

FOURTH MEETING ON THE ECOLOGY OF SHORE-BIRDS

This series of meetings of people working on the ecology of estuarine and shore-birds has been held at approximately two-yearly intervals, alternately at Durham and Liverpool. The fourth meeting, which took place at Edge Hill College of Higher Education, Ormskirk, near Liverpool from 9 to 12 April 1979, was held under the auspices of the International Waterfowl Research Bureau's Feeding Ecology Research Group (Co-ordinators Dr. R. Drent and Dr. P. R. Evans) and the local organisation of Dr. W. G. Hale. Approximately 50 people attended, including a strong contingent from the Netherlands and several from elsewhere in Europe and America. Abstracts of papers presented are given below.

Session 1. Breeding in relation to food supplies (Chairman: Dr. J. D. Goss-Custard)

The background to studies on breeding waders

by W.G. Hale, Department of Biology, Liverpool Polytechnic

To date most work on the feeding ecology of wading birds has been carried out in the winter, and on the Ribble waders take rather less than 10% of the annual invertebrate productivity. A large part of the productivity may not be available to them but it is interesting that in Alaska sandpipers on the breeding ground take more than 25% of the annual productivity (Norton 1973, Maclean 1973). This comparison is not meaningful without information on availability, but other evidence (e.g. Holmes, 1971 and Holmes & Pitelka 1968) suggests that waders are close to their food limit on their breeding grounds.

In the high arctic food may be at a premium on the return of breeding birds at the beginning of the breeding season and it may well be that the fat supply carried by the Pectoral Sandpiper Calidris melanotos enables it to exist for some days with little food intake at this time; a similar adaptation may occur in other waders.

Dispersion over the breeding area may be brought about by territoriality, which in most species wanes by the time of the hatch. However, territoriality may limit the number of young produced without directly providing a feeding area for the young. When territoriality is absent, e.g. in Redshank Tringa totanus, the population may be regulated in a density dependent manner by the availability of water holes to which the young may be led, cf. classical rose-thrip situation where climate also acts in a density dependent manner. In the high arctic a similar situation may result where pockets of good food supplies exist.

In summer the food of waders changes from marine invertebrates mainly to insect food which has a higher calorific value per unit weight. Many waders also feed on berries (Kumari 1958).

At present relatively little information exists on the feeding ecology of wading birds during the breeding season and detailed studies are required in both Arctic and temperate situations. It is suggested that initially attention should be paid to:- 1. food availability on return to the breeding ground; 2. food supply in relation to territory; 3. adult and chick weights during the breeding season; 4. the use of feeding enclosures in the feeding areas during the breeding season; 5. estimation of quality/quantity of food; 6. comparative information on summer/winter feeding; 7. moult in relation to food supplies.

- Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers. Condor 73: 93-99
- Holmes, R.T. & Pitelka, F.A. 1968. Food overlap among co-existing sandpipers on northern Alaskan tundra. Systematic Zool. 17: 305-318
- Kumari, A. 1958. Rabakuroitsaliste toitiumsest Ornitholagooilme Kogumik. 1:195-215
- Maclean, S.F. 1973. Life cycle and growth energetics of the arctic crane fly Pedicia n. autennatta. Oikos 24: 436-443
- Norton, D.W. 1973. Ecological energetics of Calidridine Sandpipers breeding in northern Alaska. Ph.D. Thesis. (Alaska)

Nest predation in relation to snow-cover as a factor influencing the start of breeding in shorebirds.
(Abstract of a paper in press in Ornis Scandinavia)

by Ingvar Byrkjedal, Zoologisk Museum, University of Bergen.

Prolonged pre-laying periods of Golden Plovers Pluvialis apricaria on Hardangervidda, southern Norway, have been recorded corresponding to the late thaw. High vulnerability to predation of nests situated on small, snow-free patches could be an ultimate factor in timing the start of egg-laying in Golden Plovers, and in other shorebirds as well. This hypothesis was tested by exposing two series of artificial nests to predation under widely different snow conditions (mid May and mid June). Each series was exposed for 6 days, and comprised 20 nests with 2 eggs of Black-headed Gull Larus ridibundus in each nest. The same nest scrapes were used in both instances. In May significantly more nests (15) were robbed than in June (8), $P=0.02$. Predators were mainly Ravens Corvus corax and Red Foxes Vulpes vulpes. It is speculated that presence of parent birds at the nests would have further increased the difference in predation between the early and the late nest series.

Resource partitioning amongst breeding waders in NE Greenland

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

During the 1974 Joint Biological Expedition to NE Greenland, information was collected on the types and amounts of ground cover occurring in the breeding territories and chick feeding areas of Ringed Plover Charadrius hiaticula, Turnstone Arenaria interpres, Dunlin Calidris alpina, Sanderling C. alba, and Knot C. canutus at four sites along Kong Oscar's Fjord. In each territory or chick feeding area the percentage cover of vascular plants or moss, lichen, open ground and water, together with 14 further subdivisions of these categories, was recorded on pre-printed cards (Green et al. 1978). The average percentages of these different cover types for each species are given in Ferns (1978). Factor analyses and stepwise multiple discriminant analyses were performed on records obtained from 108 territories and 87 chick feeding areas. The following factors each accounted for more than 10% of the variance associated with the amounts of different cover types recorded in the breeding territories of each species (the factors are given in order of importance and are separated by commas): Ringed Plover - bare ground, dry vegetated ground, stony surface, absence of water; Turnstone - dry vegetated ground, dry tundra polygons and stripes, disturbed ground, streams; Dunlin - wet vegetated ground, medium and large pools, small pools; Sanderling - sloping ground with rivers, dryness and lichen, bare and undulating ground, silty ground with lichens. No Knot territories were available for analysis. Factor analysis of chick feeding areas showed clearly that chicks moved away from the vicinity of the nest to sites with a greater cover of vegetation and water, which presumably contained more abundant food supplies (Greenwood 1978).

