

Abstracts of wader theses

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.

Behavioural ecophysiology of migratory Great Knots

(2002, PhD thesis, Australian School of Environmental Studies, Griffith University, Nathan, Queensland 4111, Australia)

Phil Battley, 2/30 Bucklands Beach Road, Bucklands Beach, Auckland, New Zealand
e-mail: pfbattley@yahoo.com.au

I studied the behaviour and ecophysiology of the Great Knot *Calidris tenuirostris*, a medium-sized migratory sandpiper, in Roebuck Bay, northwest Australia, and Chongming Island, Yangtze River mouth, eastern China. Great Knots breed on mountaintops in eastern Siberia and most spend the non-breeding season in northern Australia. They migrate north in late March and April, flying more than 5400 km direct to eastern China and Korea, before refuelling in the northern Yellow Sea and departing for the breeding grounds in late May.

A comparison of body composition of birds caught before migration from northwest Australia and birds caught after migration in China found that, in addition to the expected use of fat deposits during migration, lean tissue of most internal organs was reduced after flight. The largest reductions were in the flight muscles, skin and carcass remains. Significant decreases were also found in the salt glands, intestine, liver and kidneys. This is the first demonstration of extensive lean tissue catabolism in migrating birds, and shows that the 'airplane refuelling paradigm' of Odum *et al.* (1964: Homeostasis of the non-fat components of migrating birds. *Science* 143: 1037–1039), which claimed that only fat content varies in migrating birds, does not hold. The reduction in lean mass was reflected in a 42% decrease in basal metabolic rate (BMR) after migration. Variation in BMR was associated with variation in the flight muscle mass and intestine mass. Captive premigratory Great Knots that underwent an enforced fast showed a similar reduction in BMR. The relationships between BMR and body mass in between- and within-individual comparisons differed from the relationship typically found among species. The slopes (exponents) of log-log regressions of BMR against body mass were among the highest known in birds (intraspecific comparison, slope = 1.36; intraindividual comparisons, mean slope = 2.23). Predicting BMR from interspecific allometric equations is not possible during fuelling and migration periods.

Body composition changes indicated that migrating Great Knots conserved protein as efficiently as any bird, active or inactive, drawing as little as 4% of their energy from protein. Nevertheless, the magnitude of the flight from Australia to China resulted in substantial lean tissue catabolism. Comparison of the body composition of wild migrated knots with fasted birds indicated that both groups had broken down lean tissue from most organs in the body with the exception of the brain, though nutritional organs were substantially more reduced in the fasted birds.

Such lean tissue breakdown means that there is no 'fixed' tissue mass component in long-distance migrating birds. A

recent predictive model of bird flight by Colin Pennycuik (1998: Computer simulation of fat and muscle burn in long-distance bird migration. *Journal of Theoretical Biology* 191: 47–61) was modified to allow lean tissue breakdown from the 'airframe' as well as the flight muscles (airframe being the total mass minus fat mass and flight muscle mass). The model was also modified to allow protein breakdown in the flight muscles from only myofibrils. Predicted flight lengths for an average Great Knot caught in Australia before migration were sufficient to reach China, but only if the body drag coefficient used was much lower than the previous default values (0.10 to 0.17 c.f. 0.25 to 0.40). The model did not accurately predict the flight muscle mass on arrival, always removing too much tissue during flight.

Behavioural heat avoidance was studied during fuelling in Roebuck Bay. Birds with higher breeding plumage scores (i.e. better fuelled) had a higher incidence of heat avoidance (primarily raising of back feathers). Solar radiation also affected the frequency of heat avoidance. The study season was unusually wet and cool. In a more typical season heat avoidance may be more prevalent.

Photographs of Great Knots breeding in Russia seem to show more red feathering on the mantle and scapulars than is observed in birds fuelling in Australia. We studied the pre-breeding moult progression and plumage in knots before migration from Australia, just after arrival in China, and on Russian staging and breeding grounds (using specimens from the Zoological Museum of Moscow). Great Knots had either completed or suspended prealternate moult before departure from Australia, and birds caught after arrival in China had not resumed moult. Russian birds had greater numbers of red feathers on their upperparts. The difference between the plumage of Russian and Australian/Chinese birds could not be accounted for by the continuation of the prealternate moult. Instead, a presupplemental moult must occur in birds refuelling in the northern Yellow Sea. This is the third wader in which a presupplemental moult has been identified. The relative importance of sexual selection compared with natural selection in the evolution of this moult is unknown.

