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.

The causes of individual and seasonal variation in the metabolic rate of Knot *Calidris canutus*

(1998, PhD thesis, University of Durham, UK)

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Basal metabolic rate (BMR), an individual bird's minimum rate of energy expenditure, was followed in adult and juvenile captive Knot throughout their annual cycle, in conjunction with measurements of total body mass (BM) and body composition (lean mass and fat mass, as predicted using Total Body Electrical Conductivity). Adult captive Knot increased significantly in BM during spring, primarily due to fat deposition. Most juvenile Knot did not display fat deposition in their first spring in captivity.

A seasonal peak in BMR, often double the seasonal minimum, occurred during spring but typically took place, on average, 5, 11 and 4 days (respectively) after the seasonal peaks in BM, lean mass and fat mass. Little of the variation in BMR seen within or amongst captive Knot, irrespective of physiological state, was explained by variation in a single parameter (BM, lean mass or fat mass). As variation in BMR was not simply a consequence of variation in total lean mass, the *average* metabolic output per gram of the lean tissues must also have altered seasonally.

During fat deposition in spring, Knot exhibited a significant increase in liver mass and a significant elevation (approximately 50% higher) in the activity of succinate dehydrogenase (SDH, an indicator of metabolic activity) in the small intestine. Such adaptations may have assisted an increase in fat deposition rate. SDH activity decreased by approximately 60% in the pectoral muscle of Knot during this period. Such a reduction in SDH may also aid fat deposition as it lowered an individual's overall BMR. As Knot BM decreased after the spring peak, their BMR decreased in parallel with a decrease in SDH activity in their pectoral muscles.

The spring peak in overall BMR may indicate an increase in the maximal sustainable metabolic rate (MMR) of an individual during migratory flight. If a relationship exists between BMR and MMR, then variation in metabolic activity rather than variation in the mass of various lean tissues (e.g. pectoral muscle) will increase metabolic scope without increasing the energetic costs of flight.

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Reproductive strategies in the common sandpiper *Actitis hypoleucos*

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

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1. This study investigated the breeding phenology and reproductive strategies of common sandpipers *Actitis hypoleucos* at Heriot and Leithen Waters, Borders, SE Scotland. The study combined observational, experimental and molecular techniques to determine the genetic mating system, parental care roles and brood sex ratio variation.
2. Arrival on breeding sites was highly asynchronous although the pattern of the sexes was similar. Arrival date explained variation in timing of breeding although late females partially compensated by initiating egg laying sooner. Supplementary feeding had no effect on timing of breeding. Pair experience was a significant predictor of nest success. Breeding success was low in 1998 due to high nest depredation. Probability of renesting depended on the time of the initial failure.
3. Sandpipers showed limited reverse-dimorphism but did not pair assortatively for any morphological trait. However, birds paired non-randomly with respect to previous breeding experience. None of the morphological or ter-

ritory quality parameters measured explained female settling patterns. Both sexes were equally faithful to former breeding areas but males displayed greater fidelity to specific territories. Females tended to switch territories following breeding failure but, in most cases, this coincided with the failure of old mates to return. When both mates returned, birds usually remated. Females always switched territories when old mates failed to return, suggesting that mating decisions may be based more on mate quality than territories
4. DNA fingerprinting revealed extra-pair paternity in the population. Of 83 offspring from 27 broods, 13 (15.7%) young from 5 (18.5%) broods were identified as extra-pair. There was no evidence of intra-specific nest parasitism. Most identified copulations were within-pair and occurred more often around egg-laying. Females control the outcome of copulations. Moreover, asynchronous arrival and mate switching may promote cuckoldry by stored sperm from previous matings.
5. Males invested significantly more in parental care during

incubation (60–62%) and brood attendance (58%) than females. Supplementary feeding resulted in supplemented males significantly increasing incubation duration compared to non-fed controls while supplemented females tended to reduce their effort. Females deserted some nests and most broods, leaving males as the sole carers. However, there was no apparent effect of desertion on breeding success. Laying-date explained a significant amount of variation in the timing of female desertion. Males invest substantially in care because they gain either current (replacement clutches, increased fledging success), future fitness benefits (increased female sur-

vival and pair remating) or both. Females reducing investment may gain delayed fitness benefits.

