PhD-Dissertation Reviews

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PhD-dissertation reviews

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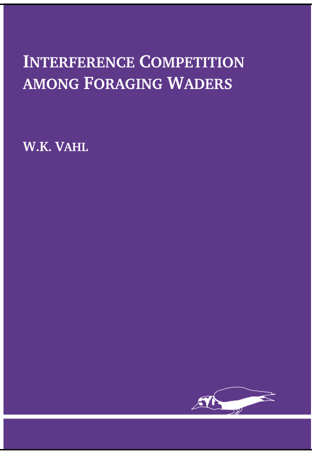
Vahl W.K. 2006. Interference competition among foraging waders. PhD-thesis, University of Groningen. ISBN 90 367 2796-0, paperback, 239 pp. Available at http://irs.ub.rug.nl/ppn/297672886.



The PhD-thesis of Wouter Vahl fits the traditional line of research by mainly Dutch and British ornithologists on the ecology of wintering waders in intertidal areas. Nevertheless, it deviates from this line in one particular aspect: the approach is almost entirely experimental rather than descriptive. Henceforth the work has been carried out in the laboratory on captive waders rather than in the field on free-ranging birds. This experimental-based approach reflects the author's strong belief that scientific progress can only be made through proper experimentation. Vahl aimed to achieve progress in the field of interference competition and with his outstanding thesis he has certainly done so!

The thesis reminds us of the central role that competition for food plays in the regulation of populations. Thus, in order to understand the ecology of populations we need to understand competition. In his so often philosophical writing style, Vahl stresses that *understanding* competition boils down to revealing the *mechanisms* of competition rather than *phenomenologically* describing competition. In the phenomenological school of thought a process is merely described without considering the actual mechanism underlying the process. Vahl strongly advocates the mechanistic approach. In doing so, he distinguishes two forms of competition: exploitative competition and interference competition. The former operates indirectly through resource depletion and its mechanisms are rather straightforward and well understood. However, the mechanisms underlying interference competition, which operates through direct interactions between individual foragers, are not well understood at all. This justifies the (mechanistic) focus on interference in this thesis.

The thesis starts off with an historical overview of the study of interference competition among waders (Chapter 1). We learn that in the previous century only a single study considered wader competition experimentally under controlled laboratory conditions (not surprisingly this was on the most studied wader-species, the Oystercatcher). All other studies were field studies that were studies in correlational ways, i.e. they described the relationships between food density, wader density and intake rate. One field study provided the exception: captive and model Oystercatchers (again!) were introduced in order to experimentally elevate wader density in a field plot. The nice thing about the study of interference competition (and about Vahl's thesis) is that empirical research grew hand in hand with theoretical developments. The 'ideal free distribution' (IFD) model, a model originally developed to predict the distribution of breeding birds among different habitats (Fretwell and Lucas 1970) was picked up by waderologists in the early 1980s (Zwarts and Drent 1981). This was elaborated by Sutherland (1983) who mathematically reframed the model to predict the distribution of foraging waders. A further theoretical breakthrough was achieved by Van der Meer & Ens (1997), who showed that small differences in how intake rate varied with both wader and food density (the so-called 'generalized functional response') had a major impact on the predicted distribution of foragers. This latter insight made clear that if we were to properly predict and understand the distribution of foragers, the actual mechanism underlying the generalized functional response needs to be known. It was this realization that sparked the PhD-project of Wouter Vahl.

Thus, Vahl sets out to understand the generalized functional response mechanistically. He does this by performing experiments in the laboratory (Chapters 2, 3 and 5) and in the field (Chapter 4) and by reviewing how the generalized functional response has been and should have been modelled from an evolutionary point of view (Chapter 6). The chapters are presented in logical structure and are enlivened by boxes, afterthoughts, reflections and many notes. These extra bits of 'discussion' enrich the thesis tremendously and are typical of the author's (self) critical attitude (perhaps not surprisingly, one of his statements [stellingen] reads: "*Science relies on scientists being (self) critical. Yet, self-criticism is scarce and criticism of others is often not appreciated among scientists*").

In his first laboratory experiment (Chapter 2), Vahl mimicked the intertidal by filling up a single tray with wet sediment in which bivalves were inserted. In feeding trials this tray was then presented to a flock of captive but hungry red knots.

