PhD-Dissertation Reviews

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PhD-dissertation reviews

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Michler S.P.M. 2009. Sex-specific strategies in a sex-biased world. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4175-0, paperback, 200 pp. Available at
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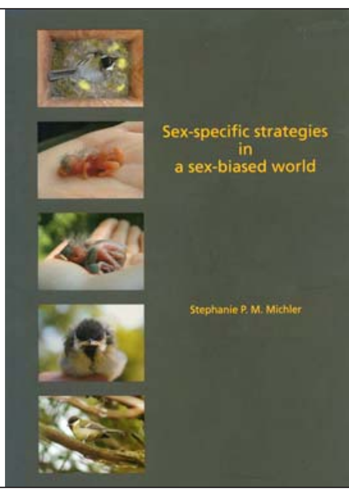

The evolution of sex allocation has generated a wealth of empirical and theoretical studies, yet we are still unable to predict the direction of sex-ratio bias in many species. In part, this has been attributed to environmental heterogeneity leading to spatial and temporal variation in selective pressures, such that male-biased allocation may evolve in one environment but female-biased in another. To complicate this further, these selective pressures may affect males and females differently (leading to conflict between the sexes over sex allocation). It is therefore vital that the local environment is taken into consideration when studying sex allocation. Stephanie Michler's thesis elegantly tackles this important research field using a combination of experimental and statistical techniques to unravel the effects that sex-biased natal dispersal, and sex-biased competitive abilities over resources, have on sex allocation.

Michler's thesis contains five data chapters and four boxes, which are structured into three parts. The first part investigates whether parental provisioning is a mechanism through which parents manipulate sex allocation, and the extent to which parental provisioning is influenced by sibling competition. The second part moves on to examine how environmental heterogeneity, primarily in terms of the local population sex-ratio, influences juvenile survival and post-fledging dispersal. The third part then asks whether females facultatively vary their brood sex-ratio according to the local environment.

Michler's first data chapter, Chapter 2, asks whether parents alter their provisioning behaviour in relation to sex, at both the brood and offspring level. This was possible due to a large-scale manipulation of the sex ratio of the first broods of Great Tits *Parus major*, in four plots in 2004 in the Lauwersmeer area, in the northeast of The Netherlands. These manipulations largely enabled separation of the potentially confounding effects of environmental or genetic variation in quality in relation to brood sex-ratio. Michler concluded, in accordance with other studies, that both parents provisioned male and female offspring at the same rate. The real insight however, was gained in the finding that although the overall amount of food provisioned did not differ with brood sex-ratio manipulation, male-biased broods were fed larger prey, less frequently. Male Great Tits are slightly larger than females and have been shown to have a competitive advantage over females under certain conditions. Altering the frequency and prey load of provisions may therefore represent a mechanism through which parents can influence the level of intra-brood competition.

The second part of the thesis takes the experiment to an impressively large scale, this time manipulating the sex-ratio and juvenile density of 12 plots, over three years, to investigate their effects on fledgling dispersal, and adult and juvenile survival. Importantly, Michler first confirms that the manipulations of brood sex-ratio in the first two years lead to sex-biases at the plot (local) scale up to five months after fledging. She also shows that the effects of the juvenile density manipulations were much weaker. Chapter 3 analyses the manipulations in 2005 and 2006 and represents the first experimental study within a natural population to show an effect of local sex-ratio on the fitness component of apparent juvenile post-fledging survival, using mark-recapture models. Apparent and not real survival was estimated because emigration could not be ruled out, due the open nature of the study site. Michler predicts that male-biased plots should experience increased competition (due to the sexual dimorphism) and that this should lead to decreased juvenile survival. Although this trend was apparent in the first year, the opposite trend was observed in the second year and no sex-specific effect was detected. Michler suggests that although the sex-ratio of the local population affects apparent juvenile survival of both sexes, context dependent factors may shape the direction of this selection pressure.

