

Abstracts of Wader Theses

Compiled by Rob Robinson

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 Rob Robinson, BTO, The Nunnery, Thetford, Norfolk IP24 2PU, UK, rob.robinson@bto.org or the Editor.

Influence of predators on the breeding success of meadowbirds in Brandenburg

(2006, Ph.D. thesis, University of Osnabrück, Germany)

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Predation as a threat to ground breeding birds has received a growing attention during the 1990s. I studied densities and breeding success of Northern Lapwing simultaneously with number and distribution of Red Foxes several years after rabies vaccination in two East German wetlands. The study areas were situated in the Havel and Oder valleys.

Since c.1995 Red foxes *Vulpes vulpes* inhabit Eastern German wetlands at similar densities like open farmland (3–4.6 litters per 10 km²) except a part of the Lower Oder valley which is flooded every spring (1.5/10 km²). They selected for dry places when excavating dens but in wet meadows along the river Havel increasing numbers of dens closer to groundwater suggested a recent immigration. Foxes regularly preyed upon birds in spring but only formed one part of a diverse guild of mammalian predators inhabiting wetlands. Thus at low fox densities other mammals like mustelids became more important as predators. Increasing groundwater tables and removing artificial dry places can help to make wetlands less attractive for foxes.

Conservation management has created attractive habitats for several meadowbird species in both areas. Nest losses due to farming activities were of relatively low importance but throughout the study period losses due to predation were usually high and productivity was insufficient to maintain local populations. Carnivores formed the majority of the predators identified and especially Red Foxes played an

important role. The only exception was a hatching success of 66% for one year in one area which is subject to regular flooding and where area mustelids appeared to be the most important predators. This occurred in 1998 after the catastrophic Oder flood of 1997 which probably led to a crash of local small mammal and mustelid populations. Thus neither culling of corvids nor attempts to control only foxes can be expected to effectively lower predation rates and future management should identify the factors limiting the entire mammalian predator guild.

Lapwing chick survival showed a decrease during summer and was strongly dependent on the availability of water and wet soils in the parents' territories. Water therefore still seems to be the most important environmental factor in wet grassland management.

Predation on Yellow Wagtail nests in the Oder valley was no important threat. Without additional losses due to mowing and grazing the local population would be self-sustaining. Similar results were obtained in other German studies and a review revealed two general patterns. Mainly large and medium-sized species of ground breeders suffered from high predation rates while songbirds are mostly unaffected. Carnivores have been identified as important predators in virtually all recent thorough studies while birds (including the regularly suspected corvids) were of minor importance.

Quantifying abundance, breeding and behaviour of the African Black Oystercatcher

(2006, Ph.D. thesis, University of Cape Town, South Africa)

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The African Black Oystercatcher *Haematopus moquini* was studied at the Koeberg Nuclear Power Station and Nature Reserve from November 2002 until June 2005. This protected mainland site has low levels of human disturbance both within the harbour area and on the adjacent beaches where a variety of terrestrial and avian predators occur. The oystercatchers breed on artificial rocky shore within the harbour and the sandy beaches. The oystercatcher is long-lived, strongly territorial and mate-faithful with a low reproductive rate. It has been studied extensively on offshore islands, Western Cape rocky shores and Eastern Cape sandy shores but not on

Western Cape sandy shores.

Breeding productivity and abundance data were collected by conducting weekly counts (adults, pairs, nests, chicks and fledglings) and each breeding pair was followed throughout the breeding season. The dates of hatching, fledging and departure from the parental territory were recorded for each chick. Total time commitment to breeding for each pair was calculated. Breeding productivity data of oystercatchers from other sites were compared. Feeding behaviour was observed and quantified. Prey was identified and correlated to sampling done at the site. Behaviour activity data were collected by

instantaneous scans of birds on the rocky and sandy shores; tide, weather, daylength and time of day were used as explanatory variables in generalized linear models. Each behaviour was modelled. Behaviour between the rocky and sandy shores was compared. Management practices and other seabirds and shorebirds breeding at the site were observed.

