

## PhD-Dissertation Reviews

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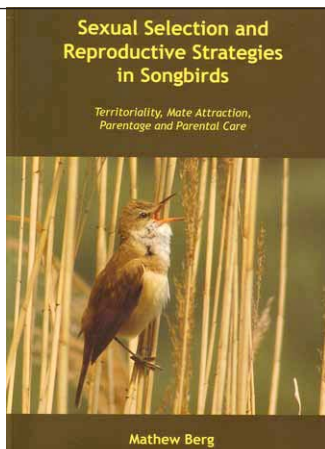
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**Berg M.L.** 2007. Sexual selection and reproductive strategies in songbirds. – Territoriality, mate attraction, parentage and parental care. PhD-thesis University of Groningen, Groningen. Paperback, 208 pp. Available at <http://irs.ub.rug.nl/ppn/300721439>.



As the title suggests, Mathew Berg's thesis deals with the many aspects of avian reproduction, from establishing a territory to caring for the offspring.

As such, it touches upon two of the main concepts in evolutionary and behavioural ecology: sexual selection (how do individuals choose their partner?) and conflict (how do individuals deal with their conflicting interests?). How different individuals of the same sex choose to follow a strategy within these two concepts in order to maximise their reproductive output, and how this depends on the physical and social environment is the main topic of the thesis. Individuals will adopt a strategy that may help them compete with their conspecifics for territories and mates, and will provide the optimal care for the survival of the offspring at a minimal cost to the parent itself. The processes and evolutionary forces driving an individual to adopt an optimal strategy have resulted in an immensely wide and complex diversity of mating and breeding system known among animals today.

An example of that complex diversity is the existence of extra-pair copulations, which appears to be ubiquitous among songbirds. Before addressing reproductive strategies in nature, the thesis starts off with chapter 2 describing some methodology used to investigate parentage and relatedness. Researchers often rely on microsatellite markers that are unfortunately often species specific. Using cross-amplification of over 100 existing polymorphic microsatellite primer pairs derived from a wide variety of avian species the use of these primers was tested for the Australian Reed Warbler *Acrocephalus australis* and the Winter Wren *Troglodytes troglodytes*. Mathew Berg managed to find a substantial proportion of polymorphic markers for both species, and thus revealed the potential of cross-amplification as a useful technique exploiting existing microsatellite markers, in particular for those from related species.

The next chapter then logically deals with the, for many animals, first part of reproduction: territory establishment. It discusses an experiment testing the 'dear enemy' effect in Winter Wrens – a phenomenon in which an individual can distinguish between neighbours and strangers. Import-

antly, although a well known effect, the role of previous experience and the constraints on recognition remain poorly studied. These are addressed in this study, by focusing on relationships as mediated *via* song. In a neatly set up experiment using the playback of large and small repertoires of neighbours and strangers, it is shown that Winter Wren can clearly distinguish between neighbours and strangers, thus exhibiting the dear enemy effect. However, it is shown here that only a single experience appears to be enough to significantly decrease the behavioural response of the focal individual, suggesting that male wrens cannot only recognise, but also rapidly adjust their response to intruding individuals based on previous experience. This likely helps to maintain stable territory boundaries with neighbours, which are not easily disturbed by brief intrusions by strangers.

Chapter 4 carries on discussing the function of song as a sexual signal, and focuses on the importance of song for territory defence and advertisement of the male's quality; both to avoid losing paternity, which may come at a considerable loss in fitness. The defence of territory and/or mate, however, is a costly behaviour and should therefore be restricted to, for instance, the female's fertile period. Following the natural territory patrolling and 'spontaneous singing' behaviour of wrens, no difference was found across different stages of the breeding cycle. However, by experimentally presenting an intruder at different stages of breeding, it turned out that males did sing their 'challenge song' more frequently during the female's fertile period. This may be an adaptation to sperm competition because it enhances the male's territoriality, keeping the strangers out, and because females may eavesdrop on counter-singing males and assess their quality. The males may thus not only advertise their quality to contesting males, but also to females. As such, males enhance their territory persistence and paternity assurance. The results presented in this chapter illustrate the importance of song as both an intra- and inter-sexually selected trait.