Stepwise multiple discriminant analysis showed that the nesting territories of each species were clearly differentiated from one another even though there was no interspecific territoriality. The most discriminating variables were the amounts of open ground and pattered ground, and the amount and wetness of the vegetation. Chick feeding areas, on the other hand, were similar in all species, including Knot.

Considerable areas were not occupied by territorial waders, especially those in which the amount of vegetation cover was low (< 30%), or in which the snow melted too late to permit successful breeding (Green, Greenwood & Lloyd 1977). Sites with less than 30% vegetation cover probably do not contain adequate food resources for the formation of eggs. The habitats occupied by each species appear to be related to the main types of feeding methods which they employ. Thus, for example, Ringed Plovers rely on speed to capture items on the surface and can thus exploit much barer areas than the other species, provided that suitable sources of settling adult insects are near at hand. Turnstones feed by pushing and probing amongst dense, dry vegetation, and disturbed soils. Dunlins feed by delicate probing in pools and wet vegetation. Sanderlings feed on small food items at the surface in sparsely vegetated areas, and by probing in streams and rivers. There is, however, a considerable amount of overlap in the range of feeding methods utilized by these species.

Ferns, P.N. 1978. Ecological distribution of wading birds. pp79-84 in Green & Greenwood (1978)
Green, G.H., Pienkowski, M.W., Brown, S.C., Ferns, P.N. & Mudge, G.P. 1978. Methods used for wader studies. pp38-51 in Green & Greenwood (1978)
Green, G.H. & Greenwood, J.J.D. (Eds) 1978. Report of the Joint Biological Expedition to NE Greenland 1974. Dundee: Dundee University N.E. Greenland Expedition.
Green, G.H., Greenwood, J.J.D. & Lloyd, C.S. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. J. Zool., Lond. 183: 311-328
Greenwood, J.J.D. 1978. Activity patterns and habitat distribution of tundra invertebrates. pp 168-182 in Green & Greenwood (1978)

The breeding biology and foraging behaviour of the Turnstone Arenaria interpres in Finland.

by D.M. Brearey, Department of Zoology, University of Durham.

A population of Turnstone was studied during the summers of 1976-1977 on the archipelago of Valassaaret (63°25'N, 21°4'E), in the commune of Björköby - within the narrowest portion of the Gulf of Bothnia. The population of approximately 200 pairs spend the pre-laying period feeding in the coves of the central islands, Storskär and Ebbskär. The coves are shallow, protected, with mud-ooze bottoms and harbour high densities of chironomids which emerged in late May and early June. The coves were communal feeding areas for the Turnstones and territories were not held there.

Feeding observations were carried out to distinguish the feeding behaviours of males and females and the effect of conspecifics on feeding performance. By measuring 6 behavioural components, used to set up an index of wariness, the following conclusions emerged: 1) birds benefit by feeding near conspecifics; 2) females better their feeding performance when in the presence of their mates; and 3) feeding within ones territory greatly decreases the amount of scanning.

Selection of breeding territories was discussed; differences between main island and islets (small surrounding pieces of land) being compared. Birds nesting on islets confined their feeding activity to the breeding territory.

Egg predation on larids by Turnstones occurs throughout the archipelago and it is especially heavy on the islets. On one islet, Yttre, (0.5 ha) predation by Turnstone on Common Gull Larus canus eggs reached 100% of all nests and that on Arctic and Common Terns Sterna paradisaea and S. hirundo reached 64% of all nests. It is not known how much of the bird's diet the eggs make up. Other differences between main island and islets were discussed.

Pairs defended their territories against intruding Turnstones and against potential predators such as Common and Herring Gulls Larus argentatus. Broods remained on the territories for several weeks.

Breeding waders on Rockcliff Marsh

By Graham D. Rankin, Department of Forestry and Natural Resources, University of Edinburgh

Aspects of the breeding biology of Lapwing Vanellus vanellus, Oystercatcher Haematopus ostralegus and Redshank Tringa totanus were studied on a dry, cattle-grazed saltmarsh, Rockcliffe Marsh in Cumbria.

There was a halosere across the marsh from the landward Lolio-Cynosuretum to the seaward Puccinellietum, in which 8 vegetation types could be distinguished. In addition, phytosociological information was obtained for a gravel area, a sea creek, and a grazed meadow behind the sea wall, for comparative purposes. The vegetation of the whole marsh was predominantly graminoid and consisted largely of hemicryptophytic species, owing to the influence of grazing and trampling by cattle.

There was a decline of invertebrate abundance and biomass across the halosere, and a concomitant decline in grazing intensity, as indicated by fresh cowpat density. Cowpat density was positively correlated with the abundance and biomass of total invertebrates. This correlation was largely due to that with Diptera abundance and biomass, rather than other invertebrates (Coleoptera, Arachnida) which exhibited no such correlation with cowpat density. The proportion of dung-associated invertebrates varied across the halosere, but over 80% of Diptera were dung-associated in each vegetation type.

There was a positive correlation between the fresh cowpat densities of each vegetation type in different years. The densities of fresh and old (from the previous grazing season) cowpats were also positively correlated. Cowpat density had, therefore, a high predictability, and was a reliable index of invertebrate (especially Diptera) abundance and biomass.