A model to evaluate reproductive effort in relation to time investment and egg production is introduced; the large variation in these explanatory variables will enable their relative importance to be detected. A graphical method to display time commitment to breeding and to provide an overview of breeding events is introduced and used to facilitate visual comparisons between different seasons and sites.

Oystercatcher density increased over 30 years; in the harbour there were 46 birds/km and 13 birds/km on the beach. The oystercatcher pairs in the artificial shore of the harbour have a similar productivity to an adjacent area of shoreline five times as long as the original shore. Over the three-year study period, the breeding productivity of oystercatchers at Koeberg was below that estimated to maintain a stable population (0.35 fledglings per pair per year). The poor productivity at Koeberg is mainly attributed to egg and chick loss as a result of predation; in addition there were high levels of human disturbance in the 2004/2005 breeding season.

Data from 18 breeding sites around the South African coastline, on different shore types, were grouped into protected island sites, protected mainland sites and unprotected mainland sites. Egg loss resulting from predation caused poor breeding success at protected mainland sites; human disturbance caused chick loss at unprotected mainland sites. Site-

specific conditions played the largest role in determining breeding success and reasons for variation in breeding success often remained unclear. However, it is clear that the best place for an oystercatcher to breed is on an island with no predators.

African Black Oystercatchers foraging diurnally on sandy shores of the Western Cape, feed mainly on polychaetes (*Scololepsis*, *Nephtys* and *Glycera*), also on small crustaceans (especially associated with the drift-line kelp) and *Donax serra*. This sandy shore offered a diverse array of possible prey items throughout the tidal cycle and although specialization was present (particularly for an individual bout of feeding) the adaptable oystercatchers used a variety of techniques and opportunistic behaviours to utilise the available prey.

The effects of several variables on the different behavioural activities of the oystercatcher on rocky and sandy shores on a Western Cape mainland site were quantified. The main difference seen is the dependence of the rocky shore birds on the tide height, especially feeding, sleeping and lying and the relative importance of all the variables (tide, weather conditions, daylength and time of day) on all behaviour activities on the sandy shore birds. Feeding on the sandy shore occurs throughout the tidal cycle but was more dependent on weather variables.

The Koeberg Nuclear Power Station and Nature Reserve meets the criteria for an Important Bird Area and a Ramsar Wetland of International Importance. The nuclear power station is a National Key Point site having strict security for entry and therefore low human disturbance within the harbour area. Practical conservation recommendations are given.

State dependent life-history strategies: a long-term study on Oystercatchers

(2006, Ph.D. thesis, University of Groningen, the Netherlands)

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The research described in this thesis is part of a long-term field study on free-living Oystercatchers (*Haematopus ostralegus*), on the Dutch Wadden Sea island of Schiermonnikoog. The study was started in 1983 by Jan Hulscher, and since then a lineage of PhD-students has investigated life-history decisions in this long-lived bird species. Most of their work has focused on understanding individual variation in settlement decisions, partner choice and reproductive decisions. Their strategy to investigate these life-history decisions has been to combine detailed behavioral observation with a long-term dataset collected over many years, and to conduct critical experiments whenever possible. The research conducted in this thesis is aimed to be a continuation, and it investigates some of the questions which are the direct result of previous work. Furthermore, we will integrate the results from many of these studies to better understand why this breeding population is declining so rapidly in recent years.

This thesis is partitioned into four main parts: (i) a general introductory part, (ii) a section on age-dependent life-history decisions, (iii) a section on state-dependent life-history strategies, and (iv) a concluding part. Each part consists of several chapters, with each chapter discussing one specific research topic. Some of the chapters are followed by a box, which discusses a topic related to the chapter, but in less detail. We end with a general discussion in the final chapter, in which

some of the results from individual chapters are brought together. In chapter 2, we continue our general introduction with an introduction to the study system by describing how this population has changed over the last twenty-one years. Breeding numbers of Oystercatchers have declined strongly in recent years on Schiermonnikoog, as well as in most other breeding areas in the Netherlands. We investigate in detail which demographic parameters have changed on Schiermonnikoog and how this relates to changes in food availability and climate change. Subsequently, we discuss what might have caused Oystercatcher breeding numbers to decline rapidly all over the Dutch Wadden Sea.