Between trials he varied the number of bivalves on offer and the number of birds in the flock. Using video, Vahl and his students scored intake rates and time budgets on a set of 'focal' birds. In his second lab-experiment (also published in Chapter 2), he repeated this design but using turnstones instead of red knots. Both experiments confirmed the idea of interference competition: the more birds feeding on the artificial patch the lower the foraging success of an individual bird (the effect of exploitative competition was ruled out here as the trials lasted too short for this to become important). However, unexpectedly and as it turned out important for the rest of the thesis, the mechanism of interference was very different from what had been assumed in interference studies so far! Time loss to fights over just encountered prey items ('kleptoparasitism') had always been considered as *the* mechanism underlying interference competition. However, Vahl's knots and turnstones hardly interacted with each other and stealing prey virtually never happened in his experiments!

These findings puzzled the author with the question why his birds nevertheless suffered from interference competition. At some point he realized that in birds handling their small prey so quickly that prey robbery is impossible (as in his birds), the mechanism of interference may act over clumps of food items rather than over individual food items. This idea made him design the next experiment (Chapter 3): a pair of captive turnstones was offered a single tray of food. The food was hidden underneath seaweed and was distributed either dispersed or clumped. Having 17 captive turnstones to choose from, the 'focal' individual during a trial either was the dominant or the subordinate member of the pair. The results were crystal clear: dominant birds feeding on clumped food were able to monopolize the food clump and thus obtained much higher intake rates than the subordinate birds. When feeding on dispersed food, multiple prey items could not be defended and thus dominant and subordinate birds had equally low intake rates. Surprisingly, however, the number of aggressive interactions was similar on clumped and on dispersed food and it was thus concluded that the amount of aggressive behaviour is thus a bad indicator of interference effects.

Elaborating on this overwhelming effect of the food's spatial distribution, Vahl performed a field experiment on free-living turnstones stopping over at a New Jersey beach along Delaware Bay (Chapter 4). There, he manipulated food spacing by varying the distance between small clumps of food (eggs of horseshoe-crabs), while keeping the number of food clumps constant. This time the results were much harder to interpret: the more food was spaced out, the more turnstones were attracted to the plot, the less often agonistic interactions occurred, whereas intake rate was unaffected.

Back in the more controllable laboratory at NIOZ, Texel, Vahl performed his final experiment (Chapter 5). So far he had manipulated the spatial distribution of the food in the horizontal plane, but now he manipulated the degree of prey patchiness in the vertical direction. A set of five mealworms was offered to captive turnstones in two ways: the worms were either buried in layers of different depths (spaced out) or buried altogether at the deepest layer (clumped). The results were consistent with those from the previous lab-experiment: clustered food was easier to defend than spaced-out food. Therefore, dominant birds feeding on vertically clumped food were better able to monopolize the food and thus obtained much higher intake rates than the subordinate birds. When feeding on vertically dispersed food, subordinates could somewhat increase their intake rate as it was harder for the dominant ones to defend 'their' food.

Chapter 6, the final chapter before the general discussion, covers a theoretical exploration as to why foragers would interfere with one another. The earliest mechanistic models on interference considered foragers as if they were 'aimless billiard balls' with no choice but to act aggressively upon an encounter with a competitor. More recently, the adaptive value of interference behaviour has been included in such models. However, each of these models takes kleptoparasitism (prey stealing) as the basic mechanism of interference. In their attempt to unify approaches, Vahl and co-workers continue to take kleptoparasitism as a starting point. This somewhat surprised me, given the empirical insights gained from this thesis that foragers often interfere over clumps of food rather than over individual prey items. Nevertheless, the aim to streamline evolutionary models of interference competition is brave and certainly warranted. I advice anyone that considers constructing a new model on interference competition to consult this chapter!