Great Knots were radio-tagged to determine individual departure dates on migration. When caught, condition indices were taken; body mass, breeding plumage score and breast muscle mass (estimated by ultrasound). Departures occurred evenly from 25 March to 13 April. Twenty-three of the twenty-seven radio-tagged knots departed on migration. Birds that remained had lower residual body masses and breeding plumage scores than birds that departed. Whether



the birds that remained were off-schedule or subadult is not known. There was no relationship between body condition at capture and departure date for the birds that migrated. Departures from northwest Australia are still six to eight

weeks before breeding starts, and time constraints probably become greater as birds migrate north towards the breeding grounds. These findings suggest that not all stages of a migration are under equally strong selection pressures.

* * *

Oystercatcher specialisation: Fitness implications and population consequences

(2001, PhD thesis, University of Southampton, UK)

Sarah E. A. Le V. dit Durell, Centre for Ecology and Hydrology Dorset, Winfrith Technology Centre, Dorchester, Dorset DT2 8ZD, UK, e-mail: sld@ceh.ac.uk

The aim of this thesis was to investigate the fitness implications and the population consequences of individual feeding specialisations. In particular, it was concerned with how individual specialisations may affect the population consequences of habitat loss or change, a subject of particular relevance to conservationists. A review is made of individual feeding specialisation in shorebirds, the mechanisms involved in such specialisations and the different benefits and risks that may be associated with particular habitats or diets. Individual feeding specialisations were found to be widespread among many shorebird groups and most shorebird feeding specialisations were found to be constrained by differences in morphology, social status or individual skill. It is concluded that individuals or groups that are unable to change foraging area, diet or feeding method for social or morphological reasons would be the most vulnerable to any deterioration in their food supply.

Research into Oystercatchers *Haematopus ostralegus* overwintering on the Exe estuary, south-west England is presented and individual feeding specialisations described. Young birds and females specialised in different diets and feeding methods from adult males. Sex ratios changed with age such that 50% of immatures and 67% of adults were male. Individual fitness was measured in terms of body con-

dition and mortality rates of ringed birds. Mussel-hammerers, the majority of which were male, had higher body condition indices and lower rates of mortality than mussel-stabbers and worm/clam feeders. Worm/clam feeders, the majority of which were females and young birds, had lower body condition indices and higher rates of mortality than mussel feeders. It is suggested that young birds and females on the Exe had higher rates of winter mortality because of the lower payoffs and/or higher risks associated with their feeding specialisations.

A modelling approach is used to predict the population consequences of differential mortality between age and sex groups. Increasing the mortality of young birds or females substantially reduced population size. Increasing female mortality resulted in a male biased population. Any increase in mortality which affected one sex more than the other resulted in a greater reduction in population size than if the increase affected both sexes the same. It is concluded that studies designed to predict the effect of habitat loss or change on shorebirds should be particularly aware of age and sex-related feeding specialisations that may lead to age and sex differences in mortality and age and sex differences in response to change.

* * *

Determinants of habitat and site use by Turnstones and Purple Sandpipers in N.E. England, and possible effects of the removal of coastal nutrients

(2001, PhD thesis, University of Durham, UK)

Mark Eaton, Royal Society for the Protection of Birds, The Lodge, Sandy, Beds SG19 2DL, UK
e-mail: Mark.Eaton@rspb.org.uk

Purple Sandpipers and Turnstones were studied on the coast of south Northumberland, with regard to the possible effects of reductions in sewage inputs into inshore waters along the Northumberland coast as a result of new European legislation. Multivariate analysis of bird density in relation to 33 habitat variables indicated that Purple Sandpiper distribution was positively correlated with the abundance of intertidal musselbeds, but negatively correlated with raptor density. Turnstone density was positively correlated with several intertidal habitats such as bare and barnacle-covered rock, as well as the amount of detached wrack deposited on the strandline. Analysis of stable carbon and nitrogen isotopes in particulate organic matter in inshore waters indicated that sewage contributed up to 60% of the total organic matter in the immediate vicinity of outfalls, and hence probably supported increased intertidal invertebrate densities.