The second section on age-dependent life-history decision we discuss how life-history traits change during a lifetime. In chapter 3, we first develop a new statistical model to separate within and between-individual effects. Our model can be useful in many biological situations, but we will illustrate our approach with two examples on age-dependent reproduction in Oystercatchers. We show that old Oystercatchers have a higher reproductive performance than young Oystercatchers for two different reasons. Firstly, individuals perform better as they age (within-individual improvement), and secondly Oystercatchers that start breeding late in life perform better than individuals that start breeding early in life (selective appearance, between-individual change). Furthermore, our

method can give much more insight in underlying mechanisms of age-dependent changes than alternative methods. In box A, we give an additional example in which the statistical model developed in chapter 3 can be used. We show that patterns of extra-pair copulation behavior not only change during the duration of a pair bond, but that pairs with high levels of extra-pair copulation behavior are also more likely to split up the next year. Following up on the role of the pair bond we show in chapter 4 that variation in reproductive performance during a lifetime is more likely to depend on how long a pair had been together, than on the age or breeding experience of individual pair members. Using observational as well as experimental data, we suggest mate-familiarity is one of the main determinants of reproductive success in Oystercatchers. In box B, we integrate patterns of age-dependent probabilities of breeding, reproduction and survival into an age-structured population model. From this model we calculate age-specific reproductive values and sensitivities which we use to discuss how the selection for earlier or delayed maturity depends on the population growth rate in Oystercatchers.

In the third section on state-dependent life-history strategies we investigate how life-history strategies depend on the conditions, mainly in relation to the habitat quality individuals breed in. In chapter 5, we first give a general description of what are the main causes of phenotypic variation in life-history traits of Oystercatchers, and what causes life-history traits to co-vary. We show that both reproductive output and survival not only depend on individual quality, but also on the quality of the partner, suggesting that life-history traits in Oystercatchers are not simple sex-linked traits. Furthermore, we discuss how our analyses can be used as a powerful ally to life-history experiments. In chapter 6, we focus on one specific life-history trait, egg size. In Oystercatchers there is substantial variation in egg size, and parents that lay larger eggs produce more offspring. However, it is unclear whether a large egg really constitute an advantage to the chick or that chicks from larger eggs do better because they are also born

in a better rearing environment. We performed a cross-foster experiment to disentangle the effect of egg quality and the quality of the rearing conditions on the survival of chicks hatched from small and large eggs. In chapter 7, we investigate the long-term consequences of being reared under favorable conditions. We show that rearing under high quality conditions not only affects life-history traits early in life, but also settlement decisions later in life. Even future offspring benefit. We discuss whether early conditions are likely to have long-term effects in many other species too, and discuss the problems associated with using short-term fitness measures. In box C, we follow up on chapter 7 by discussing why offspring reared under favorable conditions do much better, and what determines offspring quality. In chapter 8, we discuss the relationship between the life-history decisions where and when to reproduce. Oystercatchers strongly vary in the quality of their breeding habitat, as well as in their age at first reproduction. Following up on a previous study by Bruno Ens and colleagues, we further develop the idea that variation in both these traits might be the result of individuals queuing for high quality breeding territories. We improve their original model; incorporate asymmetries in settlement behavior (as suggested in chapter 7), and compare model predictions with observed patterns in the field. Finally, we discuss how queuing behavior might help us understand patterns of population decline in this species.

