

ABSTRACTS of TALKS and POSTERS

Presented at the 1991 Wader Study
Group Conference and Symposium

WADER MIGRATION

Waders and theories of bird migration

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This interesting paper reviewed several aspects of bird migration, including flight, migration speed and rates of fattening as well as orientation. It was mainly illustrated by examples of waders and terns. (Ed.)

Are dispersion patterns of Palearctic shorebirds shaped by competition?

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The hypothesis of asymmetric competition for winter resources amongst migratory shorebirds predicts that competition should decrease with distance from breeding grounds. This prediction is tested by measuring the intensity of competition at a south temperate estuary.

During the austral summer the Berg River estuary, South Africa, supports one of the highest densities of migratory shorebirds on the East Atlantic seaboard. High predation pressure by birds is maintained by high production of invertebrate prey. The observed pattern of partitioning both food and spatial resources was attributed to the superabundance of prey and to specific differences in foraging techniques unrelated to competition. The spatial redistribution of birds within the estuary was related to changes in feeding conditions on the preferred mudflats, rather than density-dependent factors mediated by competition. Aggression indices for the most common waders were either unrelated or negatively correlated with their densities.

Production and P/B ratios of invertebrates on the estuaries and coastal lagoons at temperate and subtropical latitudes are correlated positively with mean ambient temperature and negatively with distance from the equator. It is predicted that the

combination of high prey abundance and production, and a reduced level of competition in the southern hemisphere may outweigh the costs of long-distance migration.

Aspects of the migration of North Frisian Avocets

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Movements of North Frisian Avocets *Recurvirostra avocetta* during the non-breeding season were followed using sightings of individually colour-ringed birds. During moult, Avocets from the study colonies near Husum dispersed to all parts of the Wadden Sea. At the end of the moulting season, most of the North Frisian Avocets wintered in Portugal. Age and sex related distributions of wintering Avocets were discussed.

Length of stay and development of body weight of migrating waders

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The change of the body weight in connection with the length of stay of different wader species (*Charadrius hiaticula*, *Pluvialis squatarola*, *Arenaria interpres*, *Gallinago gallinago*, *Lymnocyptes minimus*, *Limosa lapponica*, *Tringa totanus*, *Actitis hypoleucos*, *Calidris canutus*, *C. minuta*, *C. alpina* and *C. ferruginea*) migrating in late summer and in autumn through the region of Langenwerder Island (Western Baltic) was shown. The variation in staging times and rates of gain of bodyweight, lead to the conclusion that different migration strategies exist. The most rapid weight increases were found in *Calidris canutus* and *Arenaria interpres*, and very low weight increase rates in *Pluvialis squatarola*, *Gallinago gallinago* and *Lymnocyptes minimus*.

Migration, wintering and moult of Little Stints in northeast Italy

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Weekly counts of Little Stint *Calidris minuta* at Saline di Cervia, between February 1990 and May 1991, were compared with capture data regularly collected at the same site and on a tidal area of the Lagoon of Venice, in order to provide a detailed phenological description of migrant and/or wintering populations occurring in northeast Italy, as well as biometrical information

from the northern edge of the species' winter range.

Counts revealed a peak during pre-breeding migration (May) and slightly smaller figures during post-breeding migration (August-October). The wintering population showed much numerical fluctuation during November-January (max. 240 birds, over an area of 800 ha) and disappeared almost completely in February of both years.

Captures allowed assessment of age class ratios within each month from August-February, and within 10-day periods during the migration season (August-October): a higher proportion of adults than previously reported was found in winter (up to 75% in February). Among captured birds (c. 500 birds), significant differences in body mass were observed according to their age, moult condition and time of year. During summer months, the mass of adults in primary moult was lower than of all other categories of birds (i.e. adults in body moult, non-moulting adults, juveniles in body moult and non-moulting juveniles) and much better correlated with date, probably as a result of a less continuous migratory turnover among these birds. During winter, significant differences in the body mass of adults and young were also recorded, the latter showing lower mean values.

Adults in active primary moult (or moulted birds), were caught in comparable numbers, with a similar effort, during 10-day periods from August-December; non-moulting adults outnumbered them till mid-September, then disappeared. Neither birds starting primary moult later than mid-August, nor any going to suspend it, were observed; the first adults which had completed their moult were recorded in late October and all adults examined after late November had renewed all primaries, with a single exception (n = 40). We observed a much later onset of body moult in juveniles than in adults, i.e. in late September and late July respectively.

MIGRATION AND POPULATION PROCESSES

Similarities and differences from year to year in autumn migration of Dunlin at the Polish coast

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The material for the analyses are Dunlins *Calidris alpina* trapped and ringed at the Vistula mouth (near Gdansk) during 1985-1991. The ringing has been undertaken every year by permanent trapping (every whole-day) from mid-July to the end of September, resulting in over 20,000 Dunlins ringed from a total of almost 500 catching days.



Every year adults have appeared in greater numbers in the study area in the second half of July. Juveniles follow c. mid-August with increasing numbers in September. Turnover of birds resting and feeding in the area is very high, but generally lower in juveniles than in adults. Over 50% of trapped adults every year have been actively moulting. Birds with 'adult-buff' coverts have appeared regularly each year and make up about 20% of the total.

The main difference from year to year concerns the number of birds ringed, which largely relates to the number of juveniles present that year in the study area. The proportion of juveniles differs between years, from 36 - 65%, but does not fluctuate regularly. The year following high number of juveniles, we observe greater numbers of second year birds. Small numbers of birds are regularly recaptured each year. Dunlins ringed as juveniles, during previous autumn migrations have been recaptured over 15 months later. The recapture of birds ringed as adults show a similar advance in primary moult.

Weight and retrap data of Dunlins staging on Schiermonnikoog, Dutch Wadden Sea

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During the years 1968 - 1988 on the island of Schiermonnikoog in the Dutch Wadden Sea, 10,104 Dunlins *Calidris alpina* were caught and ringed. Of the Dunlins ringed as adults, 3.3% was recaptured at the same ringing site.

An important question about population dynamics is: do Dunlins with apparently a lower body condition (in this study measured as body mass) have the same or a lower chance to be recaptured than the ones with a better condition? To investigate this, a comparison was made between the weights of 743 non-recaptured Dunlins and the weights of 83 Dunlins, who were recaptured later. The weights of Dunlins caught in August 1977, September 1978 and November 1978 were standardized for structural body size. There were no significant differences between the two frequency distributions of standardized weights of Dunlins.

Therefore, weight (or condition) has no influence on the chance of recapture for Dunlins on Schiermonnikoog. Dunlins with a lower body condition at the moment of capture have obviously the possibility to recover on the mudflats of the Wadden Sea near Schiermonnikoog.

Counting juvenile arctic waders in the Wadden Sea

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There is no place in the Wadden Sea where large numbers of waders are caught in late summer or autumn. Therefore it is usually not possible to get sample sizes from ringing large enough for reliable estimates of the proportions of juvenile for any wader species. Juvenile birds also tend to be caught selectively and their percentage in catches tend thus to be overestimated.