The proportion of eggs plus chicks of each species which was trampled was positively correlated with cowpat density, which indicated that cowpat density was a valid measure of grazing intensity. The cattle were introduced to the marsh during the first week of May in each year, so that annual differences in the proportion of eggs and chicks trampled were related, in part, to the timing of the laying season of each species. When the laying season was delayed, a higher proportion of eggs were at risk to trampling for a greater part of the incubation period, than if the laying season was earlier.

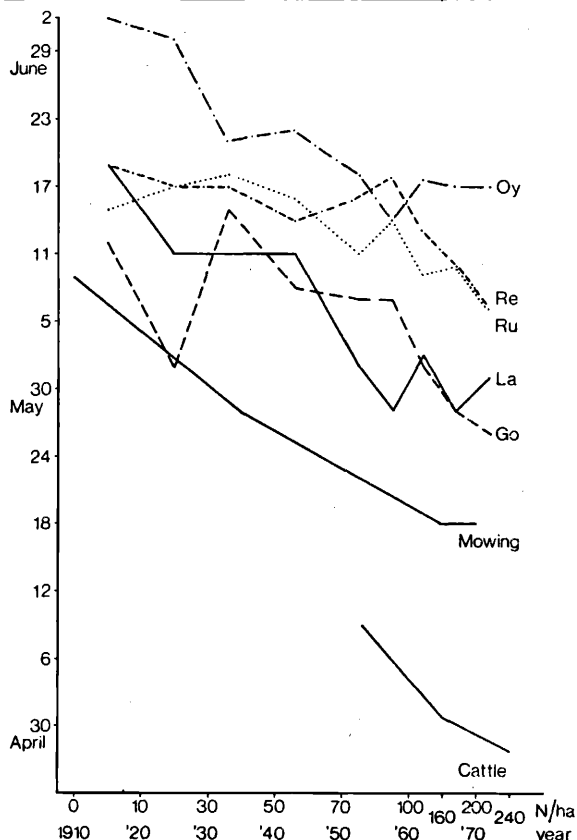
Each wader species tended to nest at a higher than average cowpat density in those areas where the mean cowpat density was low, presumably to maximise food availability, and at a lower than average cowpat density in those areas where the mean cowpat density was high, presumably to minimise the risk of trampling. On a larger scale, Lapwing nest density was positively correlated with cowpat density in each vegetation type. Lapwing nest density was also correlated with Diptera and total invertebrate biomass in each vegetation type. Cowpat density may have been a proximate factor, acting as an index of food availability, the ultimate factor.

Cowpats were not only an index of food availability, they were also a source of invertebrate prey for the waders. Faecal, pellet and gizzard samples indicated that the main prey of both adults and chicks of waders were dung-associated invertebrates.

Recent changes in timing of breeding of inland breeding wader species (meadowbirds) in the Netherlands.

by A.J. Beintema, Rijksinstituut voor Natuurbeheer, Netherlands.

The distribution in time of ringing dates of chicks of wader species can be used as an index of the timing of breeding (hatching) of these species. From these dates (figure) it can be seen that there has been a considerable forward shift in this timing between 1911 and now. Changes in the closing date of the egg-taking season of Lapwings Vanellus vanellus can not be held responsible for this. It is tempting to try to explain earlier breeding by a general warming up of the climate. However, this is not supported by the temperature records in spring. The temperature sum of 200°C (calculated by adding up all mean day temperatures from 1 January onwards, excepting values below zero) is not reached earlier nowadays than at the beginning of the century. This parameter is thought to be relevant for meadowbirds, because at this date farmers are advised to apply fertilisers, as, from then on, the grass starts to grow rapidly. However, there has been a marked change in the use of Nitrogen fertilisers during this century. This leads to an increase in grass growth, which (together with better drainage and consequently a quicker warming of the soil) in turn leads to an earlier date of mowing, and an earlier date of cattle grazing. Average dates (related to N application) are given in the Figure. The slopes of the graphs are remarkably similar to those of the median ringing dates of the Oystercatcher Haematopus ostralegus, (Oy), Redshank Tringa totanus (Re), Ruff Philomachus pugnax (Ru), Lapwing (La) and Black-tailed Godwit Limosa limosa (Go).



Why good Shelduck areas are bad for Shelducks

by Michael W. Pienkowski, Department of Zoology, University of Durham

There are natural tendencies both to regard gatherings of breeding birds as the important areas for conservation and to concentrate studies in such situations. While this may be appropriate for some species, there may be problems in this approach when applied to populations of, e.g. wildfowl and waders, which also breed in a far more dispersed pattern.

We have been studying the population dynamics, breeding biology, behaviour and feeding ecology of Shelducks Tadorna tadorna on the Firth of Forth, near Edinburgh, since 1976, following an earlier study by Jenkins et al (1975, J. Anim. Ecol. 44:201-231). Although part of the work was concerned with testing ideas of regulation in the winter flock put forward by Jenkins, this abstract will be concerned more with the breeding season studies.

In spring some pairs establish territory and breed in isolated situations, usually along linear coasts, while others are found in "colonies" holding mutually adjacent feeding territories, often in small estuaries, and breeding in fairly close proximity in nearby sand dunes. In "isolated" sites the number of fledged young per territorial adult is about seven times that in "colonies", and the "isolated" young grow faster and fledge earlier than "colonial" birds. There is, as yet, little direct data on survival of young after fledging and of adults from isolated sites but there are indications that these are at least as high as for colonial birds. Ringing has shown that the two groups experience similar conditions in the period after fledging. It seems likely that production of young at colonies is insufficient to maintain numbers, and that these are probably made up by recruitment of young reared at isolated sites.