The thesis closes with a discussion on previous attempts to scale up from interference competition to population dynamics. Most wader-studies on interference competition have merely been interested in the consequences of interference competition for population dynamics. Although Vahl clearly acknowledges the existence of such consequences, he argues that the time is not yet ripe to link the two fields. Having read his thesis one cannot agree more with that statement. The steps we would need to make when going from interference to populations are yet way too big. Vahl's work reveals *something* about the mechanisms underlying interference competition, but at the same time reveals new gaps in our knowledge. Given the importance of how food is distributed spatially, the question how foragers move through a spatially heterogeneous landscape of food in social context becomes very relevant. Given the importance of social dominance, we need to understand more about how social hierarchies come about and how they are maintained. Such basic questions need to be addressed first before we can possibly scale up to the level of populations. All in all, I think this thesis has not only taught us a great deal about interference competition, but it also teaches us that carefully making mechanistic steps is the only way up in the science of (avian) ecology!

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Reneerkens J.W.H. 2007. Functional aspects of seasonal variation in preen wax composition of sandpipers (Scolopacidae). PhD thesis, University of Groningen, The Netherlands. ISBN 90-367-2918-1, paperback, 168 pp.
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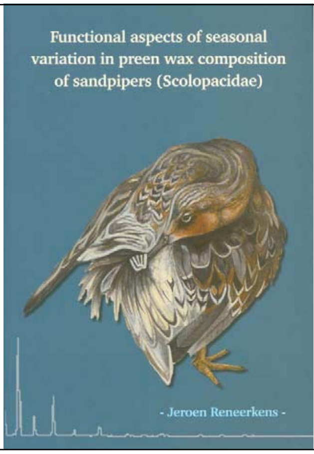

Everyone who has paid attention to a preening bird should have noticed that it over and over returns with its bill (and sometimes head) to a spot just above its tail. It is exactly there where the bird's tiny uropygial gland, or preen gland, is located. This gland secretes waxes that are efficiently spread out over the feathers during plumage maintenance. Biologists have been interested in the functions of these preen waxes, such as plumage maintenance (waterproofing, anti-degrading effects) and plumage appearance (smell and coloration). Chemists have studied the composition of the uropygial gland secretions by gas chromatography and have identified different types of waxes, in which the exact composition of preen waxes varies among bird species.

Recently biologists and chemists combined forces and discovered that the composition of preen waxes varied intra-individually in a long-distance migrant, the Red Knot *Calidris canutus* (Piersma et al. 1999). Red Knots, which secreted a mixture of monoester waxes in the non-breeding season, switched to secreting a mixture of diester waxes at the onset of the breeding season. The timing of diester wax secretion suggests that it has a certain function related to the breeding cycle. The fact that diesters are not secreted all year round indicates that the production and secretion of diesters come at a cost.

In his dissertation Reneerkens investigates the functional aspects of this seasonal variation in preen wax composition. He starts off with a survey of preen wax composition in 19 species of sandpipers (Scolopacidae) (chapter 2). His sample included species breeding at temperate to high-arctic latitudes, thus he could falsify the idea that seasonal variation in preen wax composition is a phenomenon restricted to tundra-breeding sandpipers. (Later we learn (Box C) that some species, both from temperate and high-arctic origin, do not change the composition of their waxes at all. Interestingly these species are closely related.) The most important result of the inter-specific comparison is that the secretion of diesters continued throughout the incubation period, and that non-incubating birds had the lowest likelihood of secreting diesters, indicating a functional role of preen waxes during incubation. The latter result was the reason to (again) mobilize the network of shorebird researchers to collect even more preen wax samples, this time from a selection of species with different (or even contrasting) incubation patterns, including species where both sexes incubate, where only males incubate, and where only females incubate (chapter 3). From this comparison the link between diester secretion and incubation became even more apparent: it was found that diester preen waxes were secreted almost exclusively by the incubating sex in uniparental breeders, and by both sexes in species with biparental incubation. An interesting exception to this pattern are male Curlew Sandpipers *Calidris ferruginea* and male Buff-breasted Sandpipers *Tryngites subruficollis*, which do not incubate, but do sometimes secrete small amounts of diester waxes. Most likely, the secretion of diesters in these males is a remnant of a time when both sexes incubated in these species.

Chapter 4 is more or less an intermezzo in the search for functional aspects of variation of preen wax composition, investigating whether diester secretion is under endogenous control. The authors expected that this is not the case since diester secretion is costly and the shift from mono- to diesters seems to happen on a small timescale. However, captive Red Knots changed preen wax composition in a similar way to free-living individuals, both under natural light conditions and in a constant photoperiod treatment, falsifying this idea. Changes from mono- to diesters took surprisingly long time, suggesting that this change entails considerable modifications of the biochemical or metabolic machinery.

