As a means of disseminating information about important new wader studies well in advance of formal publication, this series features abstracts from recent wader theses (bachelors, masters and doctoral). Thesis authors are invited to submit abstracts to the editor.

## Burying depth as a trade-off in the bivalve Macoma balthica

(2001, PhD thesis, University of Groningen and Netherlands Institute for Sea Research, The Netherlands)

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The bivalve *Macoma balthica* is an important prey for several wader species, such as Red Knot *Calidris canutus*, Bartailed Godwit *Limosa lapponica* and Eurasian Oystercatcher *Haematopus ostralegus*, that use the Wadden Sea as a stopover site or as a wintering area. Important features of the life history of the bivalve for these waders are density, size and depth of living. Knots for example can only feed on *Macoma* with a shell length of 12–17 mm and not buried deeper in the mud than 3 cm. It was already known that *Macoma* lives at different depths throughout the year and that they live at different depths at different places. The aim of this study was to find out which factors determine burying depth and therefore the accessibility of the bivalves for waders.

The study is outlined in the first chapter.

The second chapter describes an experiment in which burying depth of *Macoma* was manipulated by gluing the bivalves to plastic strips or by keeping them in mini-cages at fixed depths. The bivalves that were buried deep did not grow as well as those that were buried shallow. This means that living deep and being safe has a cost for *Macoma*; namely less growth.

The third chapter describes experiments in which the time of immersion (and therefore time for feeding) was manipulated. When the bivalves were immersed longer, they grew faster.

In the fourth chapter, an experiment is described in which winter water temperature was manipulated. Against expectation, colder temperatures did not lead to an increase in body condition and/or burying depth of the bivalves.

The hypothesis from Leo Zwarts' thesis "flatfish help waders" was tested experimentally. In chapter five the process of facilitation of Macoma by small plaice is discussed ("facilitation" here means the positive effect of one species on another by the action of a third species). It was shown that flatfish do indeed feed on the siphons of bivalves and that the bivalves come to the surface in reaction to the loss of part of their siphon. However, the strength of the reaction was not the same in three identical experiments. For the explanation it is necessary to understand the feeding method of Macoma. Macoma is a so-called facultative deposit- and suspension feeder. For deposit feeding, they have to bury shallow to be able to extend a large part of their siphon over the surface of the mud. Only then can the flatfish feed on the siphons. Then they force the *Macoma* to bury even shallower. This means that in different situations (time of year or food-conditions) the effect of flatfish can be very different.

This is also illustrated in the last chapter where field data and the outcome of the experiments are combined. Two sites are compared, "the Frisian coast" in the eastern Dutch Wadden Sea, where Leo Zwarts and colleagues collected data on burying depth of *Macoma balthica* from 1980 to 1986 and "Balgzand" a mudflat in the western Wadden Sea, where data were collected from 1993 to 1999.

For Knots and Oystercatchers, the study sites on the Frisian coast and at Balgzand differ dramatically in quality because at Balgzand the bivalves are much less available throughout the year than at the Frisian coast. The fraction of suitable *Macoma* in the upper 4 cm, and especially the upper 2 cm, is much higher on the Frisian coast than at Balgzand. Especially in August, when the Knots arrive in the Wadden Sea from their breeding grounds (Piersma and Davidson 1992), none of the *Macoma* is accessible at Balgzand.

The study locations at Balgzand and the Frisian coast differ in sedimentology. The Frisian coast is a much muddier site than Balgzand, the sediment fraction  $<50 \,\mu\text{m}$  being 22.5 and 1.3 respectively. At both sites the body condition of Macoma is comparable and the seasonal changes similar. However, it is also evident that siphons are lighter on the Frisian coast. It is hypothesised that for Macoma living at the sandy Balgzand study site, suspension feeding is the dominant feeding mode. Macoma on the muddy Frisian coast are forced to deposit-feed and thus run the risk of repeatedly losing part of the siphon to siphon-nippers like juvenile flatfish. A somewhat unexpected outcome of the present study is the realisation that the distribution of Macoma-eating birds, such as Knots and Oystercatchers, depends on the feeding strategy of Macoma, which in turn appears to depend on the interaction between abiotic factors and the constant threat of predation when buried shallow.

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## Influence of natural and human factors on the waders (Aves, Charadrii) wintering at Ria de Aveiro, with special reference to Dunlin (*Calidris alpina* L.)

