eleven breeding seasons of our Redshank study gives a good indication of the sexes of the majority of birds in the population.

Redshanks tend to mate for life, although some divorces have been recorded. Each sex shares incubation and brooding of young, although one bird, usually the female, may leave during the fledging period. At many nests only one bird is trapped. Possibly some males mate with two females, though this is very difficult to demonstrate, and records in the literature are open to considerable doubt as other interpretations of observations leading to the conclusion that triangles occur are possible. Occasionally a pair of Redshanks may produce a second clutch before the first one hatches, though this is unusual. Records of three birds trapped at one nest are interpreted as a single bird from another pair being attracted to a trap containing a bird.

In general, care should be taken in interpreting observations on breeding strategy where the sexes are indistinguishable, and particularly where alternative interpretations are possible.

Coexistence of Golden Plover and Dotterel on the breeding grounds: competition or symbiosis?

Ingvar Byrkjedal, Zoological Museum, University of Bergen, Bergen, Norway.

In a study area at about 1200 m altitude on Hardangervidda, S.Norway, 20-25 Golden Plover pairs and 5-29 Dotterel pairs nested each year over 5 years. The numbers breeding of the two species did not correlate. In the same stage in the breeding cycle the species showed niche overlaps of 85-99% for habitat and feeding method, and 68% for a small sample of stomach contents. Intraspecific niche overlaps at different stages of breeding were less (48-74%; habitat, feeding method) than interspecific overlaps at the same stage. Both species preferred the same part of the study area, and Dotterels seemed to nest inside Golden Plover territories more often than expected by chance. Only a few cases of Golden Plovers chasing Dotterels were seen, all in the pre-territorial and early territorial period. Golden Plovers hold large territories while Dotterels do not. The limited use Golden Plovers make of their territories for feeding suggests that the territories function mainly to achieve spacing of nests and broods to reduce predation. It is believed that the Dotterel is allowed to breed inside the Golden Plover territories as its anti-predator behaviours are so different from those of the Golden Plover.

It is suggested that Golden Plovers might gain advantage by the presence of Dotterels, as a predator is then less likely to specialise on Golden Plover nests and chicks. The Dotterel may also take advantage of the wariness of the Golden Plovers, which, by their loud alarm calls, may function as "watch dogs".

Within-season variation in the detection of Redshank *Tringa totanus* on upland moorlands

T.M. Reed, Chief Scientists Team, Nature Conservancy Council, P.O. Box 6, George Street, Huntingdon, U.K.

Changes in the detectability of Redshank during the breeding season were examined from records gathered by transect survey in Co. Durham, England in 1981. Birds were most abundant between late April and late June. Vocal registrations reached a peak in early (3-20) June, when non-vocal records were lower. Adults alarm-calling as if with young ("j-calls") occurred in 88% of all territories; 96% of registrations in the period 3-20 June were "j-calls", the same time as first hatching dates reported on nest record cards.

The number of visits was correlated with the number of registrations, but not with the number of vocal records. The number of vocal records in May and June correlated with final population estimates. Population estimates based on infrequent survey visits will produce misleading results unless careful account is taken of the timing of the visit. The optimum time for a single visit in a typical year is the first 3 weeks of June.

The social significance of breeding plumage variability in the Turnstone

D. Philip Whitfield, Department of Zoology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, U.K.

An observational and experimental study was conducted on the Valassaaret archipelago, Finland, in an attempt to ascertain why the breeding plumage of the Turnstone *Arenaria interpres* is so highly variable in comparison with some other species of waders. Two hypotheses were tested: 1) that the dominance status of individuals is signalled by plumage characteristics and, since status differs between individuals, so does plumage; and 2) plumage variability allows territory holders to recognise each other and avoid energetically costly and wasteful territorial disputes between neighbours of this highly aggressive species. The status-signalling hypothesis was rejected for several reasons, including a lack of correlation between territory quality (= dominance status) and measures of male plumage variability, and there being no correlation between plumage characteristics of males and females of mated pairs. The individual recognition hypothesis was supported by the results of an experiment using models, which showed that male Turnstones could visually discriminate between territorial neighbours and non-neighbours.