The next three chapters (5–7) of the dissertation investigate possible advantages of secreting diesters over secreting monoesters during the incubation period. Chapter 5 tackles the initial hypothesis that diester preen waxes are an avian equivalent of cosmetics, changing the appearance of the birds' plumage and act as a sexually selected quality signal during mate choice (Piersma *et al.* 1999). Although diesters absorbed more light than monoesters, this did not affect the reflectance of the plumage of Red Knots with a coating of mono- or diester preen wax, thus the shift in the composition of preen waxes has no visual function. The search continues in chapter 6 where the effect of mono- and diester waxes was studied on a feather degrading bacterium *Bacillus lichenifomis*. Removal of waxes from the feathers resulted in a faster degradation of the feathers, but there was no difference in degradation between feathers coated with mono- and diesters. The study thus clearly shows that the shift to diester secretion is not related to a presumed higher activity of feather degrading bacteria during incubation. In chapter 7, the specially trained sniffer dog Joey was involved in the project, which finally shed some light on the functionality of changing from secreting mono- to diester waxes just prior to the incubation period. In an experimental setup, Joey had more difficulties to detect a small stick when small amounts of diester rather than monoester waxes were applied to this stick, convincingly showing that diester preen waxes reduce the bird's smell. Secreting the less volatile diester instead of monoester waxes increases the 'olfactory crypsis' of the bird, reducing the probability that the nest is detected and thus predated.

Reneerkens' dissertation is a nice example of how systematic research can enormously enhance the understanding in a field where studies are almost as plentiful as controversies. Reneerkens' sound research has enabled him to both falsify and verify hypotheses. An important notion to the field of preen wax research is that results cannot simply be extrapolated to other situations, but that details like species, life history stage, and sex must always be considered.

At a first glance the uropygial gland secreting its 'funny' waxes seems to be a trivial aspect of the life of birds. However, after reading Reneerkens' dissertation, one cannot become other than fascinated by this tiny organ and its secretion products. One also realizes that shifting the composition of preen waxes is an important adaptation of ground breeding species like shorebirds to the high predation pressures brought about by olfactorially guided mammals. A comprehension we may never have acquired in a world without curiosity driven research.

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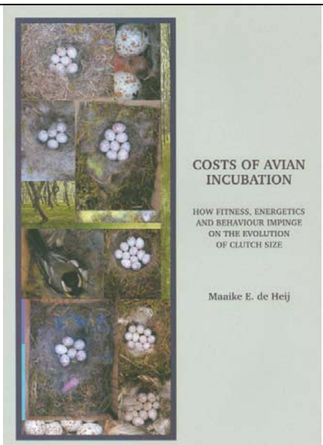
De Heij M.E. 2006. Costs of avian incubation: how fitness, energetics and behaviour impinge on the evolution of clutch size. PhD thesis, University of Groningen, The Netherlands. ISBN 90-367-2794-4, paperback, 183 pp.
Available at http://irs.ub.rug.nl/ppn/297673424.

Again the Great Tit *Parus major* proved to serve as an excellent species to study some intricate questions in biology. In her thesis, de Heij presents results that are important for our understanding of how natural selection affects reproductive decisions of altricial birds. There is a long history of studies on clutch size in birds. In 1947, David Lack concluded that clutch size of altricial birds was most likely determined by processes that took place during the nestling period. This idea was also intuitively plausible: during chick rearing, parent birds are flying on and off for days to provide their offspring the food they need. Obviously this must be a more strenuous job than sitting on a clutch of eggs. Many studies followed that tried to test the idea of optimal brood size by measuring the fitness consequences of having fewer or more nestlings than the parents had chosen themselves. A long-term study was started by Joost Tinbergen to measure how fitness is related with brood size. In the study population, situated in the Lauwersmeer area in the north of the Netherlands, the Great Tits did not seem to follow Lack's logic, because if birds were given an enlarged brood, fitness was actually increasing (Tinbergen & Sanz 2004). This was the starting point of de Heij's research. Why do those Great Tits in the Lauwersmeer not behave optimally?