In the General discussion section, chapter 9 concludes with integrating some of the conclusions from separate chapters into a more general framework. We will specifically return to what we have learned about what are the most important causes of variation in life-history traits. Furthermore, we will discuss how life-history decisions are affected by the population composition, and how in turn life-history decisions might affect population dynamics. Finally, we will discuss what might be some of the future challenges in the study of life-history evolution, and for the Oystercatcher study population on Schiermonnikoog.

Strategies of sea-level rise mitigation for breeding Redshank

(2005, Ph.D. thesis, University of East Anglia, Norwich, England)

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Amongst the key conservation implications of sea-level rise are reductions in the extent of saltmarsh and coastal grasslands, habitats which both have important nature conservation interests. This creates a situation in which (1) a trade-off between increases in saltmarsh at the expense of coastal grassland will exist, (2) options for mitigation are likely to be limited in the coastal zone and (3) improvements to inland habitat management could provide compensatory habitat. For species supported by these habitats, the relative quality of coastal and inland habitats is unknown. This thesis uses the Redshank, *Tringa totanus*, a wading bird species that breeds on saltmarsh, coastal and inland grasslands, to address these issues. Redshank populations are declining across many countries and on all breeding habitats but declines inland have been most severe. Comparisons of breeding densities and breeding success between habitats give contrasting results. Breeding densities are highest on saltmarsh and coastal grassland but breeding success is very low, due to a

combination of low hatching success resulting from predation and tidal flooding, and poor chick survival. On inland grassland, where breeding densities are lowest, breeding success is much higher than on either saltmarsh or coastal grassland. Despite extensive use of intertidal habitats for foraging, by coastal breeding birds, access to intertidal foraging areas did not improve breeding success. Schemes aimed at creating saltmarsh are unpredictable in their outcome and likely to have significant time-lags (>80 years). In contrast, grassland rehabilitation can be both rapid and effective because management can be optimised by providing shallow wet features and suitable vegetation. Thus, the higher success of inland grassland populations coupled with the success and potential for large areas of grassland rehabilitation to occur means that this could provide the best short-term solution to conserve breeding wader populations. In the long term, these populations may then act as centres for population expansion once saltmarsh creation schemes realise their biodiversity potential.

From an egg to a fledgling: A perspective on shorebird breeding ecology and chick energetics

(2006, Ph.D. thesis, Behavioural Biology, Groningen University, Haren, the Netherlands)

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Shorebirds are a diverse group of species exhibiting a variety of growth rates, reproduction strategies and behaviours which enable them to survive in the different environments in which they live and breed. Adaptations are not limited to specialised egg structure or large fat reserves to survive harsh conditions. There are other adaptations, also physiological, that enable shorebirds to survive in harsh climates; for example, metabolic adaptations in chicks. I discuss the adaptations of shorebird (Charadrii) chicks that enable them to grow and fledge successfully in their environment.

Although the breeding phenology, breeding success and population trends of African Black Oystercatchers *Haematopus moquini* over three austral summers on Robben Island, South Africa, from the 2001–2002 to the 2003–2004 breeding seasons were discussed, the bulk of the thesis considers the pre fledging growth and energetics of shorebird chicks; in particular, the Little Stint *Calidris minuta* (Scolopaciidae), Kittlitz's Plover *Charadrius pecuarius* (Charadriidae), Blacksmith Lapwing *Vanellus armatus* (Charadriidae), Crowned Lapwing *V. coronatus* (Charadriidae), African Black Oystercatcher (Haematopodidae) and Spotted Thick-knee *Burhinus capensis* (Burhinidae).

These species were selected on the basis of different adult body masses, different modes of development and different timing of breeding. Together with data from the literature I could also investigate the influence of (adult) geographical breeding distribution on the growth and energy expenditure of shorebird (Charadrii and Lari) chicks.