However, in order to be a reliable signal to both contesting males and eavesdropping females,

there should be a clear cost of song – the handicap principle (Zahavi 1977). This is the topic of the next chapter, where we move on from territory establishment to mate attraction. This is perhaps the most important chapter in the thesis, due both to the fact that song is a, for researchers, relatively easily quantifiable sexually selected trait, but also to the clarity of the result. Additionally, hitherto there is little empirical evidence for the costs of song. In this experimental study supplementary feeding is used to point out the effect of food availability on song output of Australian Reed Warblers. As expected under the handicap principle, supplementary fed males indeed sang more than controls. Using an experimental set up where the experimental group was fed on an alternating daily basis of fed and non-fed, it turned out that song is a flexible behaviour as well – a requirement for being a reliable signal. Males in the experimental group sang significantly less on non-fed days than on fed days. Therefore, this study points out that females can reliably use song output when they choose a partner and may obtain direct benefits of access to food rich territories.

Chapter 6 deals with the same issue, but now the functional significance of building multiple nests, as a 'non-bodily ornament', is investigated. Besides the 'real' nest, prior to pair formation, Reed Warblers build additional, small nest-like structures within their territories. Using the same supplementary feeding experiment as in chapter 5, Berg shows that more of these 'fake nests' are built when there is more food available. Additionally, the number of fake nests within a territory was experimentally manipulated. Somehow surprisingly, however, the number of these 'nests' was not related to pairing success. Although the fact that they are built before pair formation only does suggest a role for mate attraction, multiple confounding factors may have blurred the effect in this study. The function of these additional fake nests thus remains to be investigated. The time spent on building these structures may be, for instance, more important than the actual presence of the fake nest itself.

Chapter 7 investigates the unclear potential benefits of extra-pair copulations for females. One

reason for females to engage in extra-pair matings may be to obtain indirect, genetic benefits. Using the methodology described in chapter 2, the rate of extra-pair copulations in the Winter Wren and the role male heterozygosity plays in siring extra-pair young is studied here. Extra-pair offspring occurred in 38% of broods, and these were more likely to belong to more heterozygous males. However, once cuckolded, these males sired fewer extra-pair young, despite the fact that they seemed to be in a better condition. Additionally, no difference in heterozygosity was found between within-pair and extra-pair young. Interesting results that add to recent studies focusing on the role male heterozygosity may play in female choice, yet future studies are clearly required here to unravel this complex issue.

The last section of the thesis focuses on the question how parents decide over parental care. The fundamental trade-off between current and future reproduction underlies the decision which strategy to adopt in order to optimise a parent's reproductive output (Trivers 1972). Chapter 8 discusses this trade-off as the choice for males to care for the current offspring or to engage in additional matings with neighbouring females. Male, but not female, Australian Reed Warblers appear to significantly reduce the amount of parental care with increasing numbers of neighbouring territories. When a caged conspecific was experimentally presented, however, it turned out that the sex of this conspecific did not influence this result. Berg therefore argues that males not only likely face a trade-off between parental care and obtaining additional matings (in case of the intruding female), but also with territorial effort (intruding males). Additionally, females did not compensate for the lack of male care, and therefore nestlings grew slower when males shifted their attention towards intruding conspecifics.

The next chapter looks at how food availability may affect incubation attendance and hatching asynchrony in the Australian Reed Warbler. The supplementary feeding experiment used in previous chapters is applied here as well. Female Reed Warblers, which take up all incubation effort in

this species, showed an increase in incubation attendance when food resources were plentiful, and also advanced the onset of incubation, which resulted in increased hatching asynchrony. These results again point at the trade-off a parent faces, in this case the trade-off between foraging and incubating. Incubation and the onset thereof seem to be energetically constrained. Alternatively, a female may be willing to invest more into incubation when mated to a male that obtained a higher quality territory ('differential allocation hypothesis'; Burley 1986). The possible benefit of an earlier onset and enhanced incubation attendance may be the earlier hatching, thereby lowering the risk of nest depredation.

The final chapter, the general discussion, emphasises the main point of this dissertation: optimal reproductive strategies depend on the individual qualities as well as on their physical and social environment. It is the interplay between territorial and mating effort (sexual selection) that will dictate which is the optimal strategy with respect to the trade-off with parental effort (conflict): signalling individual quality or condition, responding to potential competitors or to mates, maintaining relationships with partner and neighbours, or 'betraying' those to obtain additional matings or to expand the territory.