Food-stealing in territorial and non-territorial Oystercatchers during the breeding season

Geir Olav Toft, Department of Animal Ecology, Zoological Museum, N-5014 Bergen/Univ., Norway

Food-stealing was studied during the breeding season at Hagavagen Bay (58°55'N 5°37'E), SW Norway, in a colour marked population of Oystercatchers *Haematopus ostralegus*. Breeding birds were faithful to the area, while non-breeders were more mobile. Individual birds fed on a range of prey items, using different feeding methods. Territorial birds found and swallowed more prey items than non-territorial birds. Territorial and non-territorial Oystercatchers attacked conspecifics at a fairly equal rate. Attacks were mainly concerned with food. Territorials were attacked significantly less than non-territorials by other Oystercatchers, and territorial birds lost significantly less prey to other Oystercatchers than did non-territorials. Territorial birds also defended their prey. Territorial birds attacked other conspecifics significantly more during the pre-hatching period (April-May) than during the post-hatching period (June-August). Non-territorials were attacked significantly more during the post-hatching period, although non-territorial birds attacked conspecifics at a similar rate pre- and post-hatching.

Territorial females stole/obtained food from their own mate, but the male never stole from his own female. Dominant polygynous females stole from the subdominant females of the polygynous associations.

Food-stealing benefits territorial/high status birds, which are apparently rewarded by their aggressive activities. Food-stealing may also favour territorial females. These may increase the quality of their eggs by this behaviour.

Feeding territories in Curlews (20Y revisited)

Bruno Ens, Zoological Laboratory, State University of Groningen, Kerklaan 30, Haren (Gr.), Netherlands.
Present address: Research Institute for Nature Management, P.O. Box 59, 1790 AB Den Burg, Texel, Netherlands

Since 1977 Curlews have been caught, colourmarked and studied along the Frisian coast of the dutch Waddensea by Leo Zwarts (Rijksdienst Ijsselmeerpolders) and collaborators, including the author. Numbers "wintering" on the tidal mudflats are similar from year to year, apart from seasonal changes. Lowest numbers typically occur in November, but observations on marked individuals indicate that this may be due to an increased amount of time spent feeding in the fields, rather than migration. Apparently, individual birds return to the area, year after year, to stay there from July until April.

Approximately 20% of the individuals defended a feeding territory on the mudflats in summer and autumn. Two hypotheses were investigated, concerning the possible benefits of territorial behaviour, offsetting time lost in aggression.

1). Territorial behaviour may slow down depletion of the food stock: Dugan (1982. *J. Anim. Ecol.* 51: 849-857) has even suggested hoarding. The marked female Curlew 20Y studied intensively in 1978, 1979 and 1980 abandoned her territory in 1979, which was accompanied by a notable decrease in intake rate. This was probably due to a decrease in the available biomass of clams *Scrobicularia*, but the impact of Curlew predation proved hard to measure. Our subsequent studies have therefore concentrated on the ragworm *Nereis* (staple food of the majority of Curlews). In 1979 territories were defended at intermediate densities of food (Ens & Zwarts, 1980. *Watervogels* 5: 155-169), as in Sanderlings (Myers et al. 1979. *Auk* 96: 551-561). In summer and autumn of 1980 worm density decreased most within territories (Esselink, pers. comm.). Curlew predation could account for only 4% of the decline, which was probably mainly due to predation by other species (birds, fishes and invertebrates) not excluded from the territories. Hence the depletion hypothesis appears untenable.

2) Short-term renewal of the food supply puts a premium on systematic foraging (maximizing the time between successive depletions of a food patch) and exclusive use of an area (review in Davies 1980. Ardea 68: 63-74). Two mechanisms seem plausible: a) depletion of a small attackable or detectable fraction of the prey population; b) prey depression due to escape behaviour on the part of the prey (Charnov et. al. 1976. Am. Nat. 110: 247-259). However, only the first mechanism seems potentially predator-specific. Initial observations indicated that feeding rate declined the more often sites of 25 m^2 had been visited previously, but subsequent work failed to substantiate this trend (Esselink, pers. comm.). Tidal changes in the availability of *Nereis* may be responsible for the conflicting results. Understanding the factors that make *Nereis* available to Curlews seems an important and potentially rewarding research goal for the future.

Body condition of shorebirds in spring: preparations for the breeding season?

N.C. Davidson, Department of Zoology, University of Durham, South Road, Durham DH1 3LE, UK.