Therefore other methods have to be developed to monitor breeding success of arctic waders in this key migration area. In 1991 we started to count the proportion of recognizable age classes of several arctic wader species in the Schleswig-Holstein Wadden Sea. This was undertaken by very experienced field observers. Adequate sample sizes were obtained for Ringed Plover, Grey Plover, Knot, Sanderling, Curlew Sandpiper, Dunlin, Ruff, Bar-tailed Godwit and Spotted Redshank.

The method also allows us to measure age-specific differences in habitat use and behaviour. Such differences were found in most species, i.e. the proportion of juveniles in the early season was correlated with the flock size. However, as interesting as the uneven distribution is, it makes it very difficult to measure the average proportion of juveniles for the whole area. The talk deals just with the preliminary results from the first half of the first season. It is hoped to develop this project for long-term monitoring of the breeding success in arctic waders.

A proposal for indexing wader populations

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The Birds of Estuaries Enquiry of the British Trust for Ornithology produces annual indices of the sizes of wader populations in Britain relative to January 1973 as base. However, for a variety of reasons, not all estuaries are surveyed each January. The present index is found by totalling the numbers of waders counted at estuaries which were surveyed in both the current year and the previous year, and adjusting the index by the ratio of these two totals. This 'chaining' property is a major weakness, because no check is made on the relationship between numbers of waders in the current year compared with the base year. In the proposed index, missing values are filled in ('imputed') by means of a parsimonious statistical

model. The new index can make use of surveys made throughout the winter months (not only the January survey). The model consists of a site factor, a month factor, and a year factor, the latter which forms the annual index.

Missing values are imputed using an iterative algorithm, assuming a simple multiplicative model. The year factor can be defined in such a way that it is computed as the ratio of the total number counted (and imputed) in the current year and the total for the base year. This eliminates the chaining problem with the current index. The site factors assess the relative importance of sites for a species, taking into account all available counts at the site. The month factors can be used to provide information on seasonality. The model can also be used to highlight observations which appear out of line with previous surveys.

GENETICS, ENERGETICS & USE OF SPACE

Hypervariable DNA control region sequences reveal global population structuring in a long distance migrant shorebird, the Dunlin *Calidris alpina*

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Hypervariable segments of mitochondrial DNA (mtDNA) as well as part of the cytochrome b gene of Dunlins were amplified with PCR (polymerase-chain reaction) and sequenced directly. The 910 base pairs of sequence obtained for each individual is the largest population survey conducted to date in birds. A total of 27 types of mtDNA were detected and all 25 types defined by the hypervariable control segments were specific to geographic regions of the total circumpolar breeding range of the species. A genealogical tree relating the types, clustered them into five populations: Alaska, west coast of North America, Gulf of Mexico, western Europe and the Taymyr peninsula of Siberia. The Dunlin is thus highly structured geographically, but high diversity within populations as well as large long term effective population sizes argue against severe population bottlenecks in promoting this differentiation.

Instead, population fragmentation in Pleistocene refuges is the most plausible mechanism of mtDNA differentiation, but at a much earlier time than that suggested with morphometric data.

Seasonal changes in metabolic rate in Knots in relation to migratory performance

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Knots are long-distance migrants and as such are subject to widely different environmental conditions over the season. As seasonal changes occur in plumage, fat reserves and body composition, along with these, changes in basal metabolic rate can also be expected. Two subspecies, breeding in the Arctic, were studied. 'EuroCanadians' *Calidris canutus islandica*, fly a relatively short distance and winter in the Wadden Sea and Britain, while 'AfroSiberians' *Calidris canutus canutus* fly nearly twice as far to winter in Mauritania or even in South Africa. Clearly, the two subspecies will face different energetic costs and constraints in their annual cycles.

Experiments were carried out with captive Knots in the laboratory, in search of annual rhythms in their energetics as mentioned above. Metabolic rates of each subspecies were measured at six different temperatures ranging from -20 to +35°C. These measurements were repeated nine times at approximately six-week intervals to cover a whole year-cycle. There were clear seasonal changes in Basal Metabolic Rate (BMR), which were related to body mass changes in connection with migration. It appears that a summer plumage provide less effective insulation than a winter plumage.

Telemetric activity recording comes on age: a microcomputer controlled system to record activity patterns and physiological variables of waders

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Activity and in particular time budgets are a fundamental tool in ecological studies to analyse the animal/environment interactions and furthermore to understand the regulation of animal populations. Radiotelemetry offers the facility to record activity patterns and physiological variables of free living animals.

The aims of the present study were:

1 To find out whether motion-sensitive transmitters can be used to monitor distinctive behaviour patterns of Oystercatchers *Haematopus ostralegus*. Adjusting the mercury switch in an angle of 12-13° to the bird's back allows to monitor the overall locomotor activity, while an angle of 47-50° is suitable to monitor foraging behaviour.

2. To test a new microcomputer-controlled system for long-term activity recordings. Major functions of the receiving station are: the rejection of interferences, the facility to compensate tem-

perature dependent frequency and pulse rate drifts of transmitters, the high sensitivity which offers long reception ranges and the direct access to the disk stored data.

It is obvious that the tested system can be used for any activity monitoring based on conventional VHF-transmitters as well as for recording physiological parameters (e.g. body temperature, heart rate).

Behaviour of a flock of wintering Avocets *Recurvirostra avocetta*

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For the last four winters, the Avocets wintering on the Tamar estuary in South-West England have been studied. During this period the numbers have increased (to a peak of 255 in February 1991), although as a percentage of the wintering population in the U.K., they continue to decline (currently about 13% compared to 95-100% in the 1950s and 1960s). Avocets have a restricted distribution on the estuary during their November-March period of residence. They make use of four distinct sites, but over 95% of their time (measured in bird-days) is spent in two of them, Weir Quay and Saltash. Of these two, Weir Quay is the preferred site, and downriver movements to Saltash are closely linked to the exceptionally high river flow rates which have occurred in three of the last four winters. The actual reason for the shift in distribution, and the mechanisms involved, remain obscure, as do the factors causing birds to select favoured areas of mudflat within their preferred site: no correlation was found between usage (mud feeding Avocet hours/m²) and either worm density (*Nereis diversicolor*, spionids and tubificids), particle size or sheer strength. From some very approximate calculations, it is tentatively suggested that Avocets on the Tamar estuary have not yet reached carrying capacity level.

SIBERIAN NIGHT

Waders breeding in northeast Taimyr

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A joint U.K./South African/Dutch/Soviet team visited Pronchishcheva Lake (75°15' N, 112°40' E), N.E. Taimyr, between mid June and early August 1991. With the aims of studying the breeding success and characterising the populations of waders present in the area, hitherto almost unknown ornithologically. As predicted,

1991 proved to be a lemming peak year in the northern Taimyr, with densities exceeding 100 per hectare in the area in which we worked. Upon our arrival on 15 June, the area was >95% snow covered, and only Snowy Owls had commenced laying; onset of wader breeding accompanied a thaw which set in within the next few days. Within our 14 km² core study area, we estimated there to be c. 100 breeding pairs of nine wader species; nests of 71 of these were found at the egg stage and broods of a further 20 located subsequently. In addition, 100 nests of non-wader species were found.

Nesting success was high, with very little predation evident; few Arctic Foxes, but many skuas were present. Over 400 birds were ringed, mostly waders and including both breeding adults and young. Biometrical information and blood and feather samples taken from adult waders will be used in population characterisation studies.