In sum, Berg's thesis addresses the full range of reproductive strategies that individual animals may follow and is an excellent illustration of its complexities, which makes it unfortunately often hard to state firm conclusions. However, mainly due to the strong experimental approach used here, this is a strong dissertation with a number of important results.

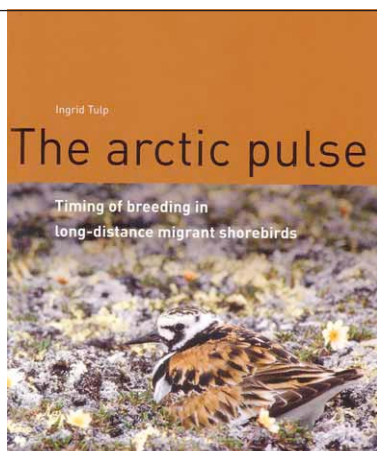
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- Zahavi A. 1977. The cost of honesty (Further remarks on the handicap principle). *J. Theor. Biol.* 67: 603–605.

### Publications from this dissertation

- Berg M.L., Beintema N.H., Welbergen J.A. & Komdeur J. 2005. Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. *J. Avian Biol.* 36: 102–109.
- Berg M.L., Beintema N.H., Welbergen J.A. & Komdeur J. 2006. The functional significance of multiple nest-building in the Australian reed warbler *Acrocephalus australis*. *Ibis* 148: 395–404.
- Eikenaar C., Berg M.L. & Komdeur J. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. *J. Avian Biol.* 34: 419–427.

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**Tulp I.** 2007. The arctic pulse. Timing of breeding in long-distance migrant shorebirds. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-9022228-8, paperback, 259 pp. Available at <http://dissertations.ub.rug.nl/faculties/science/2007/i.y.m.tulp>.



First things first. This is a beautiful thesis. The cover shot of an incubating Turnstone, its chestnut coverts, scapulars and tertials mirrored by the red-

brown cover, is as stunning as any I've seen. And the numerous portraits of breeding shorebirds, incredibly cute chicks, and evocative tundra scenes throughout the thesis all add to the package. It has clearly been written by someone who likes her study system and isn't afraid to admit it ("As an unbiased scientist you're not supposed to have favourites but I can't help it that for me Little Stints are the absolute champions among arctic breeding shorebirds"). But this thesis is not just a pretty cover.

Ingrid Tulp sets out to address one of the more difficult issues in avian migration ecology – what determines laying date in long-distance migrants? We are all familiar with Lack's well established concept that breeding in general is timed to coincide with a peak in food availability; Ingrid develops the idea that as the window of opportunity for breeding is so tight in the Arctic, studies in that zone may act as magnifying glass to the processes at play. The terminal reward model of Ens *et al.* (1994) forms the heuristic basis for the research, in which arrival date and arrival condition both influence reproductive success (and both factors may depend on decisions made earlier in the migration). As empirical data relevant to such models are scarce, Ingrid set out to measure reproductive success in a variety of shorebirds on Taimyr Peninsula, Russia, in relation to arrival date and condition.

There turned out to be a good reason why such data are scarce – birds did not stay within the study areas, nest failure rates were high and it proved impossible to measure fledging success in most species. Instead, this thesis presents a coherent, cohesive series of eight research chapters on seasonal patterns of food levels and energetic demands and performance of parents and young. They are arranged to follow the general chronology of the breeding season. The rationale behind the research is that identifying the energetically stressful periods may allow the selection pressures on the timing of breeding to be determined. Because shorebirds show different incubation strategies, it was possible to study how uniparental incubators (in which a trip off the nest means the eggs



are left unincubated) and biparental incubators (in which another adult can take over the duties) budget their time under different conditions.

The first research chapter details body condition of nine small shorebird species upon arrival on the breeding grounds and during incubation. Confirming a suggestion from earlier datasets, most species arrived weighing considerably more than they do on the non-breeding grounds, apparently having brought some nutrient stores with them. These would be sufficient to cover 0.8–2.8 days of survival if birds could not feed upon arrival. Total body water measurements via the deuterium dilution method indicated that incubating birds had higher lean tissue masses than did arriving birds. Some rebuilding of organs may be derived from imported fat stores, but as body masses also increased, exogenous nutrients must also be involved in these populations.