Both fat and protein (measured by pectoral muscle size) reserves of waders increase rapidly in spring prior to migration to the breeding grounds. Consistency of timing and level indicate that these are internally-regulated, as are reserves in winter. Distances flown with a known amount of fat are difficult to assess, since flight range estimates vary widely, but some Knots *Calidris canutus*, Sanderlings *C.alba* and Dunlins *C.alpina* can probably fly direct from refuelling sites around the North Sea to breeding grounds. Some waders may undergo a pre-migratory dehydration. This would markedly increase the flight range through an increase in effective lipid index. At this part of the annual cycle, fat is used to fuel migratory flight, as an energy reserve for survival through severe weather on the breeding grounds, and possibly to aid egg formation. Pectoral muscles are increased in size to power flight with the large (up to 50% of body mass) fat load, to aid survival in severe weather, and probably to provide a protein source to aid egg formation. Flight theory predicts that pectoral muscles decrease in size during flight, but little is known of the fat or protein condition of waders arriving in the arctic. Total mass at this time could represent anything from no fat reserves to a 15% lipid index - sufficient for survival for several days without food.

Habitat specialization in breeding shorebirds: a defence against egg-predation?

M.W. Pienkowski, Department of Zoology, University of Durham, South Road, Durham DH1 3LE, UK.

There are currently two main hypotheses to account for habitat specialization and territorial defence by breeding shorebirds: (i) to secure an adequate food supply for the start of the breeding season; and (ii) to reduce the chance of nest-predation. The latter could have evolved through improved egg-camouflage leading to a close match with a specific nesting habitat, combined with spacing out of nests. Several features occurring in many wader species cast doubt on hypothesis(i). These include (a) the large amount of feeding that occurs off-territory in many populations; and (b) the great degree of variation (even within a small area), both within and between species as to whether or not territories are used for feeding. Several other observations tend to support hypothesis (ii). These include the evidence (a) that Ringed Plovers *Charadrius hiaticula* vary their territory size inversely with the closeness of match between egg-markings and habitat; and (b) that many shorebird species nest in their highest densities in sites protected by their inaccessibility to predators, by plentiful nest cover, or by anti-predator defence by other species nesting nearby.

Unfortunately, feeding and nest-protection conditions often vary in such ways that the expectations of both hypothesis (i) and (ii) run parallel. A natural experiment occurred at Lindisfarne, NE England, between 1973 and 1983 due to the deposition of wind-blown sand over much of the area. This appeared to affect nesting conditions in some areas by covering much of the gravel previously favoured by nesting Ringed Plovers and to which their egg markings are closely adapted. No changes in feeding conditions were apparent. The numbers of breeding Ringed Plovers fell by about 50% in the areas where the nesting habitat had changed, in accordance with hypothesis (ii). It is not known whether this resulted from a redistribution of birds which had previously bred or from a failure by young to replace adults that died.

Numbers and distribution of migratory geese, ducks and waders at a new dike in the Danish Wadden Sea

Karsten Laursen, Iver Gram & John Frikke, Game Biology Station, Ronde, Denmark

In 1979, a new sea wall was built in the southern part of the Danish Wadden Sea. It stretched from Emmerlev Klev in the north, over the Danish-German border to the Hindenburg dam in the south. 11 km^2 has been reclaimed off Højer, in the Danish part. 5 km^2 has been reclaimed off Rödenas in the German part. The reclaimed areas were originally saltings and mudflats. In the remaining Wadden Sea area west of Højer and Rödenas, and in the reclaimed areas, 12 species have reduced in numbers, the numbers of 1 species is unchanged, and the numbers of 9 species have increased. The total reduction in numbers within each group of species was 50% in geese, 35% in ducks and 30% in waders. Changes in numbers off Højer and Rödenas were not the same. The reductions at Højer compared to those at Rödenas were 75% against 30% in geese, 50% against no change in ducks, and 75% against no change for waders. Aerial counts showed that these changes have occurred throughout most of the Listerdyb tidal area (450 km^2). For the Brent Goose, these changes seem to have occurred throughout the entire Danish Wadden Sea. Reasons for the changes in distribution, particularly the differences between Højer and Rödenas, were discussed. The new sea wall at Højer has been placed in the mudflats, so the upper part of the flats, which has a high proportion of the prey biomass, has been lost, together with roosting sites at the foreland edge. These conditions have been maintained at Rödenas, where the sea wall has been withdrawn to, and partly behind the foreland edge.

The effect of time limitation on cockle feeding in the Oystercatcher

L.L.M. de Bruijn & C. Swennen, Netherlands Institute for Sea Research, Texel, The Netherlands

In cage experiments it was shown that Oystercatchers divide their daily food intake equally over the two low water periods, independent of the low water being in the morning, afternoon or in the night. There was considerable variation in total daily intake. Moreover, consistent individual differences in total food intake were found. On average in winter the birds ate somewhat more than in summer.