The difference in production of young is due in part to a difference in nesting success which results from mutual interference and intra-specific brood parasitism at nests in colonies. However, more important is the much lower survival to fledging of ducklings at colonies. This results from fighting between adults during which defence of young from Herring Gulls Larus argentatus suffers. Broods may also become mixed and young suffer attacks from adult Shelducks. At isolated sites Herring Gulls are also common but the adult ducks - without the distractions of many other Shelducks - appear well able to defend their young.

We argue that Shelduck behaviour may be adapted to breeding in isolated sites and that, if such sites are not available, they may breed in colonies. Because of the low production in colonies and the probably continual input of birds bred in (and adapted to) isolated situations, it may not be possible for the ducks to become well adapted to colonial conditions.

Wader Study Group Projects

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

Although most Wader Study Group members in Britain know one another and often carry out field work together, their efforts have largely been directed towards gaining knowledge about particular local sites. Many members have expressed the view that it is high time that some advantage was taken of this efficient local network in order to conduct nationally (and internationally) co-ordinated studies. The tremendous gain in our knowledge about wader numbers achieved by the Birds of Estuaries Enquiry, shows what can be done. With this in mind, an advisory panel was set up, co-ordinated by William Dick, to assist the Group's officers in making specific proposals. The aim is not to record information centrally for its own sake (though this too can fulfil valuable functions), but rather to concentrate on a small number of specific projects which can help fill gaps in our knowledge. This year, two such projects have been initiated, one on the spring passage of Siberian Knot Calidris canutus in Africa and Europe, and the other on the spring passage of Dunlin C.alpina, Sanderling C.alba, Ringed Plover Charadrius hiaticula and Turnstone Arenaria interpres, mainly in Britain. These are fully described in an earlier Wader Study Group Bulletin (Dick 1978, Ferns 1978) and progress reports are included in the current issue. If these projects prove to be a success, and members feel they are worthwhile, further co-ordinated studies will be carried out. If anyone feels strongly that attention needs to be paid to a particular topic, their views would be welcomed.

Dick, W.J.A. 1978. Spring passage of Siberian Knot. Wader Study Group Bulletin 24: 5-7

Ferns, P.N. 1978. Spring passage of Dunlins, Sanderlings, Ringed Plovers and Turnstone through Britain. Wader Study Group Bulletin 24: 7-9

Session 2. Food selection and profitability theory/Winter feeding (Chairman: Dr. P.R.Evans)

Dr. R.H.Drent introduced this session with an unprogrammed and highly stimulating review of feeding rates and energetic requirements in various birds in relation to various models of foraging strategies, annual cycles and population limitation. Not only did this generate much discussion throughout the meeting but also led, by popular demand, to an "encore" in the final session.

Consumption and production in the Dutch Waddensea

by Cor Smit, Research Institute for Nature Management, Den Burg/Texel, The Netherlands

The Dutch Wadden Sea consists of 120,000 hectares of tidal flats and 140,000 ha of subtidal area. It is an important moulting, resting and wintering area for large numbers of ducks, geese, waders, gulls and terns from NW and N Europe, Siberia, Iceland, Greenland and the NE part of arctic Canada. In the past years all over the area bird counts have been carried out. By combining these a picture can be developed of the total number of birds.

Many species show a peak in numbers in autumn and spring. The picture of the total number of birds present per month however only shows a peak in autumn and a rather constant number in the months following (fig.1). Consumption of macrobenthic invertebrates has been computed from body weights and numbers, assuming that a bird's consumption per day amounts to its daily Basal Metabolic Rate x 5. Fig. 2a and 2b show the monthly consumption on tidal flats and in the subtidal areas.

The annual consumption of all carnivorous species amounts 10.3×10^9 g ash-free dry weight. This figure comes quite close to earlier estimations made by Hulscher (1975) and Swennen (1976). On the tidal flats 5.1 g adw/m²/year is consumed (60%), in the subtidal area 3.0 g adw/m²/y (40%). Biomass of macrobenthic invertebrates reaches its highest levels from June-August, its lowest from December-March. The amount of biomass on the flats has a mean value of 20-30 g adw/m², in the subtidal area 10-15 g adw/m² (Beukema 1976). On the flats fishes consume about 2.8-4.6 g adw/m²/y, in the subtidal area 2.75-5.5 g adw/m²/y (Zijlstra 1979).

As only few data on the annual macrobenthic production in the Dutch Wadden Sea have been published no conclusions can be drawn as to whether the amount of biomass of prey species limits the number of birds and fishes. More definitive statements can only be made if more information is available on: (1) the energy used by predator species throughout the year; and (2) the production of prey species and their availability to birds and fishes.

Beukema, J.J. 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Neth. J. Sea Research 10: 223-235

Hulscher, J.B. 1975. Het wad, een overvloedig of schaars gedekte tafel voor vogels? pp 57-82 in C. Swennen, P.A.W. de Wilde + J. Haeck (ed.). Symp. Waddonderzoek. Med. Werkg. Waddengebied; Vol 1.

Swennen, C. 1976. Wadden Seas are rare, hospitable and productive. pp 184-198 in M. Smart (ed.) Proc. Int. Conf. on the Conservation of Wetlands and Waterfowl, Heiligenhafen, 2-6 December 1974.