The same experimental approach was then used in Chapter 4 to investigate whether local sex-ratio and juvenile density affect post-fledging dispersal, and whether there are differential effects on the sexes. Female fledglings dispersed further from male-biased plots, and male fledglings dispersed further from plots that had a high density of nestlings before manipulations. This is the first experimental study in a system of wild-living birds to demonstrate that the local social environment can play a role in differentially shaping the post-fledging dispersal patterns of males and females. The costs and benefits of dispersal are central to the evolution of social behaviour; these findings therefore have widespread implication. Furthermore, this is a nice finding as it suggests that the difference in apparent survival of juveniles according to sex-ratio treatment (Chapter 3) was not due to differential emigration rates, given that no sex-bias in apparent juvenile survival was detected (and assuming that no sex-biased long-distance dispersal occurs outside of the study area).

Chapter 5 asks whether the survival of juveniles and adults are affected by local sex-specific competition, using manipulations over three years. Due to competitive asymmetries in size and age, it was expected that adults versus juveniles and males versus females would show differences in survival in relation to manipulations of local juvenile sex-ratio and juvenile density. For example, male survival may be negatively affected by an increased density of juvenile males. However, no negative effects were detected in adults or juveniles as a result of increased density of same or opposite sex juveniles. Unexpectedly Michler found that juvenile survival increased with the density of same-sex fledglings, which she proposes may be due to behavioural or physiological changes that improve sex-specific juvenile competitive ability. An additional explanation in males is that higher densities of males may increase pressure on adult males to decrease their territory size, increasing the areas available for males to settle in.

The final part of the thesis focuses upon sex allocation, starting with Box C: An investigation of the error associated with the sexing of unhatched eggs. DNA was extracted and sexed from only ca. 60% of the unhatched eggs versus over 95% of the dead hatchlings, suggesting degradation of DNA in the unhatched eggs. No sex-bias was observed in dead hatchlings, but an apparent male bias occurred in unhatched eggs, however, this is likely to be an artefact of poor quality DNA – running a positive control within each sample would confirm this. This simple analysis highlights the importance of methodological rigour and calculation of error rates.

In the last data chapter, Michler shows that both first-year and experienced female breeders biased their broods towards females after experiencing a high nestling-density plot in the previous year (natural density for the first-year birds, experimental density for the experienced birds). This is in line with predictions from the Local Resource Competition hypothesis. The experiment demonstrates that sex-specific competition in the local environment is important in shaping sex allocation, which is the central theme of this thesis. By experimentally manipulating the level of local competition, Michler provides insight into the fitness consequences of the resulting patterns of sex allocation, in terms of the dispersal and survival patterns. She also highlights future research avenues, emphasising that more studies are required to understand the exact nature of local resource competition in female Great Tits (Box D), and whether sex allocation decisions lead to realised fecundity benefits.

Stephanie Michler's thesis is a lovely example of how carefully designed experiments can unravel subtle yet biologically important effects. Her findings have widespread application, for example, showing how provisioning should be analysed at both the level of the quantity and frequency of prey delivery. Her findings also highlight the importance of scientific rigour, and of long-term analyses to control for year-to-year variation. Overall this thesis represents a sound piece of evolutionary research that adds substantial knowledge to our understanding of how the local environment can shape sex allocation.

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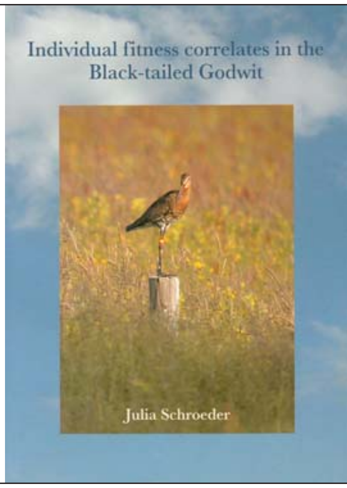
Schroeder J. 2010. Individual fitness correlates in the Black-tailed Godwit. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4157-6, paperback, 206 pp. Available at http://irs.ub.rug.nl/ppn/323774334.