Waders in their breeding habitats in East Siberia (Kolyma Delta, Bering Sea coastal area)

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During an expedition to East Siberia this year different wader breeding areas were visited and species composition and densities established. On the mainland east of Meechkyln Island Red Knot *Calidris canutus* has been spotted, while in the mountain bordering the Kolyma Delta Great Knots *C. tenuirostris* has been discovered. Spoon-billed Sandpiper *Eurynorhynchus pygmaeus*, breeding in Anadyr airport area, has also been spotted near Provideniya.

The taiga area near Omalon River is important for species like Wood Sandpiper *Tringa glareola*, Greenshank *T. nebularia*, Terek Sandpiper *Xenus cinereus*, etc. Kolyma Delta has been a reserve for eight years. With an area of 25,000 km², it is one of the most important wader areas of the former USSR. Most common species there were Red-necked Phalarope *Phalaropus lobatus*, Pectoral Sandpiper *Calidris melanotos*, Temminck's Stint *C. temminckii*, and also Long-billed Dowitcher *Limnodromus scolopaceus* and Spotted Redshank *Tringa erythropus*.

Research on waders at the Pyasina Mouth, western Taimyr in 1991

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As part of a joint Russian-Dutch-Polish expedition



we worked at the Pyasina Mouth (74° 08'N 86°45'E), western Taymyr, between 11 June and 22 July 1991. Our main goal was to study the mating system of Little Stint *Calidris minuta*. Data was also gathered on the breeding biology of other waders (especially Grey Plover *Pluvialis squatarola* and Ringed Plover *Charadrius hiaticula*) as well as Pomarine Skua *Stercorarius pomarinus*. Spring seemed to be very late in 1991 and about half the area was still snow-covered on 25 June. Lemmings were extremely numerous in mid-June, but the population crashed afterwards and not many animals survived to mid-July. Pomarine Skua bred at a density of c. 2 nests/km. Clutch predation by Arctic Foxes was very heavy.

Little Stint was the most numerous breeding species (up to 60 nests/km² on 0.25 km² of the best area), followed by the much less numerous Curlew Sandpiper *Calidris ferruginea* and Pacific Golden Plover *Pluvialis fulva*. Dunlin *C. alpina*, Grey Plover, Turnstone *Arenaria interpres*, Grey and Red-necked Phalarope *Phalaropus fulicarius* and *P. lobatus* were scarce. Ringed Plover bred along the seashore (0.6 pairs/km²). A total of 122 wader clutches (87 of Little Stint) and an additional 12 Little Stint broods were found. Almost all eggs were measured. A total of 197 waders (122 adults) were ringed - 88 adult

Little Stints also with colour rings. Adult birds were measured (wing, ulna, bill, total head, tarsus, middle toe, mass, primary moult score and primary parasite load). The time budget of incubating and chick-rearing Little Stints was studied.

BREEDING BIOLOGY

English Common Sandpiper population study

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The gradual decline of the range of *Actitis hypoleucos* in England (and Wales and Ireland) has been noted in many publications. During 15 years of study the details of a local decline have been monitored.

Fledging production per pair appears to be declining as well as the population and this appears along with lessening site fidelity. Possibly a high density is needed to stimulate breeding and cooperate alarming to protect chicks by confusing predators. The colonial tendency prevalent in shorebirds may thus also be important in a species commonly considered completely territorial. A repeated census of an area in 1990 that was thoroughly censused in 1959 confirms that smaller streams are being abandoned and an overall population decline is still occurring.

Why does it take so long before young Oystercatchers first breed?

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Waiting 14 years before reproducing for the first time (as sometimes observed in Oystercatchers *Haematopus ostralegus*), is only explicable if reproduction at an early age has disproportionate negative effects on the possibility to reproduce in the future. Three hypotheses seeking causes of disproportionate costs to first reproduction at an early age for long-lived seabirds have been put forward:

1. Foraging skill or competitive ability on the feeding grounds improve slowly with age, so that the act of reproduction is disproportionately costly to young birds (Lack, Orians, Ashmole).
2. Social competition prevents young non-breeders from settling (Coulson, Lack, Porter).
3. The social system is such that it is profitable for young non-breeders to join queues for advantageous reproductive positions (Wiley). The risk of losing priority in the Queue as a result of escalated contests may prevent individuals from challenging opponents preceding them in the queue (Wiley & Rabenold).

A detailed description of the social system of non-breeders and the ways by which non-breeders recruit into the breeding population on Schiermonnikoog strongly favours the third hypothesis.

Polygyny and polyandry in the mating system of the Little Stint *Calidris minuta*.

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Observations of colour ringed Little Stints in Taimyr, Siberia, proved polygyny and polyandry in the species. Some nests are left by females after egg laying, in others they start incubation immediately. Females laying two clutches in succession and incubating the second one were found. Males can start incubation during egg laying or leave the nest and mate then. Starting of incubation by males, seven days after clutch completion was observed as well as desertion of the nest by both parents. Nests with two birds incubating were also found. Two neighbouring nests belonging to different pairs were observed.

Breeding Black-winged Stilt at Sado estuary: habitat use

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During spring 1991 a comprehensive survey of the breeding population of Black-winged Stilt *Himantopus himantopus* was carried out at the Sado estuary, in order to understand the habitat preferences of the species. For an estimated total of 750 pairs, just over 500 nests were found: 33% in active salinas, 58% in inactive salinas, 1.5% in industrial fish-farms, 0.5% in traditional fish-farms and 6% in rice fields. However the number of nests in the rice is certainly underestimated due to difficulties in censusing. Considering only the saline type habitats (22% active salinas, 53% inactive salinas, 23% industrial fish-farms and 3% traditional fish-farms) the bird's preference is for the active and inactive salinas where most of the birds (98%) and the nests (95%) are found. Within either active or inactive salinas, there seems to be no preference between either of the two sections: crystalisers and evaporators.

BREEDING OF PLOVERS

Are Belgian Lapwings 'regionalized'? Habitat selection in Lapwings

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In Belgium, to belong to such or such region has the reputation to be 'The' question. Is this the case for Lapwings too? In my two study areas (one in the polders, near the coast in the Flemish part of Belgium and the other one in the Condroz, in the south, Walloon part of Belgium) I observed that Lapwings don't choose the same nesting habitat at the same moment. The total area covered by either meadows or crop fields, are comparable in both study sites. In the polders, first breeders prefer meadows, later ones choose crop fields.

In the Condroz, despite the lower hatching success in crop fields due to agricultural practices, Lapwings nearly exclusively choose this nesting habitat. An inquiry by Belgian ringers and bird-watchers suggest that, before 1 May (sowing time), Flemish Lapwings prefer to nest in meadows and Walloon ones in ploughing lands. After this date, all of them choose crop fields (maize, beet, garden peas).

One explanation could be related to the recent history of Belgian colonization by Lapwings. In the 1960s, they bred yet only in the northern part of Belgium. Now, they become more or less



common all over the country. Some information from other countries are still needed. I would like to call on anyone able and willing to help me by sending information about the nesting habitat (clutch habitat) used in any European region before and after sowing time, and sampling blood of Lapwing chicks during the next breeding season.