Chapter 3 compares nest characteristics of six species of shorebird varying from 30–130 g in body mass. Smaller species apparently invested more in insulating their nests, mainly through having deeper and better lined nests that reduced heat loss from eggs to the air.

Constructing an appropriate nest is one thing but incubating it adequately is another, and chapter 4 explores how frequently adults spend time off the nest ('recesses'). Small temperature sensors were placed within clutches of four uniparental incubating species to determine the frequency and duration of recesses. All four species studied tended to incubate through the cooler polar night and take recesses during the day (totalling 13–19% of the time). Recesses, especially long absences (1–8 hours), were commoner when it was cold, suggesting that adults must trade off their own body condition against incubation, periodically taking extended foraging breaks when their condition is poor.

This idea of an energetic bottleneck for small species is extended in chapter 5 to a large-scale survey of body masses of breeding Little Stints in northern Norway and across Taimyr Peninsula. Body size increased with latitude, most likely through females, the larger sex, incubating clutch-

es laid in more northerly regions while males incubated the initial more southerly clutches. Controlling for this size variation, northern birds carried larger nutrient stores than southern birds, paralleling the risk of cold weather that also increases with latitude. At all sites body masses were higher during incubation than chick-rearing. It's unclear which of two competing hypotheses would best explain this pattern – energetic stresses being higher during chick-rearing, or a lower body mass being adaptive in that period when stores are less needed as insurance once adults are freed from the time demands of incubation.

Little Stints and Dunlins come under further scrutiny in chapter 6, in which daily energy expenditure (DEE) was measured in incubating and chick-rearing adults to determine which period was the most expensive. DEE turned out to be similar in both periods for both species. But because Little Stints are solo incubators, their energetic stress (taking into account arthropod availability and the limited time available for feeding) is much higher during incubation than chick rearing. Dunlins have an intermediate breeding status between uniparental and biparental – both sexes incubate but the female deserts during chick-rearing. Their energetic stress was only slightly lower (and not significantly so) during chick rearing. This finding supports the idea that uniparental breeders like the Little Stint face the crunch during incubation.

We know already that Little Stints are champions, and their chicks do their best too (chapter 7), growing at rates above allometric predictions based on mass. However, their growth when very young was reduced in cold weather, and despite a high DEE, Little Stint chicks could not match Red Knots or Curlew Sandpipers in growth rates.

Growth rates of Knots and Curlew Sandpipers had previously been shown to be affected by climate, and chapter 8 adds the smaller Little Stint and Dunlin to the dataset of growth rates in relation to climate. The findings were largely intuitive (growth rates increased with arthropod availability and temperature, decreased with windspeed) but there were quirks. Young Dunlin grew more slowly in higher temperatures; Little Stints grew faster

with more rain; neither species showed *any* relationships with climate or invertebrate levels in the second year of the study, when a late season and short peak in prey availability meant that the best food conditions had passed when chick growth rates were being measured. The contrasting seasons also influenced a proxy for survival – whether or not chicks were relocated and caught 2 days or later after initial capture. A seasonal decline in apparent survival in 2001 was lacking in the later, more synchronised breeding season of 2002.

The final research chapter uses long-term climate data to predict historical arthropod levels in an attempt to determine the variability in resources that tundra-breeding shorebirds may encounter. Revealing one inadequacy of the English language, the authors use the term “hindcasting” for this process. Alas such a word does not, to my knowledge, exist (does it in Dutch?), though I can confirm the absence of a straight antonym to “forecasting”. Hindcasting it is for the moment, then. Four seasons of climate-arthropod data were used to construct models capable of explaining 70–90% of the seasonal variation in arthropod biomass in pitfall traps; these were then applied to a 33-year climate record from Dickson, Taimyr Peninsula. The conclusion is that the date of peak invertebrate abundance has become earlier over time, advancing by seven days in three decades.