Little Stint chicks at Medusa Bay, Siberia (73°N), grew relatively quickly; their growth rate coefficient was 14% greater than the prediction (from Beintema & Visser 1989) for a bird their size. Their total metabolisable energy, TME, over the 15-day pre fledging period was 107% greater than the allometric prediction (from Weathers 1992) for a bird the size of a Little Stint. Therefore their small size and large surface area-to-volume ratio may have resulted in greater relative heat loss and thus impacted their energy expenditure and growth. To obtain the observed growth rates, chicks had to rely on a high rate of food intake.

Kittlitz's Plover, Blacksmith Lapwing and Crowned Lapwing chicks were studied in a warm, sub-tropical environment, in South Africa (34°S). Body size, timing of breeding, mode of development, and habitat all impacted the growth and energetics of the three species. Their small growth rate coefficients, low resting metabolic rates (RMR) and low daily energy expenditure (DEE) may be adaptations to low food availability and mild ambient temperatures. The three precocial species exhibited slower growth, longer fledging periods and lower daily energy expenditure than arctic and temperate zone relatives of similar size.

African Black Oystercatcher chicks are semi-precocial; they are mobile soon after hatching but are parentally fed. Growth rate influenced fledging success, the length of the pre fledging period and mass at fledging. Chicks exhibited a large variation in growth rate coefficients and chicks with comparatively slow growth rates were able to fledge. These chicks exhibited retarded growth of all body measures except wing length, thus enabling them to fledge in a shorter period

of time than their slow growth would otherwise have allowed. Sibling rivalry occurs in African Black Oystercatchers and once a dominance relationship is established the larger chick remains so throughout the pre fledging period. The larger sibling fledges earlier and at a heavier mass and may thus have improved its chances of survival.

Spotted Thick-knees are also semi-precocial shorebirds, feeding predominantly at night. The observed average growth rate coefficients of African Black Oystercatcher chicks on Robben Island (33°S) and Spotted Thick-knees in the Western Cape (34°S) were similar to that predicted from the Beintema & Visser (1989) allometric equation. Their relative (observed versus predicted) growth rate coefficient was closer to the predicted value for shorebirds than those of three precocial, self-feeding shorebird species in the Western Cape. The growth rate coefficient of African Black Oystercatcher chicks was smaller than that of other oystercatcher species which may be a consequence of differences in body size and differences in climate and food availability. RMR, peak daily metabolisable energy (DME) and total metabolisable energy (TME) of African Black Oystercatchers and Spotted Thick-knees were similar to those expected for the species (from Weathers 1992 and based on comparisons with the Eurasian Oystercatcher). African Black Oystercatchers spent less time foraging and more time inactive than precocial species. The potential negative impact of nocturnal feeding on Spotted Thick-knee chick growth may be countered by parental feeding reducing chick energy expenditure on thermoregulation and activity and adults potentially extending their foraging time into the day as their chicks become larger. Therefore their mode of development enabled oystercatcher and thick-knee chicks to reduce energy costs from thermoregulation and activity, enabling them to grow relatively faster than precocial shorebird species in similar climatic conditions.

Through a study of shorebirds (Charadrii) as a group and through comparing them with other Charadriiformes (Lari) we were able to investigate the importance of adult body mass, mode of development and latitude in shorebird growth and energy expenditure. Shorebird growth rate coefficients decreased whereas energy expenditure increased with increasing adult body mass. Semi-precocial shorebirds exhibited faster relative growth rates than precocial species at similar latitudes; e.g. comparing the growth of African Black Oystercatcher and Spotted Thick-knee chicks to that of precocial shorebirds in southern Africa. Habitat type and food availability are a consequence of latitude. The growth rate coefficients and metabolisable energy expenditure of shorebirds increased with increasing latitude, thus food availability and habitat type are influencing factors in shorebird growth and energetics. Shorebird chicks at higher latitudes spend their time brooding or foraging and spent little or no time in other activities whereas shorebird chicks in the Western Cape did not seem to be limited by time available for foraging but rather by food availability. Chicks at higher latitudes may be able to compensate for their greater energy expenditure due to greater thermoregulatory energy costs through greater food intake than chicks at lower latitudes.