Julia Schroeder is the first to graduate on the research program started by the Animal Ecology Group of the Centre for Ecological and Evolutionary Studies at the University of Groningen on Black-tailed Godwits in southwest Fryslân, The Netherlands. It is after a long time (since Albert Beintema in the 1970s and 1980s) that this 'King of the Meadowbirds' is subject of more fundamental research in The Netherlands. The context is even more urgent than before because of the rapid and ongoing decline as a breeding bird in the Dutch wet grassland habitat. This decline was a motive for Julia Schroeder to aim her study on mechanisms of natural selection in a changing environment on Black-tailed Godwits. More specifically, she studied fitness correlates and the way natural selection by man-induced forces (intensification of grassland management, climate change) works out on them, in the hope this may deliver clues to divert the decline of the Black-tailed Godwit breeding population in The Netherlands.

For her studies Julia used the substantial population of colour-ringed breeding Godwits that had been built up since 2004 in southwest Fryslân. In Chapter 2 she reports space use during settlement at a previously used or a new nest location. Earlier reports on nest-site faithfulness (Groen 1993) were confirmed in the sense that all birds returned first to their previous nest site (within 390 m on average), but decided to stay or move depending on the actual suitability of the site. Nine out of 21 observed birds moved. These movements (interpreted as prospecting in other areas) became clear ca. 15–10 days before egg-laying. The reason for moving was suggested to be the short swards that resulted from Barnacle Goose *Branta leucopsis* grazing into April and that prevented concealment of the nests for predators and might delay insect availability relative to hatching.

A Box reports a distinguished quality of early breeding birds compared to late breeders (before or after 24 April). Early breeders were in better body condition, had a higher daily nest survival probability, laid bigger eggs and had heavier hatchlings. These findings highlight two fundamental issues. First, is body condition at the start of the breeding season determined by local food conditions or by food conditions during winter and/or migration? Chapter 9 in the thesis reveals some answer: females that carried the characteristic stable N-isotope ratio from Spanish rice fields (hence used the Extremadura staging sites), arrived earlier on the breeding grounds, were heavier and laid larger eggs than birds with the isotope characteristics of Portuguese rice fields. A carry-over effect from favourable conditions during migration (being early) may link with gathering more nutrients for egg laying and reach a higher weight during incubation. The relative importance of both sites and the extent to which local food conditions can compensate for less favourable staging conditions remain to be revealed. Secondly, the importance of undisturbed breeding early in the season. Less than thought before, replacement clutches can compensate for early losses. In Chapter 3 Schroeder and co-authors report on hatching dates and hatchling weights over the period 1976–2007. This is relevant to study since Schekkerman (2008) showed that Black-tailed Godwits renounced from further advancing their laying date from c. 1970 onwards. From 1930–1976 Black-tailed Godwits matched deleterious effects of grassland management intensification by laying two weeks earlier. Although warmer weather suggests better laying conditions in early spring, the Godwits did not respond with earlier breeding, but with early females laying larger eggs and late females laying smaller eggs than in the past. It was already shown that larger eggs produce heavier chicks that survive better. The author can only speculate about causes of not further advancing laying dates. She suggests constraints in reducing the interval between arrival and egg laying and obstacles during other moments of the annual cycle for arriving earlier on the breeding grounds.

In Chapter 4 a quantification of plumage dimorphism between male and female Black-tailed Godwits is presented. This reveals a larger overlap in bill length between the sexes than expected on the basis of literature data. The most systematic difference was present in the amount of white feathers on the neck, with females being lighter than males. The most revealing result of the thesis is that male Black-tailed Godwits plumage became paler over the last 170 years, as the author concluded from studying male ornamentation in museum specimens. An explanation may be that selection pressure in favour of strong ornamentation and associated aggressiveness has been waning over time because of improved food conditions due to increased fertiliser use on the Dutch grasslands in comparison to the original breeding grounds in bogs, swamps and river plains. This intriguing example of swift adaptation is supported by the finding that a close relative, the Icelandic Black-tailed Godwit *L. l. islandica* shows the opposite pattern: in parallel with expanding its breeding range on Iceland into areas with lower habitat quality, Schroeder *et al.* found that the more ornamented males had females with larger eggs. Both results indeed indicate sexual selection on plumage ornamentation in godwits.