Zijlstra, J.J. 1979. Qualitative aspects of the role of fishes in Wadden Sea food chains. pp 124-132 in N. Dankers, W.J. Wolff and J.J. Zijlstra (ed.) Fishes and fisheries of the Wadden Sea. Final report section "Fishes and fisheries" of the Wadden Sea Working Group.

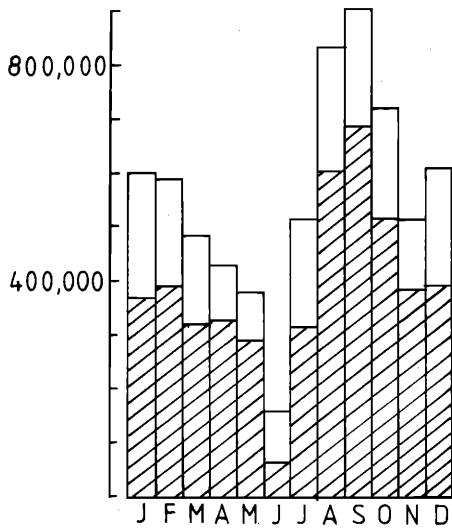


Fig. 1. The total number of carnivorous ducks, waders, gulls and terns in the Dutch Wadden Sea. Hatched; birds foraging on the tidal flats.

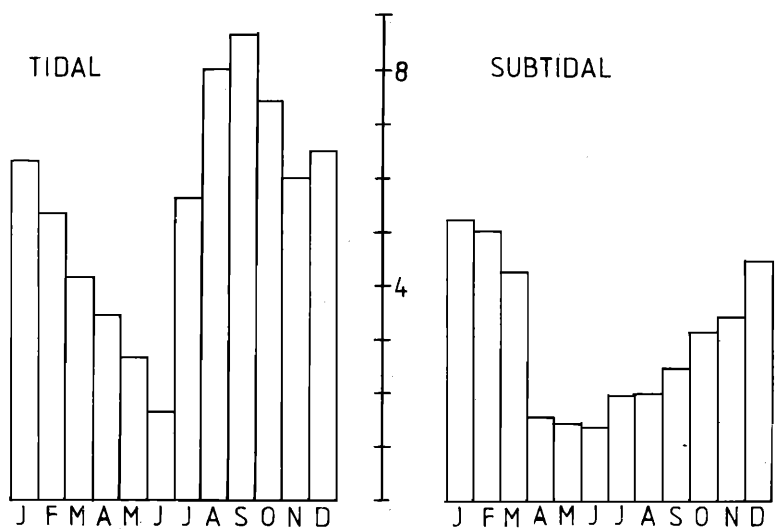


Fig 2. The monthly consumption (in ash-free dry weight x 10⁸) of all carnivorous birds on the tidal flats and in the subtidal area in the Dutch Wadden Sea.

Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds

by C.J. Reading, Institute of Terrestrial Ecology, Furzebrook, Dorset

The seasonal relationship between shell length and depth buried in *Macoma balthica* (L.) was studied on an area of intertidal flats on the east coast of the Wash. Although the larger animals buried deeper than the smaller ones very few (0.28%) occurred below a depth of 7.5cm. The study showed that *M. balthica* migrated vertically within the substratum apparently in response to daylength, so that they were nearest the surface in June and buried deepest in December. The maximum depth buried, in December, by an animal was found to be proportional to the length of its inhalent siphon. The result of this behaviour was to reduce the amount of *M. balthica* biomass accessible to Knot (*Calidris canutus* (L)) from > 90% in June to 4% in December. *M. balthica* was, however, accessible throughout the year to waders with bill lengths greater than 7.5cm, e.g. Bar-tailed Godwit *Limosa lapponica*, and Curlew *Numenius arquata*. The results are detailed in: Reading, C.J. & S. McGrorty 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. Estuarine and Coastal Marine Science 6: 135-144

The use of feeding tracks in locating Macoma by the Oystercatcher

by Jan B. Hulscher, Zoölogisch Laboratorium, Haren Gr., Netherlands

Do Oystercatchers Haematopus ostralegus use surface feeding tracks of Macoma in finding them, or do they not? Experiments were made with a captive bird feeding on plots of experimentally manipulated and natural Macoma populations. Manipulated Macoma populations were made by planting Macoma's in quadrants with sieved mud; thus other species were absent.

In a series of experiments the bird fed in daytime on manipulated plots of one square metre with 50 small (shell length 15mm), 50 large (shell length 19-20mm), or 25 small + 25 large Macoma, either when the tracks of Macoma were or were not erased just before observations started. Within corresponding size classes it took the bird more time to find a Macoma when the tracks were erased. When tracks were not erased small and large Macoma were found equally quickly, but when tracks were erased large Macoma were found more quickly than small ones. It may be concluded that, on manipulated plots, Macoma are found more quickly when feeding tracks are available than when they are not.

When feeding in daytime on erased or not erased plots of the natural Macoma population the results were not conclusive. On average Macoma was found more quickly on plots where tracks were erased.

Results from parallel experiments in daytime and at night suggest that the bird did not localise Macoma by visual track recognition on the natural mudflat. The success of the free birds in daytime on the natural beds corresponded with the success that could be predicted from the results of the captive bird when feeding on corresponding Macoma densities.

The question if Oystercatchers use surface tracks in the natural situation must be left open. A natural flat is covered with tracks of different animal species, many looking very much alike. For the human observer it is practically impossible to pick out Macoma tracks specifically, and probably for Oystercatchers too. On the manipulated plots, where all other animals, except Macoma, were removed, the surface tracks were very obvious, even to the human observer. Apparently the presence of surface tracks of Macoma is not a prerequisite for finding them.