Breeding biology of Lapwing *Vanellus vanellus* in south-Hungary

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Breeding biology of Lapwings was studied in a Hungarian alkaline grassland 'puszta' during two years. The size of eggs, clutch size, distance of nests, breeding success, plant composition around the nests and vegetation cover were investigated.

The hatching success of Lapwings was 50-60%. The most common reason of failure were predators, particularly birds (Magpie and Marsh Harrier) and mammals (straying dogs). The study revealed that the breeding success of Lapwings may be too low in the small, patchy alkaline grassland in south Hungary to maintain the population, thus endangering the status of even such a common wader as Lapwing.

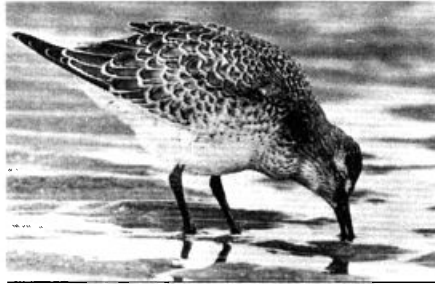
The Kentish Plover at Fuentepiedra, Spain: a progress report

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Fuentepiedra is an inland saline lake, with an estimated population of over 200 adult plovers. The lake is protected. This year we have banded 200 adults and chicks, and followed over 90 nests. Water levels fluctuate widely between years, and undoubtedly would affect most breeding parameters. Nesting can be solitary to colonial (on islands).

Avian predators include Gull-billed Terns, shrikes and raptors. Among mammalian predators domestic dogs are important, but Foxes and Badgers also occur. Predators may destroy 60% or more nests, and when the lake dries up plover colonies on islands abruptly become vulnerable. Nevertheless, during the early season the island nests are extremely important for recruitment.



SYMPOSIUM: SHOREBIRDS AND THE AVAILABILITY OF THEIR BENTHIC PREY

Variability in the macrozoobenthos living on tidal flats of the Wadden Sea

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A 22-year series (1969-1991) of quantitative data on the numbers and biomass of the macrobenthic animals living on the tidal flats of Balgzand (a 50 km² area in the westernmost part of the Wadden Sea) is available to discuss long-term changes and year-to-year variability.

The western part of the Wadden Sea has experienced serious eutrophication during the last few decades. As a consequence, numbers and biomass increased in about half of the species and total biomass doubled. Severe winters exerted an even greater and unpredictable influence, lowering overwinter survival in about one third of the species, but enhancing reproductive success in several species during the subsequent summer. Recruitment failed in important bivalve species after the mildest winters. A succession of three such winters (1988, 1989, 1990) and unrestricted fishery caused a depletion of the stocks of both cockle and mussel and starvation in Eiders *Somateria mollissima* in 1990-1991.

Exploitation of a chironomid-rich feeding area by Avocets and Black-tailed Godwits

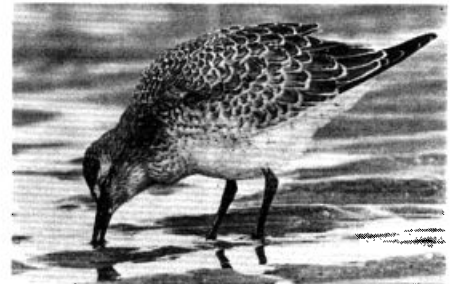
Anne-Marie Blomert & Jan van der Kamp

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The Oostvaardersplassen, a man-made shallow freshwater lake in the centre of The Netherlands, harbours in the late summer ten thousands of waders, predominantly Black-tailed Godwits *Limosa limosa* (max. 30,000) and Avocets *Recurvirostra avosetta* (max. 10,000). Avocets and Black-tailed Godwits can only feed when the water depth is 18 cm or less. Due to the annual variation in water level, there is also a large

variation in the numbers of waders feeding in the area. Faeces analyses reveals that both species take large chironomid larvae and ignore the larvae smaller than c. 14 mm. The prey are taken at a high rate (30-40 prey per minute) and since both species feed in very dense flocks (1000-2000 birds per ha), the predation pressure is extremely high. The food supply is entirely depleted when the birds feed for 4-5 hours on the same spot. The flocks move around, however, and rarely revisit areas where they foraged earlier.

Avocets feed 13 hours a day, mainly early in the morning and during the afternoon and evening; they continue to feed during moonlit nights, and probably also during dark nights. Black-tailed Godwits feed 14 hours a day, the entire daylight period and also at moonlit, but not at dark nights. The estimated energy intake of Avocets and Black-tailed Godwits is equivalent to 3-3.5 times the basal metabolic rate.



What determines the densities of foraging birds on Wadden sea mudflats? - a progress report

Georg Nehls & Ralph Tiedemann

WWF-Wattenmeerstelle/Institut für Haustierkunde, University of Kiel, Germany

On the way to evaluate the carrying capacity of tidal flats for predatory birds we felt it necessary first to assess the utilization of the various habitats of these areas. This is most easily expressed as densities of foraging birds. Densities of foraging birds, especially of waders, in the Wadden Sea are influenced by several factors acting on different time scales, of which the most important are tides and seasons. Seasonal and tidal variation in the densities of foraging birds were studied on mudflats of the Königshafen on the island of Sylt. Densities were measured on plots of 50 x 50 m of different substrates by 10-minute counts over whole tidal cycles. Intake rates were noted for some of the species present. First results indicate that the influence of the tides may overrule preferences for certain areas. The tidal behaviour varies seasonally. For several species it appeared that their foraging behaviour is strongly related to the moving tide line during the cold months but much less in late spring and summer. For some species seasonal changes in the tidal behaviour and in the densities of foraging individuals can be correlated with changes in prey choice and food availability.

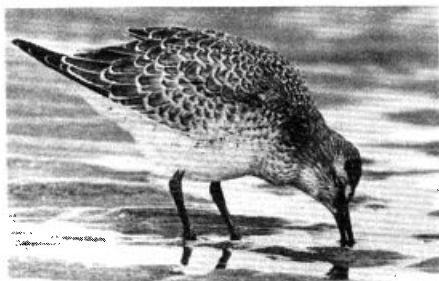


Shorebird-prey relationship in a south temperate estuary.

Bozena Kalejta

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa

The density of migratory shorebirds (Aves: Charadrii) is exceptionally high at the Berg River estuary, South Africa. The impact of shorebirds on invertebrate prey was studied from December 1987 to April 1989. Compared with the theoretical energy consumption the most common waders on the estuary had negative energy budgets throughout most of austral summer, however, they were not food limited. The highest predation pressure of waders coincided with the maximum reproductive output of invertebrates. Increased energy demands of birds in the pre-migration time were paralleled by increased nocturnal foraging. Absolute predation pressure by waders at the Berg River estuary is one of the highest recorded on the east Atlantic seaboard, but represents only 17% of the annual production of invertebrates.



Prey availability and their harvest by shorebirds in intertidal habitats

Leo Zwarts

Rijkswaterstaat, Directie Flevoland, Lelystad, The Netherlands

Worms, crabs and shrimps are the most important prey for the majority of the 14 wader species occurring on the intertidal flats in northwest Europe. Waders face a fluctuating food supply caused by the variation in the densities of the approximately twenty species of prey living in the intertidal flats (see abstract of J.J. Beukema). The variation in food supply that is actually utilised by the various wader species may even be greater than appears from the consideration of the annual total biomass of the prey. Waders generally only consume part of the prey occurring at and in the tidal substrate. This implies adjustment of the diet and aggravates the problem of how to locate reliable food resources.