In Chapter 7 the link between less melanin ornamentation and less aggressiveness in male *L. l. limosa* is made plausible by the findings that paler male godwits breed in higher densities, their nests were defended by a larger number of birds and their eggs had a higher probability of hatching. As an explanation the authors argue that a recent amelioration of habitat quality (by fertilization of the grasslands) may have led to relaxed competition for nest sites and females may choose for paler males that tolerate breeding in higher density where fitness is predictably higher. This once more indicates the fitness advantage for godwit males of being pale.

Chapter 8 reports a genetic foundation of differential fitness, namely difference (polymorphism) in the CHD1-gene that is used in sexing individuals. Males and females with the Z*-allele expressed less breeding plumage, had higher body mass, bred earlier and had larger eggs, but did not differ in annual survival. Strikingly, birds with the Z*-allele (14% of 251 birds) were only found in nature reserves and none in intensively managed farmland (of 33 birds). Although the CHD1-gene is known to be not directly responsible for fitness differences (it only has a role in gene transcription and expression), it is thought to be linked to other genes that affect fitness traits. Although Höglund *et al*. (2009) did not find differential genetic structuring in the Dutch Black-tailed Godwit population, the link between occurrence of the Z*-allele and habitats of different quality suggests a possibility of 'cryptic' genetic population structure, which needs further study.

In the Synthesis, Schroeder describes the observed breeding response on changing selection pressures in a context of life history characteristics. She concludes that not further advancing the laying date but investing in limited earlier breeding with larger eggs, is a life history strategy that does not meet the needs of the chicks but the needs of the adult, i.e. a strategy that maximizes longevity for maximum life time reproduction. Although this is a sound explanation in accordance with ecological theory, the thesis unfortunately gives hardly any clue on the *causal factors* behind not further advancing laying date. For Godwit preservation in The Netherlands this may be a crucial factor, especially on intensively used farmland, but also in reserves in which vegetation development and insect availability is speeded up by climate change. In an appendix Schroeder c.s. demonstrate the inevitable downfall and perhaps even extinction of the Black-tailed Godwit as a breeding bird in The Netherlands in the coming decades when strong measures will be neglected. This may work in two ways: measures at wintering and staging sites when it can be proven that those conditions block further advance of laying and/or strong measures that meet the requirements of non-advanced breeding, i.e. sufficient good quality habitat for chick survival by mosaic management, higher water tables and postponed mowing, on a substantial area of modern farmland. Although I think this last strategy still has perspective, it is a hard one. Therefore further research by the Groningen Animal Ecology Group on possible obstacles for further advancing laying dates may importantly contribute to preservation of the 'King of the Meadows' in the Dutch polder landscapes.

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Höglund J., Johansson T., Beintema A. & Schekkerman H. 2009. Phylogeography of the Black-tailed Godwit *Limosa limosa*: substructuring revealed by mtDNA control region sequences. J. Ornithol. 150: 45–53.

Schekkerman H. 2008. Precocial problems. PhD Thesis. University of Groningen, The Netherlands.

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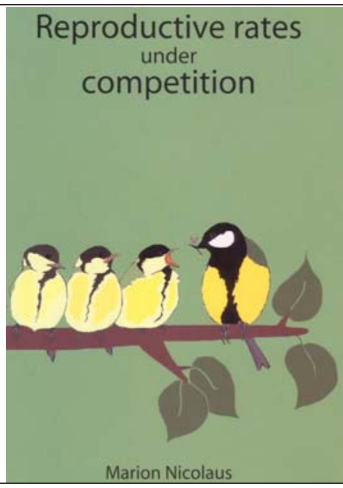
Nicolaus M. 2009. Reproductive rates under competition. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-367-3965-8, paperback, 224 pp. Available at http://irs.ub.rug.nl/ppn/322212324