Purple Sandpiper numbers were unlikely to be limited by

food resources, but birds sought to feed in areas that offered the highest food intake rates, in order to reduce the time spent feeding and therefore minimise the risk of predation by raptors. Social status determined where birds could feed, with larger and older birds excluding subordinates to poorer feeding areas. Social status in Turnstones was determined by sex and age. By feeding on the richest intertidal food resources, dominant individuals (males and adults) minimised the time spent foraging on ephemeral deposits of strandline wrack over high water, which carried a greater risk of predation. Dominant individuals of both species were able to carry less stored fat and hence improved their chances of escaping attacks by raptors. While both species are unlikely to decline in numbers as a direct response to lower food densities, subsequent changes in foraging behaviour and distribution could result in greater mortality.



Foraging site selection of turnstone *Arenaria interpres* on the Wash estuary

(2001, BSc dissertation, University of East Anglia, UK)

Jennifer Smart, School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK
e-mail: jennifer.smart@uea.ac.uk

[The substance of this dissertation is currently in press as: Smart, J. & Gill, J.A. Non-intertidal habitat use by shorebirds: a reflection of inadequate intertidal resources? *Biological Conservation*]

1. Turnstone *Arenaria interpres* wintering on the Wash generally forage on inter-tidal habitats. However, since 1998, they have also used a man-made port for foraging where they feed on food spilt during dock operations. Long term ringing data for the Wash population were analysed to examine movement patterns and weight differences between local populations. The factors determining distribution patterns between the port habitat and adjacent inter-tidal habitats and arable farmland were studied. Detailed studies of the use of the port and the food resource were also carried out.
2. Analyses of local movements within the Wash showed a higher degree of site fidelity to the east and west shores of the estuary when compared to the south, both within and between years. A comparison of weights showed that the port population was significantly lighter than the east shore population.
3. Distribution patterns were associated with month, time of day and tidal state. Throughout January and February, inter-tidal habitat use by radio-tagged individuals was restricted to the area east of the mouth of the River Nene. Foraging on the edge of the River Nene was highest during morning, low tide periods. Arable farmland was also used and the use of this habitat increased from December to February and was highest during afternoon, high tide periods.
4. The prey species were cockles *Cerastoderma edule* on the inter-tidal, barnacles *Balanus spp.* on the Nene edge and beetles and earthworms in the fields.
5. The number of turnstone present at the port was negatively related to time from high tide and daily temperature. The presence of colour-ringed individuals showed that the use of the port was tide dependent in November and December and daytime dependent in January and February.
6. The main food available at the port was wheat and the density of wheat available determined intake rates. There was no evidence of interference competition. Foraging occurred in discrete bouts. The bout length was higher with larger flocks and with low port activity. Bout rate was determined by daily temperature and the time between foraging bouts was higher following the appearance of an avian predator.
7. The results of this study suggest that turnstone use the port habitat in accordance with the "supplementary food hypothesis" and the availability of this habitat could be contributing to the maintenance and increase in this population.

* * *

Feeding ecology of shorebirds (Charadrii) spending the non-breeding season on an Australian subtropical estuarine flat*

(2002, PhD Thesis, University of Queensland, Australia)

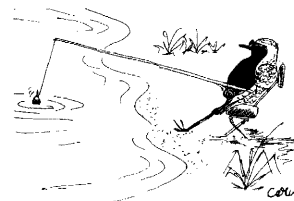
Yuri Zharikov, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
e-mail: zharikov@sfu.ca

This study examined six aspects of the foraging ecology of Eastern Curlews *Numenius madagascariensis* and Bar-tailed Godwits *Limosa lapponica* on a subtropical estuarine intertidal flat in Moreton Bay, Queensland, Australia. The topics studied were:

1. Exploitation of food resources by the shorebirds and food-resource predictability

The results of a large-scale experimental study showed that in the warm climate wintering area of Moreton Bay, Bar-tailed Godwit intake rates are directly limited by prey density. This conclusion is supported by the quick functional and numerical response of the birds to an experimentally induced decline in prey abundance, a strongly linear relationship between their capture rates and the density of their principal prey and high (>100%) estimated seasonal reduction of prey

stocks present at the start of each non-breeding season. These findings suggest a high level of exploitation of food resources by shorebirds in subtropical estuaries and imply that predictability of food supply for the shorebirds in the system is higher in comparison with colder-climate wintering areas.