Perhaps the nestling period was not providing the full picture. What if incubation was actually much more strenuous than thought? Then, brood size manipulations would only be able to explain part of the observed parental reproductive behaviour. Measuring selection pressures during the incubation period could be a way out of this impasse. By employing state of the art experiments, De Heij did exactly that. Moreover, what is most laudable is her effort to also come to grips with the underlying mechanisms by measuring the energetics of the birds. This results in a very comprehensive picture of the problem of clutch size decisions in Great Tits.



The thesis comprises 7 papers plus an introductory chapter, a synthesis and a Dutch summary. The chapters 2–4 discuss fitness consequences of incubating different clutch sizes, while chapter 5–8 treat energetic and behavioural costs of incubation. The first paper, chapter 2, can be considered the most important paper because it answers the question that was at the basis of the project: do Great Tits behave suboptimal? In three years clutch sizes were either reduced or enlarged at the second day of incubation and restored to their original size at the 11th day of incubation. Subsequently, fate of parents, eggs and nestlings was measured until the following breeding season. This revealed that clutch size affected the probability of successfully raising a second clutch in the same season, and that local survival of the parents until the following year was lower for the enlarged clutches. The latter effect was only apparent in the 2 years with a high proportion of second clutches in the population. After tallying the various fitness components it is concluded that costs of incubation were strong enough to cause stabilizing selection. Hence, the Great Tits did behave after all.

In chapter 3 de Heij tries to separate parent-related and egg-related fitness components. To do this, a complicated manipulation experiment was necessary. Clutch sizes were again either enlarged or reduced, but now eggs from one clutch were divided among the different nests. Each nest of a manipulation triplet (reduced, control and enlarged nest) now contained eggs that originated from the three different nests. At the end of the incubation period clutch sizes were again restored and the eggs were returned to their original nest. One familiar with clutch or brood size manipulations will appreciate the stamina required for such an enterprise. A nest therefore contained nestlings that were incubated while belonging to small, control and large clutches, while raised by their original parents in nests with equal numbers of siblings. This experiment showed that nestlings that hatched from eggs that had been incubated in enlarged clutches tended to develop slower, resulting in smaller fledglings.

Chapter 4 analyses how fitness relates to natural and experimental variation in clutch size and laying date based on 10 years worth of data. It shows that selection on clutch size varies through the season, with selection for large clutches early and for smaller clutches later in the season.

The next chapters describe measurements on the energy budget of incubating female Great Tits. In Great Tits only the females incubate while the role of the male during incubation is more elusive. Chapter 5 describes the findings that females that incubate in a nest with little lining at the bottom delay the onset of full incubation, while their eggs have lower probability of hatching. A thin nest is worse insulated and the female needs to spend more energy warming the clutch. Together with correlations found with clutch size and laying date, it is concluded that energetic stress early in the reproductive phase is of major importance. In the remaining chapters energy metabolism measurements are presented, showing the impact of incubation on the energy budget of females. Using a mobile oxygen meter she measured the energy expenditure of females during nocturnal incubation in the field; a technically challenging piece of work. By measuring a female while incubating different numbers of eggs it could be shown that 3 extra eggs increased energy expenditure by 6–10%. The main conclusion from these measurements is however that the effect of air temperature overrules the effect of clutch size. Energy expenditure changed by 43–49% each 10°C. The other important conclusion is that energy expenditure during incubation is high: twice the basal metabolic rate, or 20–60% above the metabolic rate of a non-incubating female. This is similar to the energy expenditure during chick rearing.

The energy expended by females on a daily, 24-h basis was related to air temperature but not to clutch size (chapter 7). This raises the question whether females compensate behaviourally or physiologically when spending more energy incubating an enlarged clutch. In chapter 8 the daily energy budget of the female is partitioned in nocturnal energy expenditure, day-time energy expenditure during foraging and during incubation. This book keeping exercise results in the intriguing conclusion that the energy intake rate a female needs to achieve during the off-bouts from the nest is extraordinarily high, in fact twice the value she needs to achieve during chick rearing. The possibility is discussed that the male partner plays an essential role during these moments by leading the female to good foraging spots, or perhaps even by feeding the female.

With the appearance of this thesis we cannot longer ignore the incubation phase of a small altricial bird.

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