The thesis of Marion Nicolaus investigates the density dependence of various reproductive rates using experiments as well as long-term data in one of the most popular avian study species, the Great Tit *Parus major*. The main experiment manipulated the social environment of nestlings and thereby aimed (1) to investigate how this affected the fitness consequences of different reproductive decisions and (2) to determine the spatial scale at which selection on individual decision works. The experiment ran over a period of three years and involved a complex design of manipulations of the social environment in terms of both the density and sex ratio carried out at both a local (brood) as well as population (woodland) scale. Due to the vastness of this experiment Nicolaus' thesis primarily focused on the role of competitor density, while another thesis investigated the role of sex ratio variation in full detail (see review of thesis by Stephanie Michler (2010) in this Ardea issue).

Nicolaus first starts out by analyzing the results of an earlier experiment in which over a period of eleven years 3 out of 8 woodlands were given a high density of nest boxes (resulting in high breeding densities). The results point out that although density dependence is a simple concept, the mechanisms by which it works are often less simple. Natural breeding density increased over time and clutch size decreased simultaneously over time, suggesting reproduction is density dependent. Nonetheless, within years birds from high density plots did equally well as birds from low density plots in terms of the number of eggs produced. This result suggested that competition works on a different spatial scale or in a different life-stage (e.g. after the nest-stage) and thereby set the stage for the thesis' main experiment.

In contrast to the previous experiment (and to most density experiments in other species) the main experiment carried out by Nicolaus and co-workers did not involve manipulation of adult breeding densities, but manipulations of nestling densities. By swapping around nestlings within and between nests of 12 woodlands, plots were created with either high or low nestling densities and with either a male biased, female biased or an equal nestling sex ratio (full factorial design). In addition to the large scale density manipulations, local nestling numbers were also manipulated among broods within plots (reduced, control or enlarged broods). One can only wonder about the logistical complexity of carrying out such a huge multifactorial experiment, as all nestlings had to be sexed in the lab before they could be swapped and they were all swapped at day six of age (some nestlings from control groups were even swapped to account for effects of swapping *per se*).

In a series of chapters Nicolaus disentangles step-by-step how the density manipulations at the brood- and woodland-scale affected the offspring performance from the nestling stage, via the post-fledgling stage to the settlement-as-breeder stage. Nestling growth and nestling survival turned out to be negatively affected by local density (brood size). Regrettably, due to mixed results the effect of population density proved to be more difficult to interpret. However, most interestingly, both sexes were not affected equally by competition within broods. Females had lower survival than males, probably because they were outcompeted by the larger and more dominant males in this sexually size-dimorphic species. The sexual size-dimorphism was largest in enlarged broods, suggesting that especially females in low condition suffered most from competition. Competition is thus asymmetrical between the sexes and likely state-dependent.

High densities may not only indicate severe competition for limited resources (e.g. post-fledging survival was also lowest in high density woodlands in this experiment), but may also function as a signal that habitat is of high quality (public information). Thus when investigating the effects of conspecific density on settlement-as-breeder decisions the density experiment offered an opportunity to test both hypotheses simultaneously. Consistent with the 'competition' hypothesis, juveniles avoided settling in natural high density woodlands. This behaviour may reduce direct competition with experienced breeders and immigrants.

Interestingly, in agreement with the 'public information' hypothesis juveniles also settled more in former male biased woodlands. Male biased woodlands carried more of the philopatric sex which led to higher local juvenile densities during the post-fledging period and thereby may have appeared attractive for settlement. Population numbers can thus contain mixed aspects of information for birds, and their interpretation may depend on the time of the year when the information is gathered.

In subsequent chapters Nicolaus switches her perspective from offspring performance to discuss the effects of density experiment on the parents in relation to their cost of reproduction and selection on brood size. Although theory suggests that there should be a fundamental trade-off between survival and parental effort, empirical evidence is actually rare. To explain discrepancies among studies, Nicolaus proposes that the costs of reproduction depends on the ecological context, and therefore is not always detectable. One would expect adults with increased parental effort to pay higher reproductive costs (that are more easily detected) under a high level of intra-specific competition, meaning in high density and male biased populations. And indeed the cost of reproduction was found to covary with the social environment. In male biased woodlands, parents rearing enlarged broods had reduced survival rates compared to those in female biased plots. A similar pattern was found for the probability of starting a second brood. An increase of parental effort may thus have affected parental competitiveness and increased their costs of reproduction under a high competitive regime. As such, this chapter provides the first experimental evidence in the literature that the cost of reproduction depends on the ecological context, and it provides a convincing framework to reconcile empirical results with theory.