6. Using PCR amplification, I show that the brood sex ratio (0.62 males) at the population level differed significantly from unity in one year (1999). However, variation between broods was not different from a binomial distribution. Sex-ratio variation was unrelated to timing of arrival, breeding or parental characteristics, but was weakly related to the proportion of shingle edge on territories. There was no strong evidence of differential mortality

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Life history decisions in Oystercatchers*

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A life history approach was chosen to answer behavioural questions against an ecological background as: Where to settle? With whom to mate and reproduce? When and how much to invest in offspring? Both causal and functional questions on these topics were considered and I paid attention to the full scope from individual variation in behaviour via population structure to fitness consequences.

The research was carried out on a free-living, colour-marked oystercatcher population on the Wadden Sea island of Schiermonnikoog in the years 1990–1997. Individual oystercatchers have been followed in this population since 1983. Oystercatchers are predominantly monogamous waders, black and white with a pronounced red bill, and long-lived (mean life expectancy is fifteen years). They breed on the island and feed on the adjacent mudflats. Males and females are highly cooperative in territory defence, incubation (taking shifts) and feeding of the chicks. Differences in breeding territory quality are one of the important factors on which oystercatchers base their life history decisions. In a high-quality breeding territory (a so-called "*resident territory*") a pair produces *ca.* 0.65 fledglings annually, whereas in a low-quality breeding territory (a so-called "*leapfrog territory*") a pair produces only *ca.* 0.20 fledglings annually (Ens *et al.* 1992, 1995 and Chapter 3).

In the first part of the thesis I describe the social system and try to understand oystercatcher settlement decisions. Not all oystercatchers acquire a breeding territory, despite strenuous efforts. About half of the birds fail to settle and remain "*nonbreeders*" (Chapters 2 and 3). These stay on high tide roosts and clubs during high tide. Only a low percentage of nonbreeders acquired a breeding territory annually, settling both in resident and leapfrog territories. But why should nonbreeders accept a low quality breeding territory (leapfrog), when they might have tried harder and acquired a high quality breeding territory (resident) instead? Ens, Weissing and Drent (1995. *American Naturalist* 146: 625–650) proposed that density-dependent effects during the nonbreeder life history stage might level out the apparent fitness differences between residents and leapfrogs. They constructed a

model to show how this might be achieved, the so-called "queue model". In Chapters 2 and 3 we have tested several assumptions and predictions of this model. We show there is less competition for the leapfrog territories, which appeared also five times more numerous than the resident territories. Hence, nonbreeders more readily acquired leapfrog territories than resident territories in both relative and absolute terms. Nonbreeders settled in a leapfrog territory when they were on average six years of age, whereas they settled in a resident territory when they were on average eight years of age. Therefore, leapfrogs had on average two more breeding seasons to produce offspring compared to residents. These results supported the "queue model" both qualitatively and quantitatively. Hence, we conclude that nonbreeders competing for the leapfrog territories can expect equal lifetime reproductive success compared to nonbreeders competing for the resident territories. Or stated more formally: the strategy of competing for a leapfrog territory is evolutionary stable with the strategy of competing for a resident territory (an ESS: "*Evolutionarily Stable Strategies*").

However, three of our findings could not be accommodated by the "queue model". First, cooperation between the male and the female to acquire and keep a breeding territory appeared very important (Chapter 2). We conclude that the costs and benefits of cooperation need to be assessed. Second, the model assumed all offspring have equal opportunities of settling in a resident or leapfrog territory. But in fact, the leapfrog offspring had more difficulties acquiring a breeding territory compared to the resident offspring (Chapter 3). Leapfrogs fledged with a lower body mass compared with resident fledglings. Therefore, leapfrog fledglings had lower survival in their first winter compared to resident fledglings. No leapfrog fledgling ever settled in a resident territory directly, although some used a leapfrog territory as a stepping-stone to a resident territory. In contrast, resident offspring settled both in leapfrog territories (*ca.* 75% of all settled resident offspring), and in resident territories (*ca.* 25%). Hence, we conclude oystercatchers show the "*silverspoon*" effect (offspring inheriting the social status of their

* Copies of this thesis may be obtained from the author.

parents). However, probably in contrast to most human societies, in evolutionary terms, the "wooden-spoon" leapfrog fledglings are equally well off compared with the "silver-spoon" resident fledglings, since they can expect equal numbers of offspring produced over their life time. Third, the "queue model" assumed all leapfrogs have equal opportunities of acquiring a resident territory. In fact, only leapfrogs breeding close to the residents had a low, but nevertheless important, annual chance of acquiring an adjacent resident breeding territory. Hence, we propose to split the leapfrogs in categories ("rows"), measured as the number of territories between their nesting territory and the nearest resident nesting territory, in future versions of the "queue model" applied to the Schiermonnikoog population.