There are five reasons why waders do not take part of the prey:

1. prey may live out of reach of the bill;
2. prey may be too large to be ingested;
3. small prey have a lower probability to be encountered due to their smaller 'touch area';
4. prey are rejected when they are unprofitable; or
5. available prey may occur in such a low density that the waders cannot actually feed on them.

Without information on these factors, it is impossible to define the food supply which is actually relevant for different wader species.

Hence the availability constraints is that it shows the outcome of the evolutionary arms' race. Waders make continuously decisions to maximize their intake rate, but for prey it is a matter of life or death to escape the predator.

Do the survivorship curves of macrobenthic animals reflect their accessibility to waders?

Jan H. Wanink & Leo Zwarts

Rijkswaterstaat, Directie Flevoland and Zoological Laboratory, University of Groningen, Haren, The Netherlands

Several authors have addressed the relationship between burying behaviour of intertidal macrobenthic animals and their accessibility to waders. Large individuals appeared to bury deeper than smaller ones in most of the investigated species, although the depth ranges of separate size classes often were rather wide and overlapping. Predation risk within a size class was negatively correlated with burying depth.

Benthos from the temperate zones showed seasonal variations in burying depth. At any time, the fraction accessible to waders varied strongly between species.

If predation plays an important role in the regulation of macrobenthic populations, accessibility of macrobenthic animals to waders may be reflected in their survivorship curves. Here we present survivorship curves for a few macrobenthic species from an intertidal mudflat in the Dutch Wadden Sea. We investigate whether the mortality rates are related to seasonal trends in burying depth and wader density in the study area.

Predation of waders (Charadrii) on prey populations: an enclosure experiment

Tamás Sézkely & Zsuzsa Bamberger

Department of Zoology, Kossuth University, Debrecen, Hungary

The impact of waders on mud-dwelling invertebrates in central-Europe was studied by an enclosure experiment. The most common invertebrates in the mud were Chironomid larvae, which accounted for 90.5% of all invertebrates. The invertebrate density was measured before the experiment and after 13 days of exposure. At the end of the experiment, the invertebrate density was lower in the control sites (1,593.7 ind.m²) compared with enclosures (11,937.5 ind.m²).

Thus birds, particular Black-tailed Godwits *Limosa limosa*, Spotted Redshanks *Tringa erythropus* and Ruffs *Philomachus pugnax*, removed 86.6% of the prey stock. Prey biomass was also significantly lower in the control (1.3 g m²) than in the enclosures (9.5 g m²). The impact of waders on the density of preys was also estimated from observations of the feeding rates of the birds. The number of prey estimated to be taken by Black-tailed Godwits was 5,765.3 prey.m² for 13 days of the experiment while the estimates for Spotted Redshank and Ruff were 1,257.7 and 574.8 prey.m², respectively. The total number of prey removed by Black-tailed Godwits, Spotted Redshanks and Ruffs was 7,597.8 prey.m². This compares with the 10,343.8 ind.m².

The difference between the estimates may be due to predation by other birds, such as other waders or ducks, or to the high variances of both estimates.

The number of Black-tailed Godwits, Spotted Redshanks and of Ruffs declined during the experiment. The rate of food intake of Black-tailed Godwits, Spotted Redshanks and of Ruffs also declined as the food stock was depleted. However, the number of roosting birds increased (but not significantly) during the experiment.



A man-made reserve: shorebirds and a high-productive habitat

Mark Rehfisch

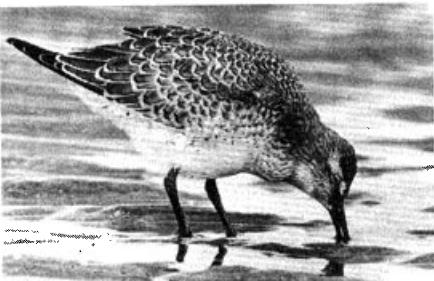
British Trust for Ornithology, The Nunnery, Nunnery Place, Thetford, Norfolk IP24 2PU, U.K.

Blacktoft Sands, an RSPB-reserve since the 1980s, centred around several brackish (mixo-oligohaline) man-made lagoons of 1.4 to 7.3 hectares area, rarely flooded to more than 89 cm. The vegetation is dominated by Phragmites and couch grass. The lagoons are linked by sluices to the Trent, a river which flows into the Humber Estuary, U.K.

The lagoon levels can thus be manipulated to optimise conditions for passage waders in spring and autumn.

Of the lagoon benthos, 98% was made up of Chironomidae. The maximum mean biomass and productivity of the Chironomidae was 5.0 g m² and 30.8g m²yr dry weight, respectively. These are high values for brackish waters in temperate regions. Waders were observed feeding on the larval and adult Chironomidae and may have accounted for an estimated 14% of the total production. This is a small offtake in comparison to that in intertidal areas but partly due to some of the four lagoons being kept flooded to depths which did not allow the birds to feed.

The reserve's aims of attracting a wide variety (25+ spp.) and density (200 per ha) of waders are met by these artificial lagoons. The high productivities recorded show the potential of man-made habitats at a time of increasing pressure on natural environments.



Specialist foraging adaptations of waders on braided riverbeds

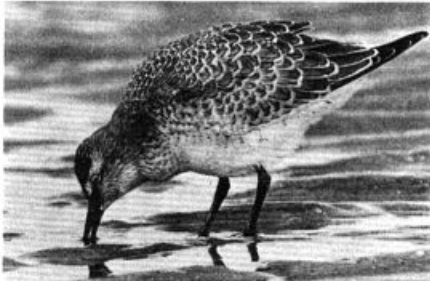
Ray Pierce

Department of Conservation, Northland Conservancy Office, 12 Kaka Street, Whangarei, New Zealand

On montane and subalpine gravel riverbeds foraging conditions are regularly severe, particularly for those species of waders that occur there

year round. Low water temperatures in winter and spring mean that aquatic prey are inactive and hidden beneath stones for much of the day. A negative phototaxis of many invertebrate prey species adds to the pressure on the daily feeding routines of waders. In addition, spring flooding, although providing temporarily abundant food in the drift, may quickly deplete prey stocks.

Three specialised riverbed waders, the Black Stilt *Himantopus novaezelandiae*, Ibisbill *Ibidorhyncha struthersii* and Wrybill *Anarhynchus frontalis* are adapted to dealing with these problems. They exhibit a startling range of bill morphologies - straight, down curved, sideways curved - each



used in a different way and at different types of aquatic feeding station. The degree of tactile foraging varies seasonally and between years, being greatest in very cold periods. The specialist bill morphologies and feeding methods may be of greatest survival value during climatic cooling.

If aquatic food becomes totally inaccessible or depleted, aquatic foraging may be replaced by riparian foraging, or as is sometimes the case in the Black Stilt by shifting to alternative habitats. Species like the Pied Stilt *Himantopus himantopus leucocephalus*, however, which are recent colonists of riverbeds, are poorly adapted to riverbeds where they have become opportunistic foragers.