Together, these studies provide a valuable window into the life histories of small Arctic-breeding shorebirds. The choice to focus on a uniparental breeder, the Little Stint, was an inspired one for both theoretical and practical reasons (they are apparently much commoner and/or readily caught than all other species), and the comparison between uniparental and biparental incubators is summarised in the general discussion. Uniparental incubators are affected more by weather during incubation, they desert nests more, and invest more in nest insulation, all of which suggests that they have slim energetic margins. Adults might be best served by delaying breeding slightly until weather conditions improve, but this would conflict with the needs of chicks, which would then face declining prey levels when growing.

The final part of the discussion states that the ‘terminal reward function’ in optimal migration models has in fact now been derived in another publication (Ens et al. 2006), with the findings of this thesis being used indirectly to aid this process. The general approach involved is outlined, and necessitated data on stores held by adults upon arrival, the length of the prelaying period, nest survival, the probability and survival of replacement clutches, and chick survival. It’s easy to see that Ingrid Tulp’s thesis was not able to directly measure many of these, but it is nevertheless a valuable body of work based on an impressive amount of logistically challenging fieldwork.

Ens B.J., Piersma T. & Tinbergen J.M. 1994. Towards predictive models of bird migration schedules: theoretical and empirical bottlenecks. NIOZ-report 1994-5. Den Burg.

Ens B.J., Schekkerman H., Tulp I., Bauer S. & Klaassen M. 2006. Modelling the flyway of arctic-breeding shorebirds. Parameter estimation and sensitivity analysis. Alterra/NIOO, Alterra-report 1290, NIOO-report 2006-01.

#### Publications from this dissertation:

Tjørve K.M.C., Schekkerman H., Tulp I., Underhill L.G., de Leeuw J.J. & Visser G.H. 2007. Growth and energetics of a small shorebird species in a cold environment: the little stint *Calidris minuta* on the Taimyr Peninsula, Siberia. *J. Avian Biol.* 38: 552–563.

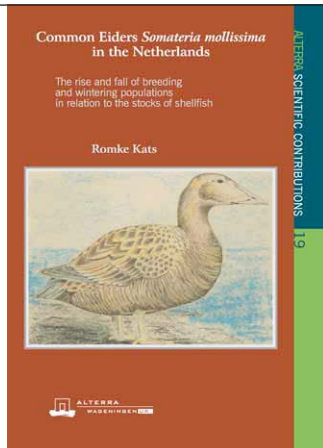
Tulp I. & Schekkerman H. 2006. Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *J. Avian Biol.* 37: 207–218.

Tulp I. & Schekkerman H. Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic*, in press.

Tulp I., Schekkerman H., Chylarecki P., Tomkovich P., Soloviev M., Bruinzeel L., van Dijk K., Hildén O., Hötter H., Kania W., van Roomen M., Sikora A. & Summers R. 2002. Body mass patterns of Little Stints at different latitudes during incubation and chick-rearing. *Ibis* 144: 122–134.

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**Kats R.K.H.** 2007. Common Eiders in the Netherlands: The rise and fall of breeding and wintering populations in relation to stocks of shellfish. PhD-thesis, University of Groningen, The Netherlands. ISBN 978-90-367-3005-1, paperback, 336 pp. Available at <http://irs.ub.rug.nl/ppn/301030170>.



Coastal ecosystems have come under strong human pressure during the second half of the 20th century, in particular fishing pressure increased dramatically (Jackson *et al.* 2001). As a part of this increasing pressure, exploitation of shellfish was intensified worldwide. The Wadden Sea and especially the Dutch Wadden Sea is no exception in this respect. As a consequence, shellfish eating birds in the Wadden Sea and elsewhere have experienced a strong decline during recent years (Scheiffarth & Frank 2005). The Common Eider, as the most important shellfish consuming bird in the Wadden Sea, entirely depends on bivalves. It has a highly specialised foraging mode, swallowing whole bivalves and crushing the shells in the gizzard. Therefore, the quality of bivalves, namely the energy content in relation to shell mass, is of paramount importance for the birds to gain enough energy from their food (Nehls 1995).