Finally, in the last research chapter Nicolaus discusses how varying population densities may cause selection pressures to fluctuate over time and could have differentially affected the outcome of brood manipulation experiments in various years. Nicolaus' work on cost of reproduction had already suggested that a high parental effort decreases the competitiveness of birds, resulting in a higher cost of reproduction in years with severe competition. As a consequence, one might expect selection for smaller brood size in years with high densities. By comparing the outcome of brood size manipulations in two periods (1995–1998 vs. 2005–2007) in the same meta-population of Great Tits, it was shown that as expected there was selection for larger broods when population densities were low (period 1), while there was selection for smaller brood size when densities were high (period 2). More specifically, selection on the offspring fitness component was positive in period 1 but non-existent in period 2, while selection on the parental component was non-existent in period 1 and negative in period 2. These results underline the importance of repeating experiments in multiple years under a variety of ecological conditions, as performing experiments in single years (as is common practice in field biology) can give highly non-generalisable results. At the same time this study also highlights the difficulty to explain differences in outcomes between years, as any other factor besides population density that varied between the two periods may explain the fluctuating selection pressures equally well. Moreover, a logical next step would be to use the available pedigree to determine the heritable basis of the reproductive rates and whether selection works at the genetic or environmental components of these traits.

In conclusion, this thesis describes a unique approach that combines multi-factorial experiments (manipulating local density as well as population density and sex ratio) with a long-term perspective (experiments repeated in many years). Very, very few studies achieve this. At several points Nicolaus shows that combination of these factors affect the reproductive performance of Great Tits (e.g. enlarged broods had a higher cost of reproduction in male biased woodlands), which convinces the reader of the unique insights a multi-factorial approach can give and also points to the complex way in which competition can work. By repeating experiments in multiple years, it becomes clear that understanding how selection depends on the ecological context, such as population density, will be important to understand discrepancies between studies and reconcile them with theory.

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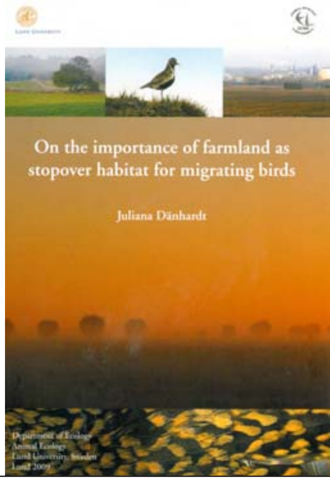
Dänhardt J. 2009. On the importance of farmland as stopover habitat for migrating birds. PhD thesis, Lund University, Sweden. ISBN 978-7105-292-6. Paperback, 126 pp.



Due to the large-scale agricultural changes in land use a lot of inland waders face big problems. Dramatic effects are for instance the crash of Dutch breeding populations of meadow birds, and declining numbers of migrating waders (Versluys *et al.* 2009, Limosa 82: 194–207; Verkuil *et al.* in press, J. Anim. Ecol.). For the Golden Plover *Pluvialis apricaria* changes in numbers on staging sites have been documented well, based on data collected by 'Wilster catchers' in The Netherlands (Jukema *et al.* 2001, KNNV, Utrecht) and the recent studies of farmland birds in Britain (Gillings *et al.* 2007, Ibis 149: 509–520).

For the management and protection of important stopover sites it is necessary to gain more knowledge about farmland regions, also outside the usual Nature 2000 areas and wetlands, where numbers of migrating birds are still doing fairly well. In Scania, the most southern province of Sweden, numbers of staging Golden Plovers in autumn are bigger than ever. That's where the PhD thesis of Juliana Dänhardt comes in.