Waders in an exotic place: feeding on exotic dishes?

Petra de Goeij & Ingrid Tulp

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

The Roebuck Bay and Eighty Mile Beach area in tropical northwest Australia has only recently been discovered as an important wintering and stopover site for nearly half a million waders. Waders use this area as a last fuelling or refuelling site before they leave for their trip northward: for some species this invokes a 5,500 km non-stop flight to China. We studied the feeding ecology of a number of wader species in February-May of 1991, concentrating mostly on knots, since the co-occurrence of the Red Knot *Calidris canutus rogersi* and the Great Knot *Calidris tenuirostris* offered good possibilities for comparison.

How the birds prepare the northward flight during their premigratory period was the main topic we concentrated on. Therefore we studied both the foraging behaviour of the birds and their respective prey species. Samples of the benthic fauna in the area provide information on prey species, densities and biomass. Visual observations of prey choice, time budgets and habitat choice were made.

Compared to the Dutch Wadden Sea, the total benthic biomass of the tidal flats in Roebuck Bay is very low (respectively 40 and 15 g AFDM/m²). The benthic fauna is characterized by large numbers of very small prey items, a situation similar to the one on the Banc d'Arguin, Mauritania. Echinoderms (especially sea cucumbers) made up nearly half of the overall biomass. Though the number of bivalve species suitable as wader prey equals that at other important wader sites (Banc d'Arguin, Wadden Sea), the densities are not high (usually <50 ind./m²). Only Great Knots have bivalves as their main prey. Red Knots seem to live on tiny prey which are hard to observe when being swallowed.

Food and feeding of spring migrant Knots in north Norway in spring

Nick C. Davidson

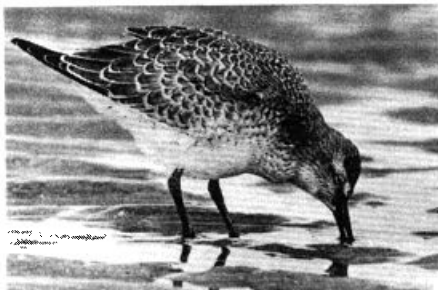
UK Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY, U.K.

Up to 28,000 Knots *Calidris canutus islandica* use Balsfjord in northern Norway for 2-3 weeks in May, before flying to their breeding grounds in Greenland and northern Canada. A high rate of food intake is needed at this staging site, since birds must both replenish fat and protein reserves used during their flight from Britain and the Wadden Sea, but also store additional reserves for their onward flight and as aid to survival once they reach their breeding grounds. In Balsfjord they find abundant supplies of small slow-growing, Baltic Tellins *Macoma balthica* and Mussels *Mytilus edulis*, all of which are on the surface or in the upper two cm of the sediment and so are available to the birds.

Analyses of pellet, faecal and stomach samples in 1985 and 1986 showed that in most places Knots fed chiefly on small (4-9 mm) *Macoma*. On the tidal flat where birds fed most frequently, however, *Mytilus* formed the bulk of the diet. Feeding rates were generally high: in early May 1985 and both early and late May 1986 birds took about 3.5 prey/min., resulting in an intake of about 0.2-0.3 mg AFDM/min. In late May 1985, however, feeding rates were almost double the earlier rates. Furthermore these birds fed on the mud-flat with the largest *Macoma*, resulting in the very high intake rate of up to 0.55 mg AFDM/min. This increased feeding rate may be a compensatory response by birds that had arrived in



relatively poor fat and protein condition in mid-May. Knots in Balsfjord seem to make their very rapid rates of mass gain (averaging 3.8 g/day) whilst feeding at much lower rates than they achieve. Such high quality late spring staging sites can offer Knots a vital final opportunity to compensate for shortfalls in body condition occurring earlier during their northwards migration.



When and why are Knots Macomaniacs, and are Macoma too dumb to do anything about it?

Theunis Piersma & Phil Battley

Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, and Zoological Laboratory, University of Groningen, The Netherlands

The Balthic Tellin *Macoma balthica* is a rather thin-shelled and meat-rich bivalve, and a common prey of Knots *Calidris canutus* in intertidal areas around the North Atlantic, according to the literature. However, in only half of the intensive investigations carried out by our group in the Wadden Sea, did *Macoma* actually comprise the largest part of the Knots' diet. Often alternative prey species like Cockles *Cerastoderma edule* and Mud snails *Hydrobia ulvae* formed the bulk of the diet, though in all study areas *Macoma* did occur. Of course not all *Macoma* are ingestible (some are too big) or profitable (too small), and there is always part of the *Macoma* population which is buried too deeply to be within reach of the Knots' bills (3.5 cm long). It appears that only in areas where the biomass of profitable, ingestible and available *Macoma* is higher than 0.5-1 g ash-free dry mass (AFDM)/m², they form the main prey species of Knots.

This biomass-threshold is pretty well predicted by a preliminary functional response curve, assuming a minimum of 0.2 mg AFDM intake per second feeding. But why would *Macoma*, with their ability to bury as deeply as 15 cm, put themselves at risk at all by living close to the surface of the sediment? Apart from those individuals which appear forced to do so by a high parasite load, the habit of shallow living by *Macoma* is probably the outcome of a trade-off between predation risk (the higher the higher) and feeding opportunities (the higher the better, since more of the inhalant siphon can be used for deposit feeding and a larger sediment surface area be sucked clean). The trade-off equation is inferred to change in the

course of the season, 'making' *Macoma* most at risk in their period of intense feeding for growth and reproduction, in February-May. Thus, although life may not seem easy for a small homeothermic predator like the Knot, being a Balthic Tellin does not appeal like an easy alternative either.

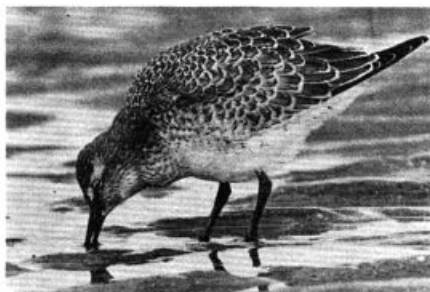
Prey switching of the Oystercatcher on Schiermonnikoog

E.J. Bunschoke

Saffierstraat 40, 9743 LJ Groningen, and Zoological Laboratory, University of Groningen, The Netherlands

During the breeding season in 1986, Oystercatchers *Haematopus ostralegus* on the island of Schiermonnikoog, Dutch Wadden Sea, switched from eating mainly the bivalve *Macoma balthica* to a diet dominated by

the polychaete worm *Nereis diversicolor*. This diet switch was not unique for 1986, and must be due to a preference switch of individual Oystercatchers. The switch in prey choice is accompanied by a change in relative availability of the prey species, and therefore fits in the optimal foraging theory.