We used molecular techniques to assess whether the inheritance of social status might lead to within-population genetic substructuring. Oystercatchers were blood sampled, DNA extracted and seven polymorphic microsatellite DNA markers were analysed per individual (Chapter 4). We detected no significant genetic divergence between residents and leapfrogs on Schiermonnikoog. We conclude that the exchange of offspring between residents and leapfrogs prevents genetic substructuring. With the help of other ornithologists, three additional groups were blood-sampled and compared with the Schiermonnikoog population (on the islands Griend and Texel, and on the mainland at Holwerd). Again, we detected very low levels of genetic divergence between these groups, suggesting a considerable amount of genetic mixing within the Wadden Sea. We present evidence that this is due to the dispersal of offspring, particularly females, to other breeding sites (Chapters 4, 10 and 12).

In the second part of the thesis I address the evolution of the oystercatcher mating system. Oystercatcher pairs are usually monogamous and very cooperative, and we argue that they use frequent copulations to signal to both breeders and nonbreeders their willingness to cooperate with each other (Chapter 5 and 12). We call this the "copulation-signals-cooperation" hypothesis. Nevertheless, some oystercatchers engaged in extrapair copulations (or EPCs, Chapter 5). As shown with DNA fingerprinting of parents and their nestlings, sometimes these EPCs resulted in "illegitimate" offspring: offspring not fathered by the attending male. We provide evidence that the breeders, particularly the females, engage in EPCs to change mate. Female breeders readily switched mate to a neighbouring widowed male breeder, particularly if he occupied a high quality territory (Chapter 2).

Some females, usually nonbreeders, did not wait for a vacancy to arise in the breeding population. Instead, they tried to evict a female breeder from her territory. In these cases, the females engaged in severe combat, which sometimes lasted several weeks. Usually one of the females succeeded in winning these fights, but sometimes neither was capable of winning or willing to retreat (Chapter 6). The females reached a "stalemate", and had to share one male in a so-called polygynous pairbond. In half of these cases, each female defended her half of the territory and built her own nest with the male. The females remained highly aggressive towards each other; hence we refer to these polygynous matings as "aggressive polygyny". The male tried to attend both nests, but with little success: many eggs were lost to predators. Hence, we show that the aggressive polygynous males produced less offspring compared with the monogamous males. In the other half of the cases, the two females stopped fighting and started to cooperate with each other: so called "cooperative polygyny". Cooperative polygyny was accompanied by two interesting phenomena. First, these females engaged readily in lesbian copulations, besides copulating with the male. This observation fits nicely in the "copulation-signals-cooperation" hypothesis, as described above. Second, the females shared and defended one territory with the male and laid their eggs in one large nest (a so-called "joint nest"). Joint nesting is a rare phenomenon: it has only been described in about 35 bird species (Chapter 12). However, oystercatchers appeared not capable of effectively incubating a composite clutch, nor did they engage in egg tossing or joint incubation, as some other joint nesting species do. Hence, since these joint clutches were incompletely incubated, and the birds moved the eggs around from incubated to not-incubated, many eggs failed to hatch despite thirty days of incubation. Thus, despite their cooperative efforts, polygynous females produced less offspring per season compared with monogamous females. Nevertheless, we propose that these females remain in the polygynous territory, because it offers higher future fitness returns compared to leaving the territory and becoming a nonbreeder. More interestingly, the polygynous male also experienced lower offspring production compared to a monogamous male. This challenges the common belief that males always benefit from attracting more females. We think this is the reason why male breeders do not attract secondary females, but instead usually chase them away (Chapter 5). Sometimes however, a female intruder might provide a better breeding partner, so the male might invite her to usurp his female by not chasing this intruder. Thereby he takes the risk of ending up mating polygynously.