First of all a survey was carried out in Scania in the autumn of 2005, counting all birds using organic and conventional farmlands (Chapter 1). The extrapolated total number of birds is at least 14.7 million birds in the 5732 km^2 large agricultural landscape, based on the assumption of an average turn-over of seven days, in the period of mid-August to 1 November. This number represents about 5% of the Swedish and Finnish post-breeding populations. To make clear how important the Scanian farmland is, criteria of the Ramsar Convention were discussed and comparisons were for instance made with the slightly smaller Wadden Sea, which is used by 10–12 million waterbirds throughout the year. That makes clear that the Scanian farmland actually should be considered as a staging site of international importance.

Considering the importance of this agricultural area as a staging site and the effects of agricultural intensification and changes in landscape structures all over Europe on many farmland birds, Chapter 2 is a welcome contribution to the growing amount of research done on landscape-dependent effects of organic farming. Describing the effect of organic farming and landscape structure, not only organic and conventional farms were compared, but also heterogeneity of landscapes was taken into consideration. As expected more birds, both seed- and invertebrate-feeders, were found on organic farms, although this trend was non-significant. The main result seems to be that bird numbers were highest when farming organically in homogeneous landscapes, especially in the case of waders, corvids and gulls. This pleads for keeping the landscape open to stimulate migratory bird diversity and species richness, including the Golden Plover of course. Earlier studies proposed to promote biodiversity with increasing heterogeneity by creating non-arable habitats in homogeneous plains. So here it is stated that that is not a good idea when it comes to a lot of typical migrating waders in Western Europe.

In Chapter 3 the study is taking onto the level of the single species, the Golden Plover. Standardized data were collected along transects in 2003–2007: recording the behaviour of flocks of Golden Plovers and documenting habitat use. Large numbers of roosting Golden Plovers were using coastal habitats. Foraging flocks were mainly observed on arable land with low vegetation. Grassland was used much less than expected. This shows that Golden Plovers do not necessarily depend on grassland. Besides that, the study makes clear – as in Chapter 2 – that large open areas in large-scale arable landscapes are important to species like Golden Plovers.

The main question is possibly found in Chapter 4: can intensive arable farmland be favourable for birds during migration? To answer this question Dänhardt studied the stopover ecology of the Golden Plover in Scania, making use of trapping of birds and radio-tagging. In this way, ecological variables such as duration of the stay, fuel deposition and moult were studied. It turns out that the Golden Plovers stayed relatively long (three months), moulted in the area and deposited significant fuel loads, although the fuelling rates were not that high. It seems that the Golden Plovers are doing pretty well in intensive arable farmland in Scania. One question one might have is what the definition of 'intensive' is, meaning: is intensive in Sweden as intensive as for instance in The Netherlands and Lower Saxony? By also studying the spatial and temporal variation in food abundance in this kind of intensive arable farmland (Chapter 5) more is understood of the habitat use by the migrating Golden Plovers. Large roosting flocks are found in coastal areas during the day, but at night Golden Plovers scatter in small flocks to forage inland. The main reason for foraging inland seemed to be that the earthworm availability was significantly higher on inland farmland during night compared to coastal fields, while the number of predator attacks and the frequency of kleptoparasitism were low in both areas. Interestingly, a new method to assess worm availability was introduced by 'surface sampling', consisting of simply visually counting earthworms on the surface, using torches at night.

It may be that the results in this thesis are not that shocking and that it more or less confirms what was already suspected. However it makes very clear what a migrating wader such as the Golden Plover prefers on a stopover site of growing importance and it reinforces the importance of farmland for migrating birds. Furthermore the thesis offers good opportunities to make comparisons with farmland sites where numbers of Golden Plovers have decreased significantly over – let's say – the past thirty years. Could it be that the Golden Plovers prefer Scania nowadays because it got really worse in the Dutch and German farmlands? Last but not least the plea for homogeneous landscapes with organic farming is valuable and should be voiced loudly!

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