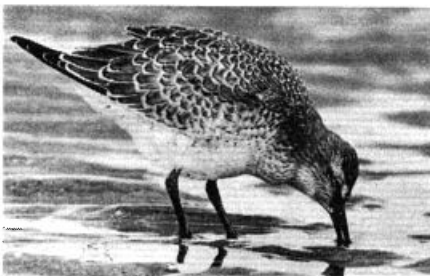


Oystercatchers quickly depleted the thin-shelled mussels from an experimentally created musselbed

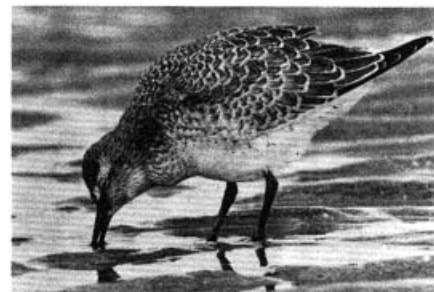
Dieko Alting & Bruno J. Ens

Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

When an experimental musselbed *Mytilus edulis* was created in 1987 on the mudflats south of Schiermonnikoog, Herring Gulls *Larus argentatus*



immediately increased in numbers, consuming starfish and damaged mussels. The build-up of Oystercatchers *Haematopus ostralegus* was more gradual, but persisted for longer. Oystercatchers either hammered or stabbed mussels. Initially, hammering Oystercatchers achieved the highest intake rates, while they specialized on small and thin shelled mussels. Several lines of evidence indicate that the fraction of 'hammerable' mussels was severely depleted by the end of August. By that time many Oystercatchers switched to stabbing mussels or feeding on alternative prey.



Why is prey availability so important?

William J. Sutherland

School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K.

I have been asked to sum up this interesting symposium on 'Shorebirds and prey availability' and in doing so I wish to outline four points that I think are of wider interest outside the field of wader biology.

(1) Variation prey availability.

A number of workers are trying to predict the factors that determine the number of birds that a site can sustain. For theoretical convenience it is usual to assume that this is constant. However, as the studies of Beukema on the Wadden Sea and Pierce on New Zealand rivers show, the prey density and availability varies markedly over time. Furthermore, the number of birds wishing to use these sites also varies markedly between years especially depending on the breeding success. Thus both the ability of sites to sustain wader populations and the demand for such sites will vary. It could thus be that, when thinking about the capacity of estuaries to sustain birds, the average years may be less relevant and we may need to concentrate more on extreme years.

(2) Measures of prey availability.

At any one time there is an excess of prey present for waders: the limiting factor is that most of it is not available. Availability is of crucial importance for almost any aspect of population ecology such as optimal foraging theory, functional and numerical responses, migration



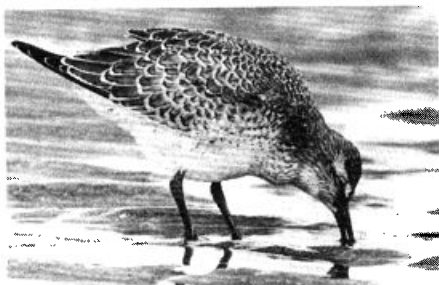
strategies or predator-prey relationships. The various studies by Zwarts, Alting & Ens and Wanink & Zwarts show that wader biologists have gone a long way towards understanding prey availability and being able to measure it. These issues are real stumbling blocks in many other studies. The simple point I wish to make is that this work by wader biologists is a real development of widespread interest and the authors should not be too modest about it!

(3) The shellfish gene.

Recent work has shown how human fishing practices, such as using a certain mesh size to avoid catching the smaller fish, have changed the life-history of fish - for example many species grow more slowly and breed when smaller than they did previously. Waders and their prey have been co-evolving for a massively longer period of time. I think it is thus exciting from the work of Piersma & Battley to see how *Macoma* have evolved with the conflicting selection pressures of being able to feed more efficiently when near the surface, yet better able to avoid Knot if buried deeper in the mud. Similarly the poster by Ens *et al.* considers the behaviour of both Whimbrel and Fiddler Crabs and the relationships between the two. There are probably many aspects of the morphology, behaviour and life-histories of prey that can be considered in this framework.

(4) Specialisation.

Bunskoeke quantified the remarkable degree of specialisation shown by Oystercatchers with different individuals feeding on different prey species or feeding using different techniques. Is this a consequence of bivalves being difficult to tackle so different Oystercatchers exploit different weaknesses in the prey? Alternatively, is it a consequence of the relative ease with which Oystercatchers can be studied combined with the huge numbers of obsessive Oystercatcher researchers? There is some evidence that other species such as Turnstone and Curlew also possess a degree of individual specialisation but the question remains as to whether this phenomenon is common to most other wader species and to a similar degree.



POSTER PRESENTATIONS

Migration pattern and fattening of Curlew Sandpiper at an Italian stopover site

Nicola Baccetti, Ariele Magnani & Lorenzo Serra

INBS, via Ca' Fornacetta 9, I-40064, Ozzano Emilia BO, Italy

The occurrence of Curlew Sandpipers *Calidris ferruginea* at Saline di Cervia (northeast Italy) during post-breeding migration (study season:

30 July - 30 October) is described on the basis of census and capture data.

The median date of passage (28/8) fits the OAG Munster's grid squares (*WSG Bull.* 1987), and also reflects substantially the pattern observed in northern European countries. Although our juveniles are slightly more represented than adults in our catch sample (56.6%, $n = 115$), the ratio seems more equally balanced than in northern Europe, where juveniles generally form the bulk of samples relative to post-breeding migration.

Among adults, the sex ratio also appears rather balanced (males 46.9%, $n = 49$), considering that we lack data from the beginning of migration (July). Mean values of body mass in juveniles (70.3 g) and adult (69.7 g) do not differ significantly, but only adults show a significant mass increase during the study season ($r = 0.39$, $p < 0.006$). Of adults, 69.6% and of juveniles, only 6.2% had signs of active body moult. All adults without body moult showed, however, traces of new (winter) plumage. Adults in active body moult had a significantly higher mean mass than non-moulting ones (72.7 g vs. 61.3 g, $p < 0.0006$). These observations, confirmed also by fat score analysis, could support the idea that Curlew Sandpipers suspend their body moult before migration, but may resume it once they reach good refuelling areas. Two adults with suspended inner primary moult (3-6), and one in active primary moult were also examined.

How to risk your life: size-dependent feeding decisions of the Fiddler Crab *Uca tangeri*

Bruno J. Ens, Leo Zwarts, Marcel Klaassen & Anne-Marie Blomert

Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

During low tide, Fiddler Crabs *Uca tangeri* can stay inside their burrow, feed on the substrate around their burrow high on the beach or move in flocks to downshore feeding areas. Measurements on the rate of predation indicate that

feeding in flocks is the most risky activity.

Only the larger crabs feed in flocks, but the minimum size of crabs joining the flock decreased when flock size increased. When small crabs were offered a choice between 'beach substrate' and 'downshore substrate' near their burrow, they preferred the latter. With increasing body size the crabs have to feed at increasing distances from their safe burrow due to their increased demand for energy. At a critical body size feeding around the burrow becomes so risky anyway that the crabs have no other option than to cot their losses. This they do by emerging in maximum numbers at certain tides only, thereby swamping the predators, like Whimbrel *Numenius phaeopus* defending territories on the beach.

Effects of experimental habitat structures on feeding waders on a tidal flat near Sylt

Kathrin Metzmacher

Rimpaustrasse 8, D-3000 Hannover 1, Germany

An experiment with changed habitat structures on a tidal flat was carried out to investigate their influence on feeding waders. Green macro-algae mats caused a short time increase of feeding time spent on the manipulated patches. Heaps of Mussels *Mytilus edulis* showed different results depending on bird species and relative position on the flat.