(1999, PhD thesis, University of Aveiro, Portugal)

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Ria de Aveiro is a lagoon on the west coast of Portugal. For centuries, it has been conditioned by human use and now comprises largely artificial habitats, though some natural areas can still be found. Even so, wintering waders are abundant and varied and include two species – *Recurvirostra avosetta* and *Charadrius hiaticula* – for which the Ria is of international importance and nine others for which it is of national importance.

The aims of this work were to study the way in which wintering waders organise and distribute themselves in the lagoon, the processes through which they exploit such an artificial wetland and adapt to the conditions and the factors involved in the regulation of the number of birds present. Comparisons between a natural and an artificial study area within the lagoon were made. Although other species were investigated, the main study species was *Calidris alpina*. Not only was this the most abundant species in the Ria but it also provided the most important results.

Fieldwork covered each winter from 1990/91 to 1995/96. Study of spatial organisation was carried out in a natural area and in the artificial saltpans. Methods used were counting, bird capture and marking and radio-tracking. Difficulty experienced catching the birds in winter led to the use of several different techniques and traps, and to design a new type of net, similar to those usually described as "cannon-nets", fired electronically at a distance. Birds were marked with picric acid and rodhamin, according to a marking code which allowed distinction between adults and juveniles.

Significant differences were observed between the number of birds captured and dye-marked and the number observed later, suggesting a distress effect associated with the capture and/or marking procedures.

Bird counts were carried out at high-tide and low-tide and movements were recorded at the boundaries of the two study areas.

The quality of the roosts was determined using a method developed for the purpose (and described in Luís, Goss-Custard & Moreira 2001, *Wader Study Group Bull.* 96: 71–73). The method evaluates roosts according to nine main characteristics, grouped under three categories: disturbance, predation risk and energetics. The roosts were then rated, according to each characteristic, on a scale of 0–3, and the global quality was determined by the sum of points given for each, with a maximum score of 27.

Results showed that individuals of the study species restricted their activities to limited sectors of the Ria, adopting routines that they maintained throughout each winter. The Ria may, therefore, be considered as divided into "functional units" (of an unknown total number), each being defined as a selection of feeding areas and high-tide roosts, used by a group of birds, during a certain period of time – in this case, winter. This kind of spatial organisation, already studied in ducks, has not previously been the object of a specific study in waders.

The comparative study of the natural area and the artificial saltpans concentrated on *C. alpina* and comprised (i) determination of the quality of the high-tide roosts, (ii) research of the disturbing effect of commercial shell-fishing and, in the saltpans, hunting, (iii) study of the feeding habits and behaviour of the birds and (iv) determination of the characteristics of the groups of wintering birds.

According to the roost-score methodology, the quality of the roosts used by the birds wintering in the saltpans (mainly working saltpans) was superior to that of the roosts in the natural area, since, among other characteristics, they provided not only the possibility of feeding during high-tide, but also more protection from wind and rain.

Shellfish gatherers occupied only a small percentage of the total area available for feeding, and the disturbance they caused resulted mainly from the area they occupied rather than their behaviour or activity.

In the saltpan area, hunting appeared to cause the birds to congregate in larger numbers for short periods, both at hightide and at low-tide. However, it was not possible to evaluate the effect of hunting on the survival of individuals. The study also showed the importance to the birds of alternative, undisturbed areas when hunting was taking place.

The feeding habits of the Dunlin were similar in both study areas and, though there were some differences, the gastropod *Hydrobia ulvae* was the main prey of birds wintering in the two areas. Birds usually occurred where the sediment was more penetrable. Abandoned saltpans, used as low-tide feeding areas in the saltpan area, were probably of lower quality than the mudflats in the natural area.

The birds wintering in the saltpans fed for longer than those in the natural area and seemed to have a different strategy of which high-tide feeding in active saltpans was an important part. Active saltpans may therefore play a major role, and a sharp drop in the number of working saltpans may be the reason for a decline in the number of wintering birds. Nevertheless, despite these differences, the saltpans – where human intervention has been great – host a group of wintering birds (particularly *C. alpina*) which does not differ – at least in respect of the studied characteristics – from that of the birds wintering in the natural area.

Studies in the natural area, showed that intraspecific competition occurs among the *C. alpina* wintering there, but it was not possible to identify the processes involved.

This study showed that the saltpans of Ria de Aveiro are important for the number of birds and species they support. Moreover the information obtained will be of great value, in conservation management and in building or rebuilding wader habitats elsewhere.



## Space use, habitat preferences, and time-activity budgets of non-breeding Dunlin *Calidris alpina pacifica* in the Fraser River Delta, B.C.