Mate choice is important, because some individuals are able to produce substantially more offspring than others do. In the third section of the thesis I address oystercatcher reproductive decisions and the reasons for this variation in reproductive success. A major part of this variation was due to individuals occupying low and high quality territories (see above), and part of this variation was related to differences in the timing of breeding. Early laying females (e.g. laying at the beginning of May) produced larger clutches, hatched more eggs and raised more offspring to fledging compared with late laying females (e.g. laying at the beginning of June, Chapter 7). This is a widespread phenomenon in birds. We show individual female oystercatchers consistently laid early in the season, while others were consistently late. Moreover, most individual females started breeding earlier when growing older: on average five days earlier in ten years time. By experimentally supplying some females with food in the prelaying period, I was able to show that food availability (partly) determines these differences in individual laying dates. Early laying females were in better breeding condition compared with late laying females, when caught on the nest. By detailed behavioural observations, food measurements in the territories, and calculations of the territory size, I was able to show that this variation is not due to differences in territory quality or food intake rate. However, early breeding females spent less time in aggression close to egg laying, and might have maintained a superior body condition during the winter, compared with late breeding females. This might explain their ability to breed early. Being early is crucial, because swapping experiments in five breeding seasons confirmed that laying date was causally related to the fledgling production (Chapter 8). To give an example: when I gave late

laying pairs an early hatching clutch, they produced more fledglings compared with the control late laying pairs. And vice versa: when I provided early laying pairs with a late hatching clutch, they produced less fledglings, compared with the control early laying pairs. Also the pairbond seems important in this respect: males and females that had bred for some years together, produced more offspring than "new" pairs. Both food supplementation experiments during chick rearing (during two years) and the observations on chick feeding indicate that food provisioning plays a role in these differences in fledging success. Moreover, many chicks died in the large broods, when food availability was low (Chapter 9). Leapfrogs appeared to respond to changes in food availability, since they produced smaller clutches, with larger differences in egg mass, resulting in smaller broods with large differences in hatchling mass, in years with lower food availability, compared to years with higher food availability. Residents did not show this response (Chapter 9). Moreover, the results indicated that the effects of food on resident chick survival were smaller than expected. Probably, this was due to loss of many chicks to predators, wherein food plays only an indirect role. Unpredictable egg and chick predation might also explain why leapfrogs seem to start with a clutch they never can raise to fledging, given the large transport costs of food to their chicks. In fact, complete leapfrog broods died from starvation before they fledge, whereas the parents might have raised one chick if they had stopped feeding the others.

Another potential cause of the high chick mortality might be infections with parasites (Chapter 11). We show that oystercatcher chicks were infected with a wide range of gut parasites, depending on the environment they were raised in (polder or saltmarsh). In contrast, we did not detect blood parasites in either chicks or parents. We treated a sample of hatchlings with an anthelmintic drug, which resulted in lower infection grades of these chicks at fledging compared with untreated hatchlings. However, contrary to our expectation, significantly lower numbers of treated chicks survived to fledging compared to untreated chicks. We propose that this might be due to the treated chicks failing to acquire an appropriate immune-response due to our treatment removing all challenges to the chick's immune system. Hence, when the treatment ceases to have effect, the treated chicks might die from the first infections they have to combat without the assistance of our anthelmintic drug.

Finally, we studied the relationship between the sex ratio of the brood (the proportion sons), territory quality and parental attributes, using molecular markers to sex offspring (Chapter 10). We did not detect correlations between the sex ratio and the territory quality, the laying date or the clutch size. Instead, we found a trend with female age: older females produced relatively more sons. We have no adequate explanation for this trend. In total, equal numbers of sons and daughters fledged from our study population. Nevertheless, only a few daughters settled in our breeding population, to breed themselves. In contrast, many sons returned to the island, and quite often settled in a breeding territory close to their natal territory. Hence, I calculated that approximately three out of four daughters disperse from the island of Schiermonnikoog, and start breeding somewhere else (Chapter 12).

The work in the Schiermonnikoog population is and has been continued by Leo Bruinzeel (PhD), Martijn van der Pol (PhD), Simon Verhulst (PostDoc) and Kees Oosterbeek (technical assistant), see http://www.biol.rug.nl/animalecology/.