Optimal migration schedules: reserve dynamics as constraint

Theunis Piersma & Bruno J. Ens

Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel; Zoological Laboratory, University of Groningen; and Research Institute for Nature Management (RIN), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

For a bird to fly a long distance, it first has to store sufficient fuel (during the storage episode) and then to expend this fuel during the flight to a destination (the expenditure episode). A full migration, one between West Africa and Central Siberia for example, involves a varying number of such flights. A bird's migration schedule is set by the timing and patterning of these flights and the rates of fuel storage at stopover sites. During the northern spring, birds move north to breed. If reproductive success predictably varies with arrival time and mass, specific departure times and masses will be selected for. By working backwards from date and mass dependent variation in reproductive success, the optimization of migration schedules can possibly be charted. Since carrying fuel entails a cost of transport and a cost of survival, birds in general should minimize the period of mass gain and maximize fuel



storage rates. The upward limit of the rate of fuel storage is set by physiological constraints (the rate of food processing). Under many circumstances rates of fuel storage are not maximized since feeding rate or feeding time is limited. Since birds fly as fast as winds blow, the fuel-stores remaining after a flight are strongly influenced by the wind conditions en route. Unpredictable variations in feeding conditions at stopover sites as well as in wind conditions during flights, provide strong stochastic elements of migratory performance. To avoid arriving too late or too light on the breeding sites due to worse than average flight or feeding conditions, it may pay birds not to maximize rates of fuel storage during the first legs of the migration. Risk aversion may thus help explain why Knots *Calidris canutus canutus* and Bar-tailed Godwits *Limosa lapponica* show lower rates of mass gain during the first storage episode in West Africa than during the second (and final episode) in the Wadden Sea.

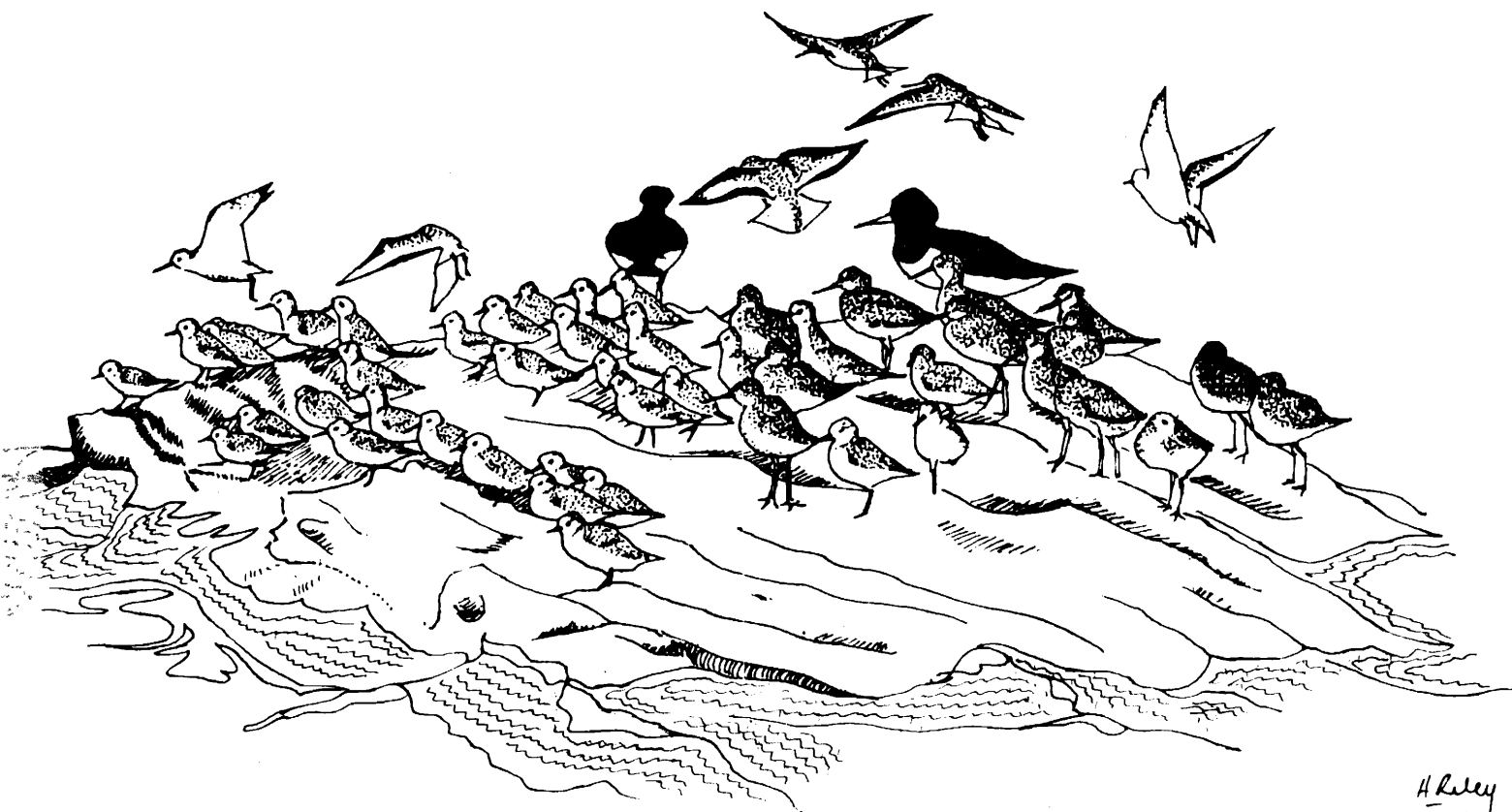
Food availability, food intake and time budgets of Knots *Calidris canutus islandica* at their late autumn staging grounds in the eastern part of the Dutch Wadden Sea

Martin Poot & Bernard Roelen

Netherlands Institute for Sea Research (NIOZ), Texel; Zoological Laboratory, University of Groningen; and J.P. Coenstraat 82 A bis, 3531 EX Utrecht, The Netherlands

Food availability puts limits as to where birds can spend the winter. In autumn 1990, we studied the way in which Knots of the subspecies *Calidris canutus islandica* cope with a deteriorating food situation on the mudflats south of Schiermonnikoog, in the eastern part of the Dutch Wadden Sea. In the course of autumn, the Knots encountered a declining availability of their main prey *Macoma balthica*, since the bivalves buried deeper in the sediment. At the same time, the

energy expenditure of Knots must have increased due to a decrease in air temperatures in combination with strong winds. We found no significant seasonal decline in feeding rates. This implies that as the food conditions deteriorated, Knots compensated by an increased foraging effort. However, foraging time per low water period increased considerably. In this way the birds might have been able to pay for the increases in thermostatic costs. Especially in the second half of the low water period, more time was spent foraging. Earlier in the season birds spent part of this time preening, standing and sleeping, activities which later on only occurred on the high tide roost. Since our results are so far preliminary, further desk work has to substantiate our claim that Knots have an increasingly hard time to balance their energy budget in the eastern Wadden Sea, with decreasing prey availability and increasing thermostatic costs. When in late October all 20,000 Knots left the area, probably for British estuaries, did they do so in direct response to the outlined difficulties?



H. Reley