(2001, PhD thesis, Simon Fraser University, British Columbia, Canada)

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I investigated aspects of the ecology of non-breeding Dunlin *Calidris alpina pacifica* in the Fraser River Delta, British Columbia, the most northerly site supporting a sizeable population of the subspecies in winter (approx. 40,000 birds).

I used radio telemetry, direct observation, and Geographical Information Systems to document site fidelity, space-use patterns, habitat preferences, and time-activity budgets of individual non-breeding Dunlin throughout the 24-hour day and twice-daily tidal cycles. Site fidelity and habitat preferences were examined at both regional and local scales. Space-use was quantified by estimating home range and core area sizes, and by examining core area placement, macrohabitat choices (marine versus terrestrial), and movement patterns within the home range. By following individuals through time and calculating within-bird means by tide stage, macro-habitat, and time of day, I minimized sampling biases and produced a detailed picture of the individuals' behaviour.

Dunlin were trapped in three areas within the Delta during two non-breeding seasons (1995–96 and 1998), and categorized by sex, and, where possible, by age. I used a maximum likelihood mixture model to assign sex, based on culmen length.

Dunlin were site faithful, both regionally (to the Fraser Delta) and locally (within the Delta). I used compositional analysis to show that Dunlin chose habitats non-randomly at both regional and local scales, and there were differences among sex and site categories. Marine habitats were ranked highest. I assessed marine invertebrate prey densities (large and small annelids, crustaceans, and molluscs) for intertidal micro-habitats throughout the Delta, to examine their relationship with space-use by Dunlin. Across sites, marine home range size decreased as prey density within the home range increased, with prey density accounting for 63% of the variance in home range size. Within a single site, both marine home range and core area size decreased as prey density increased, with prey density explaining 89% of the variance in home range size and 80% of the variance in core area size. Dunlin marine core areas contained higher densities of crustaceans and small annelids than did the rest of the home ranges. Most Dunlin also used a range of terrestrial habitats, particularly at night. Soil-based agricultural crops were preferred at a regional scale, and pasture was the only agricultural crop that was highly ranked and significantly preferred at both regional and local scales.

Dunlin spent on average at least (depending on season) 15.7 hours per 24-hour day foraging, and at least another 3 hours per day flying (measured in spring), leaving on average at most 5.3 hours per day for activities such as roosting, preening, vigilance, and aggression. The percentage of time that Dunlin spent feeding did not differ between day and night, nor between marine and terrestrial macro-habitats. Dunlin spent on average at least 7.1 hours foraging at night, of which at least 2.9 hours occurred in terrestrial habitats, although the relative use of marine and terrestrial habitats varied considerably among individuals. Females spent less time foraging than males, but there was no difference between age classes.

Finally, I compared the sex ratios and within-sex body sizes of Dunlin wintering in the Fraser River Delta with those wintering in central California, where ecological variables might favour smaller birds. Although female Dunlin are larger than males, both populations were similarly malebiased, and I did not find significant within-sex size differences between latitudes.

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## Genetic variation and migration of waders

(2001, PhD thesis, Lund University, Sweden)

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One difficulty in the study of bird migration is to follow the same birds throughout the annual cycle, as they move between their breeding and wintering habitats. Populations may mix on migration and the breeding origin of the birds is usually unknown. A way of addressing this problem may be to develop genetic markers that can be used to reveal the breeding origin of birds caught on migration or on the wintering grounds. This was one of the aims of the thesis. The genetic analyses are also applied in another context: to reveal aspects of the species' history. The occurrence of bottlenecks, population expansions or declines is tested, previous population structure and mixing between populations is investigated and long-term effective population sizes are estimated. Apart from the genetic analysis, stable isotope ratios in feathers are also tested as a tool for identifying the origin of migrating waders.

Three species of waders are studied: Dunlin *Calidris alpina*, Curlew Sandpiper *C. ferruginea* and White-rumped Sandpiper *C. fuscicollis*. The genetic variation within these species is described mainly using two molecular genetic methods: mitochondrial DNA-sequencing and microsatellite analysis. The birds are also sexed genetically.

In the Dunlin, previous work by Wenink *et al.* (1993, 1996) has demonstrated that there are five groups of mitochondrial DNA in the Dunlin throughout the world. Here, the distribution of these groups of Dunlin is investigated further in various breeding populations in the Palearctic (Papers I, V). The mitochondrial DNA shows clear geographic structuring



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