* Copies of this thesis can be obtained on CD-ROM from the author



2. Potential competition for the same resource between humans and Eastern Curlews

At present, the rates of harvesting of the callianassid shrimp *Trypaea australiensis* by bait collectors do not pose a threat to the stability of the foraging environment of Eastern Curlews. In fact, curlews may themselves exert a much higher predation pressure on the populations of this crustacean in terms of the number of prey removed per unit area than bait collectors. However, there was no evidence that substantial depletion of *Trypaea* stocks in the presence of heavy Eastern Curlew predation occurred. It is hypothesized that this stability of *Trypaea* stocks may be facilitated by continuous recruitment into the prey population.

3. Seasonal trends in shorebird diet composition

In the study area, Eastern Curlews restricted their diet to three decapod crustaceans: mictyrid crab *Mictyris longicarpus*, callianassid shrimp *Trypaea australiensis*, and ocyropodid crab *Macrophthalmus crassipes*. The contribution of *Trypaea* to the energy intake of the birds increased during the period of pre-migratory preparation in each of the three field seasons of the study (1998–2001). It appears that seasonal diet composition in the Eastern Curlew is determined largely by the relative profitability of the different prey types and therefore the intake rates that can be achieved, and possibly also the nutrient requirements of the shorebirds prior to migration.

4. Digestive constraints to energy intake in the Eastern Curlew

In this species, neither crude intake rate (the rate of intake calculated over all foraging time, including inactive pauses) (0.22 g DW or 3.09 kJ min^{-1}) nor the rate of gastric throughput (0.15 g DM or 2.81 kJ min^{-1}) changed significantly between the mid-wintering and pre-migratory periods. An asymptotic relationship between crude intake rate/gastric throughput rate and intake rate while actively foraging strongly suggests that the birds experience a digestive bottleneck, i.e. a pause in active foraging has to take place when the whole (or perhaps part) of the digestive system is full. Likewise, gastric digestive efficiency of organic matter (averaging 91%) did not change between these periods nor did energy assimilation efficiency (estimated at 62.8% in

November–December and 57.9% in February). It is argued that the apparent physiological constraint to the rate of energy acquisition restricted the choice of foraging strategies available to the birds during the time of pre-migratory nutrient reserve deposition to lengthening time spent foraging within that allowed by the duration of tidal exposure.

5. Food-resource based territoriality in the Eastern Curlew

An inverse relationship was found between feeding territory size of Eastern Curlews ($0.52 \pm 0.21 \text{ ha}$, $n = 25$) and the dry biomass density of its important prey, the callianassid shrimp *Trypaea australiensis*. This explained 69% of the variation in territory size. The rate of territorial encounters between curlews holding adjacent territories and the proportion of time spent engaged in this behaviour were not related to territory size, suggesting that no immediate cost was involved in holding territories with higher prey biomass densities and thus intake rate. These results, although correlative, are consistent with the territoriality hypothesis, which proposes that individuals can assess food resource density and adjust the size of the area they defend accordingly without any effect of competitor pressure.

6. Sex-specific habitat use in the Bar-tailed Godwit

It was found that in an area with two habitats, seagrass *Zostera* beds and unvegetated sandflats, male Bar-tailed Godwits occurred almost exclusively in seagrass while females occurred at equal densities between the two habitats throughout the non-breeding season. Estimated intake rates achieved by individuals foraging in seagrass were higher than on sandflats ($0.114\text{--}0.128 \text{ g DM min}^{-1}$ compared to $0.064\text{--}0.087 \text{ g DM min}^{-1}$) and comparable with intake rates recorded for godwits elsewhere. Based on behavioural observations, males appeared to be less well adapted for foraging in sandy habitat than in seagrass and the presence of the females in the same habitat could interfere with their foraging there. The reasons for the equal distribution of the females between the habitats are not clear. However, it is probable that one of the habitats (sandflats) supports the maximum sustainable density of females, ultimately because of prey depletion and proximally because of interference.