Feeding ecology of Curlew

by Leo Zwarts, Rijksdienst voor de IJsselmeerpolders, Lelystad, Netherlands

This study was performed in the former land reclamation works along the Frisian coast (Dutch Wadden Sea). We pegged out 300 sites (0.1 ha) where the infauna was sampled. The numbers of birds of all species present were counted from towers built near these sites. This short note summarises some data on the feeding ecology of the Curlew Numenius arquata.

Numerical response. In the Curlew the observed feeding density on the mudflats appeared to be unrelated to the density of its main prey species, the ragworm Nereis diversicolor, the shorecrab Carcinus maenas and the clam Mya arenaria. This unexpected result could be explained in several ways. Firstly, the assumed positive correlation between Curlew density and the distributions of the various prey species was masked by the negative correlations between the distributions of the prey species. Secondly, the fact that some Curlews defended feeding territories (see abstract by Bruno Ens) made it more complex to relate Curlew density to food density. Thirdly, there was little overlap in the diet of the (short-billed) males and the (long-billed) females, so that it made less sense to determine curlew density for the counting sites; in fact, this had to be done separately for males and females.

Size-dimorphism and food-selection. Observations on colour-ringed Curlews (trapped by Piet Zegers) showed that the prey-selection was dependent on the length of the bill. Marja de Vries (Groningen University) found that only Curlews having a bill of at least 13 cm preyed upon the clam. For these Curlews at least 40% of the biomass of the clam population (13 g/m²) was attainable. Short-billed curlews which were present in the same study sites took worms (ragworm, lugworm Arenicola marina and sand mason Lanice conchilega) and siphons of the bivalve Scrobicularia plana. It was possible to quantify the food intake of Curlews feeding on clams since the handling time was a good estimator for the quantity of flesh taken from the shell, although this regression line was different for each individual Curlew being studied.

Pellet-analysis. Pellet-analysis showed that our estimates of the sizes of ragworm and shorecrab taken by the Curlews were correct, so that it was possible to calculate the food intake for these prey species too. With the aid of the pellets collected on the same tidal roost in the course of the year, the selection on shorecrab and ragworm could be related to the size frequency distribution of both prey species as found in the samples of the infauna. The small shorecrabs (though very common, being the main prey for Redshank Tringa totanus, Spotted Redshank T. erythropus and Greenshank T. nebularia) were not taken by the Curlews probably because it is more profitable to take only the larger ones.

Territoriality in Curlews Numenius arquata

by Bruno Ens, Zoological Laboratory, Haren (Gr.), Netherlands

A preliminary report was given of a study (concerning feeding ecology, foraging behaviour and intraspecific competition) on a partly colour-ringed wintering population of Curlews, feeding on the tidal mudflats of the Dutch Waddenzee. This was conducted, under the stimulating guidance of Leo Zwarts, by Joke Bloksma, Bruno Ens and Marja de Vries in the summer and autumn of 1978. In 1977 it was found that an increase in Curlew density correlated with a decrease in food-intake of the "average Curlew" (Zwarts, in press). In the 1978 study in Moddergat (Frisian coast) the concept of an "average Curlew" had to be abandoned, because it was found that some Curlews defended territories, whilst others did not.

Territory-owners could be distinguished from non-territorial birds in three ways: (1) For many consecutive weeks they confined most of their activity to a relatively small space (3 territories measured between 0.5 and 0.8 ha). (2) "Yodelling" (the well-known song of the Curlew) occurred against intruding birds and even against Curlews only flying overhead. If intruders did not leave, they were chased. (3) "Border disputes", lasting on average a few minutes, took place between neighbouring territory-owners. In a typical posture the birds walked slowly side by side, occasionally making short runs or pecking at dead shells or at our plastic marker-pegs. Only very rarely did border disputes end in real fighting with pecking and wing-beating.

We agree with Brown (1969) that territorial behaviour should be understood in terms of costs and benefits. Probable costs are time (and energy) lost in border disputes and chasing. Chasing is a cost, because there are more non-territorial than territorial Curlews, so that, per chase, a territory owner loses on average more time than a non-territorial bird.

Because of the present state of our analysis, we could only look at "securing a food-supply" as one of the many possible advantages. A necessary condition, namely that the presence of the territory-owner actually decreases Curlew-density, could be verified in the case of 20Y, a female on which we did most of our observations. Also in accordance with this possible advantage was her predation on her summer food, crabs, of which she took more than 30% during daylight tides. But, although not all clams (which were her main food from August onwards) are available (see abstract by Leo Zwarts), predation pressure, as estimated by our current methods, was still so low, that the defended food stock could only be meant for the whole winter, or even the next year (during the previous winter she was observed on the same site).

Other results of our study indicated that 20Y spent more time preening and sleeping on average than the other Curlews. Finally it was found that, within their sex class, 3 territorial curlews had among the highest trapping weights and 3 non-territorial curlews had among the lowest trapping-weights.

Among the many mysteries to be unravelled next year, we feel one to be especially intriguing: why do territorial Curlews chase out animals of the opposite sex, despite differences in food (see abstract by Leo Zwarts) and habitat-preference between females and males? Concerning the latter: all 10 colour-ringed Curlews observed feeding in the surrounding meadows appeared to be males, as, in our opinion were most of the unbanded Curlews feeding in the meadows.

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The use of space by individual Grey Plovers *Pluvialis squatarola* and Curlews *Numenius arquata* on their winter feeding grounds.

by D.J. Townshend, Department of Zoology, University of Liverpool

The feeding areas used by Grey Plovers *Pluvialis squatarola* and Curlews *Numenius arquata* were studied on Seal Sands in the Tees estuary, north-east England during the three winters 1975-78. To permit long-term observations of individuals, 44 Grey Plovers and 82 Curlews were individually marked with colour rings.