Although Common Eiders are nowadays one of the characteristic bird species in the Wadden Sea, they have long been absent from the avifauna of this area (Ens & Kats 2004) with a recolonisation

of the breeding colonies on Sylt in the 1810s and on Amrum in 1877. The first recent birds breeding in The Netherlands were found in 1906 on Vlieland. Early numbers of wintering Common Eiders in The Netherlands are not well known, as these birds are difficult to record outside the breeding season. Certainly, there were only a few birds wintering in the first half of the 20th century. In the 1960s a strong increase of wintering numbers was observed.

Wintering and breeding numbers of this species are nowadays well known, however remarkably little research is done on this prominent Wadden Sea species. As Common Eiders are important predators in the Wadden Sea ecosystem, conflicts between the fishing industry and nature conservation bodies emerged. However, quantitative knowledge on the dependence of Common Eiders on shellfish is scarce. Romke Kats' intention for his thesis was to do a first step to fill this knowledge gap for the Dutch wintering and breeding populations.

Romke Kats' thesis consists of 11 chapters with partly unpublished material and the study was done in the framework of the NWO research programme 'Sustainable use and conservation of marine living resources'. It starts in chapter 2 with a description of the Baltic/Wadden Sea population, which experienced a 36% decline from 1991 to 2000. Different reasons for the strong decline are discussed; however no final conclusion is drawn, as a large discrepancy between breeding and wintering numbers seemed to exist. Chapters 3 and 4 describe the diet of Common Eiders in the Wadden Sea. In particular chapter 4 analyses the diet of birds feeding north of the Wadden Sea islands and tries to reconstruct the shell sizes of *Spisula subtruncata* and *Ensis directus* on the basis on prey remains. A new approach was to use shell thickness as a parameter to reconstruct shell length. As a control for the method, feeding trials with known bivalves were made, validating the proposed reconstruction methods; a step not often done in the diet reconstruction from remains. Both chapters form the basis for the further, more detailed studies on the relationship between food sources and population development.



In chapter 5 the mass mortality event of the winter 1999/2000, when approximately 21 000 Common Eiders died in The Netherlands alone, is analysed. The hypothesis is supported that birds died due to food shortage as a consequence of overexploitation of shellfish since the beginning of the 1990s. Chapter 6 analyses the role of parasites in the mass mortality event. High parasite prevalence and infection intensity was proposed as one of the hypotheses causing the high mortality. To this end, parasite load of birds found dead in The Netherlands and birds shot as hunting bag in Denmark were compared. As there were only minor differences found between these two groups, it was concluded that the hypothesis of the mass mortality caused by parasite infestation had to be rejected.

The population development and the large-scale distribution of the Common Eider in The Netherlands are analysed in chapters 7 and 8. This large-scale approach showed how the birds distribute in relation to the shellfish stocks. The major determinant for the distribution of Common Eider flocks were medium sized subtidal mussels. Cockles did not predict the distribution of birds. In all, there was no firm evidence that mussel cultures benefited Common Eiders, as mussel seed is transported from subtidal beds to culture plots or even exported from the Wadden Sea area.

Chapters 9 and 10 deal with the Dutch breeding population. In chapter 9 the analysis of the long-term data from Vlieland revealed that during the recent decline of the breeding population, in addition to an elevated mortality, relatively large numbers of non-breeding females were present around the colonies. This is a nice result of a modelling exercise of the population dynamics of the Vlieland colony and shows the value of long-term ringing data to calculate mortality rates. Chapter 10 deals with the relationship between the breeding population and the feeding conditions. For the local breeding females sufficient food in the vicinity of the colony is decisive. Here, intertidal mussel beds build a factor determining the size of the breeding population.

In chapter 11 Romke Kats synthesises his findings and gives suggestions for further research as a

basis to reach a science based management plan for the Wadden Sea. The thesis shows clearly how human overexploitation of a marine system affects the population dynamics of a top predator. Romke Kats' thesis shows also that we need to combine large-scale population studies with detailed studies on the population dynamics to get an idea how behaviour of animals is transferred to population patterns. Romke Kats' merit is that he worked up all information resulting from the research started in The Netherlands after the mass mortality in 1999/2000. Still, there are many open questions left that address the functional relationship between food sources and the population dynamics of this species. This might be a topic for another PhD thesis on this characteristic Wadden Sea bird species. Romke Kats himself states that for sound conservation measures of the Common Eider further research is urgently needed.

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