Birds with chisel-shaped bills invariably stabbed their cockles open, while individuals with blunt bills hammered a hole in the shells. On an average stabbers had a high intake at the beginning of the low water period, a lower intake in the middle and a higher intake again at the end. Hammerers started feeding slowly and gradually increased intake rate towards the end of the low water period.

Mean total intake in the series of trials with a steady duration of low water period of 6, 4, 3 or 2.5 h was equal. In trial series with unpredictable lengths of the low water period, including 6, 4, 3, 2.5 h and periods in which the flat stayed submerged, the intake increased with increasing length of low water. Even though the mean low water period length was 3.2 h in these series, mean total intake was the same as that achieved during the 6 h low water period schedule. During all of the series the birds maintained a steady weight.

In the low water periods of reduced length, the birds used a greater proportion of the available time for foraging, and, in addition, had a higher intake rate while foraging.

Use of space by Grey Plovers: Why do individuals differ?

D.J. Townshend, Department of Zoology, University of Durham, South Road, Durham, DH1 3L. UK.

The movements and use of space of individually coloured-marked Grey Plovers Pluvialis squatarola were studied at Teesmouth, N.E. England from 1975 to 1983. Individual Grey Plovers showed strong year-to-year fidelity to both their use of space within Teesmouth, and their patterns of movement to and from the estuary. This fidelity demonstrates that these individuals did not adopt a behaviour pattern each year after assessment of their position in a social hierarchy, or of food density and distribution at Teesmouth. Instead, it was the spacing behaviour and movements of juvenile Grey Plovers in their first autumn that determined their behaviour in subsequent winters.

Juveniles arriving at Teesmouth in autumn competed for feeding territories with adults returning to territories they had held in the previous year. Some juveniles gained territories, others stayed and fed non-territorially, and some left the estuary. In subsequent winters, surviving individuals were faithful to the pattern adopted at this time in their first winter.

The pattern of behaviour adopted by a juvenile was related to its body size (as measured by wing length). The mean wing length of juveniles that stayed all winter was significantly larger than that of the rest of the marked population of juveniles. Also, juveniles showing territorial behaviour in autumn were significantly larger than those not doing so.

The competition between juvenile and adult Grey Plovers on the main territorial areas in autumn suggests that defence of a feeding territory was the favoured strategy for Grey Plovers at Teesmouth. One would, therefore, expect the mortality of territorial birds to be lower than that of other birds. The (low) annual mortality rates of the two groups are similar, but over the winter period (when these feeding territories are defended at Teesmouth), limited data suggest that territorial birds had a lower rate of mortality than other adult Grey Plovers.

Grey Plover time budgets - A hard day's night

A.G. Wood, Department of Zoology, University of Durham, South Road, Durham, DH1 3LE, UK.

Measurements of energy intake in a variety of birds have shown that most species require between two and four times Standard Metabolic Rate (SMR) averaged on a daily basis. Yet estimates of food intake of the Grey Plover by previous wprkers have shown that by day in mid-winter, they acquire energy at the rate of only about one times their presumed SMR, estimated by extrapolation from SMR/weight relationships. Measurements of the SMR of the Grey Plover confirm that the estimated values of SMR from metabolic rate/weight relationships are not too high. Therefore the only way a Grey Plover could balance its energy budget would be for it to forage by night.

Territorial Grey Plovers at Teesmouth by day spend in excess of ninety-five percent of the time for which they are on territories (the five hours around low water) in foraging activity. Observations by night with an image intensifier could not detect any significant difference between the daytime and the nocturnal time budgets. So for the Grey Plover at Teesmouth, night-time activities are at least as important as daytime in terms of foraging time.

A closer look at individual birds, using radio telemetry, indicated that territorial Grey Plovers usually used their low water feeding territories both by day and by night. However on some dates territorial birds used areas other than their recognised territory. This use of 'odd' foraging locations was probably a response to extreme weather conditions. To investigate what constituted extreme weather conditions for Grey Plovers, principal components analysis was carried out on a range of metereological variables.

This analysis identified one component which was strongly correlated with the occasions on which territorial birds used 'odd' foraging locations, namely a component highly correlated with temperature variables but poorly correlated with windspeed and other variables. This indicates that it is extreme temperature which is the significant factor in effecting a change in behaviour of territorial Grey Plovers.