During each tidal cycle, individuals changed their feeding sites according to a predictable pattern. For a single bird this pattern was constant over periods of several weeks or months, and sometimes repeated in successive winters. In both species, four basic patterns of use of space could be identified. These patterns were distinguished by: i) whether one or more than one feeding site was used during a tidal cycle, and ii) whether or not a territory was defended on a feeding site. The strategy employed by an individual bird on a site could be predicted from two characteristics of that site: i) the time after high water at which the site became exposed, and ii) the rate of drying of the substrate. These characteristics determined the availability of *Nereis diversicolor*, the main prey of both species on Seal Sands.

Defence of a territory may confer short-term and/or long-term advantages on an individual in relation to its food supply. It is the most common strategy employed by Grey Plovers in their main feeding area. Evidence from changes in behaviour of Grey Plovers both during and between winters suggests that defence of a territory on a mid-tidal level is the preferred strategy for Grey Plovers on Seal Sands.

Unlike Grey Plovers, Curlews show marked sexual dimorphism in bill length. Bill length influenced the strategy employed by an individual Curlew on Seal Sands. It determined the maximum depth at which the Curlew should capture *Nereis* buried in the mud. Most long-billed Curlews remained on the mudflats all winter. In contrast, many short-billed individuals (which are chiefly males) fed upon the low-lying pastures surrounding Seal Sands rather than on the mudflats. This was particularly noticeable in mid-winter when *Nereis* was buried deeper in the mud. Thus no preferred strategy common to Curlews of all bill-lengths can be determined.

Changes in the body composition of shorebirds during winter

by N.C. Davidson, Department of Zoology, University of Durham

As part of a study of how waders adapt to poor feeding conditions, I have examined the fat and muscle protein levels in various waders from Teesmouth and Lindisfarne in NE England. This allows comparison with the pattern found in Bar-tailed Godwit *Limosa lapponica* at Lindisfarne (Evans & Smith 1975). Fat is the main energy reserve, and Godwits reach a peak fat level of 13% in December, during the shortest days, rather than in January, during the lowest air and mud temperatures and hence lowest prey availability. Similar peak levels are reached by Knots *Calidris canutus* (15%) in December and Dunlins *C. alpina* (13.5%) in December and January. Adults and juveniles have similar

levels of fat reserves in all three species. Redshanks Tringa totanus peak at 14.5% fat in November. Grey Plovers Pluvialis squatarola also peak in December, but at a much higher level (35%) fat, similar to those of Golden Plovers Pluvialis apricaria and Ringed Plovers Charadrius hiaticula.

It is of advantage to plovers to carry higher fat levels because they encounter greater difficulties in finding food in cold weather than do other waders (Pienkowski 1979). During two periods of freezing weather, Golden Plovers (6 days in February 1978) and Grey Plovers (12 days in January 1979) used energy reserves at 2.6 x Standard Metabolic Rate and 3.1 x SMR respectively. This probably supplied most of their energy requirements, only a small fraction coming from feeding. Most Dunlins during the same cold spell in February 1978 did not lose condition, but some juveniles were in poorer condition after the cold weather than before.

Muscle protein is metabolised primarily to balance Nitrogen excretion when there is insufficient protein intake from feeding. In most species there is little change in the level of protein reserves, measured by the weight of the pectoral muscles, through the winter. Godwits, Dunlins and Knots have similar levels, but Golden Plovers have a larger reserve. Redshanks differ from other species in that, although their protein level in autumn is similar to that of other tactile feeders, it declines rapidly between November and February. Lipid levels also decline markedly during the same period. This suggests that Redshanks in NE England, unlike other wader species, are unable to maintain their condition during normal winters. The higher mortality of Redshank than of most other species during cold weather (e.g. Pilcher 1964) is not surprising since they have little energy reserve during mid-winter to use when feeding conditions deteriorate. This is in marked contrast to the other waders studied which have little difficulty in surviving through periods of cold weather.

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Session 3. The adaptive significance of migration (Chairman: Dr. W. G. Hale)

Some questions and hypotheses concerning the timing of migration in shorebirds

by P.R. Evans, Department of Zoology, University of Durham

Most shorebirds have to fit several major physiological events into each year: breeding, moult, two migrations and a non-breeding period. It has often been argued that breeding will be timed to occur when the chances of survival of the chicks are greatest, and that migration is timed to bring birds to the nesting areas by the "best" time for breeding. However, these statements need modification. An individual bird should attempt to breed at such times of year that it maximises the total number of off-spring (which survive to breed themselves) produced in its lifetime. Very little is known of the way in which chick survival, or adult survival, varies with the date of breeding in most waders, so that a "best" time cannot be specified. However, there is evidence that suitable breeding habitat may be limited for some species, and that territorial behaviour excludes some birds, which are physiologically capable of breeding, from even making an attempt to rear young. Thus migration may be timed to bring birds to the breeding areas as soon as they are tenable, and not in relation to the date of subsequent breeding. The penalty of migrating too early is starvation (particularly in the arctic). Conditions in the arctic in a particular spring probably cannot be predicted from conditions in the non-breeding and "migration stop-over" sites, since these are usually south of the polar climatic zone. Hence one might expect arctic waders to migrate to their breeding areas at about the average date by which snow melt allows the first territories to be occupied. Hence the date of their departures from the temperate zone will be similar from year to year, unless the density of available food on the non-breeding sites fluctuate markedly between springs, to such an extent that it delays fat deposition in some years. To avoid such delays, waders might move from the areas used in mid-winter to "fattening grounds", areas either of early production (growth and/or reproduction of the prey) or of high density of prey. The latter might be sites to the north and east of the mid-winter feeding areas, sites which the birds had to leave in autumn (because prey became unavailable when temperatures fell) before prey density had been appreciably reduced by the birds themselves.

After attempting to breed, many adult shorebirds move south almost immediately, even if they lose the nest early in the summer. One or other sex often deserts the brood soon after hatching. This has been interpreted as leaving more food for the chicks, but since most chick losses appear to be the result of predation, not starvation, desertion of the brood by one parent seems counter-productive. Perhaps adult survival is higher away from the breeding grounds. It has been suggested that there is an advantage to be gained by arriving early at migration stop-over points in temperate areas; however there is a disadvantage in moving too far south too early, since high summer temperatures (as well as near-freezing conditions) severely depress prey availability.

Densities of shorebirds are higher on non-breeding than breeding areas. Hence competition for food or feeding space is assumed to be more severe during migration. Recher (Ecology 1966) suggested that species could minimize such competition by differences in their size and anatomical structure, by habitat and micro-habitat selection, by using different migration routes and/or by staggering the timing of their movements. The last suggestion seems unlikely to be effective, if all species attempt to reach arctic breeding areas on approximately the same date, as argued earlier

Selection for size in the Ringed Plover in relation to migration and climate

by R.C. Taylor, Department of Biology, Liverpool Polytechnic

Investigations carried out into selection for size in birds have tended to concentrate upon one or a few selective factors, and to have over-simplified the complex interrelationships between the birds, their environment and their inherited characteristics. In any migratory species there are three problems which need to be considered. Firstly, what is "size"; secondly, where do the different breeding populations winter; and thirdly, what group of potential selective factors are amenable to study? This paper discusses a method of analysis rather than specific results.

Wing-length and weight have traditionally been used as indicators of size in birds, but the temporal variation in these characters reduces their reliability. A multi-variate factor called the discriminant function is generated by simultaneously assessing variation in several characters. The first discriminant function in the Ringed Plover Charadrius hiaticula is probably a better indicator of overall "size" differences than any single character (Taylor 1978).

Ringed recoveries can be used to determine the winter quarters of several breeding populations. For those populations where no ringing recoveries exist but from which measurable specimens are available, the "allocation" sub-routine of the linear discriminant analysis has been used to generate hypothetical recoveries. A comparison of hypothetical with ringing recoveries indicates that this form of analysis is sufficiently accurate in its predictions to make it a worthwhile tool for use in regions where few ringing data are available (Taylor in press).

The selective significance of a series of climatic factors was investigated using multiple regression techniques. "Size" (the first discriminant score), bill length and tarsus length were separately compared with temperature and precipitation variables from the breeding and winter quarters. "Size" in both sexes shows a significant negative correlation with the winter mean precipitation. In the females there is a greater degree of correlation between "size" and the summer climatic variables than in the males. Bill length in both sexes is positively correlated with temperatures in the breeding season, and varies independently of body size. Tarsus length varies independently of body size and is very significantly correlated with mean precipitation. In both sexes, birds with long tarsi tend to breed in wet regions and winter in dry ones.

The conclusions to be drawn are that climatic factors in both winter and summer environments contribute towards selection for overall body size and bill and tarsus length in the Ringed Plover.

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AN INLAND FLOCK OF CURLEWS *Numenius arquata* IN MID-CESHIRE, ENGLAND

by Dennis Elphick

Introduction

When I moved to Cheshire in 1976, I was interested to find that during the winter up to 170 Curlew Numenius arquata were feeding regularly at a group of several fields, about 25km inland of the Mersey Estuary. I could not find reference to such a flock in the county avifaunas but there were a few records in recent Cheshire Bird Reports (CBR). Local bird-watchers suggested the flock was probably a regular feature, but unrecorded because the area was not regularly watched. Regular observations made over a period of several years at two other sites (one 6km to the south-east of my own site and one 12km to the north) showed that up to 100 and 60 birds respectively used these sites in March and April. Since then discussions with local farmers have revealed that feeding flocks have regularly used this part of the Cheshire Plain for at least 25 years and probably for 50 or more! Some reported a big drop in numbers during the severe weather conditions of the 1962/63 winter and said that numbers had increased since but not to their previous level. Farmers' comments also indicated that birds were seen at various sites from late summer, through the winter and in spring.

During the period July to October 1977 I found many more regular feeding sites. There were indications of other sites and some were found when looking for birds dyed yellow in December 1978 (see below). There are seasonal preferences for certain sites; some are only used in spring, others only in late summer/autumn and others only in winter. However, some of the last are used throughout and there is probably some overlap between the last two categories. Farming activities probably determine which areas are most favourable at a particular time. Some sites used in winter are still under silage during the autumn and others are being cultivated in the spring. Newly sown pasture or short permanent pasture, especially adjacent to brooks and streams or in wet, marshy areas appear to be preferred.

Records in the 1975 CBR indicated that birds were regularly seen flying NW at dusk away from the area of my 1976/77 winter observations. On following up these flight lines during September 1977 I located the roost on a lime-bed complex some 20km inland. The roost was not visible from adjacent public roads but permits were quickly obtained to visit the site on a regular basis. During the first few visits in October it was obvious that several hundred Curlews were using the roost, coming from feeding sites in an arc spanning from the NE through E to the south.