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Author: Wiersma, Popko

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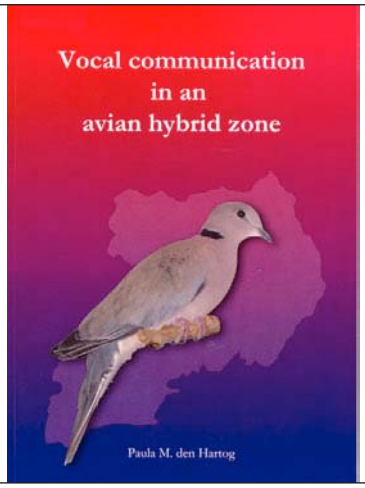
*Popko Wiersma*
*Animal Ecology Group, University of Groningen,*
*P.O. Box 14, 9750 AA Haren, The Netherlands*
*(popkowiersma@hotmail.com)*

**Den Hartog P.M.** 2008. Vocal communication in avian hybrid zone. PhD thesis, Leiden University, The Netherlands. Paperback.




Avian hybridisation is one of the evolutionary and ecological topics with ups-and-downs within the last century. Especially the biological species concept lead to the ignorance of hybrids during a long time. But the times they are changing: Since the thrive of molecular ecology, the study of hybridisation has received some kind of a revival. As we know from the study of hybrid zones in birds and in animals in general, most hybrid zones are stable over time, and are rather narrow in comparison to a species' range. Interestingly, there is lack of evidence, why this is so in avian hybrid zones. Although there have been some 100 or so theoretical models that invoke assortative mating as key factor in stabilising hybrid zones, only very few studies look at behavioural differences.

This thesis fits into the set of others within the last years that try to establish a more complete picture by combining different methods of research. This is one of the major strengths of den Hartog's thesis: she combines molecular analysis and analyses of vocalisations, the latter both in the field and in the lab. Everyone who has ever worked in the field (a matter that was more or less 'normal' during earlier years of ornithological research) knows how difficult field work can be and how unpredictable working conditions are, especially in an African environment. The study system comprises two species of doves from the genus *Streptopelia* (*vinacea* and *capicola*), that form a hybrid zone in Uganda. This hybrid zone seems to have emerged rather recently, and not to be an ancient one, so it is possible to study 'evolution in action'.

After giving an Introduction to the thesis, chapter two is mainly based on genetics where den Hartog used different methods, for both nuclear and mitochondrial DNA, but also analysed morphological characteristics and plumage traits to investigate the hybrid zone. This is especially worthwhile, because modern studies should not focus on one single method or give preference to one method over the other. Interestingly, the zone indeed seems a hybrid zone (by definition) and consist of hybrid swarms, i.e. most individuals within the zone are hybrids. Such 'real' hybrid zones are rare. What is often found are zones of overlap and hybridisation, which were often wrongly labelled as hybrid zones. The data indicate an asymmetric introgression into *vinacea*. This is especially interesting and it adds to the very few studies that show a unidirectional hybridisation in birds. For example, in Wirtz's (1999) overview on vertebrates, there are only two clear studies on hybridisation in birds from a molecular (mtDNA) perspective, and both supposed a bi-directional hybridisation. This thesis here suggests that more *capicola* females are mating with *vinacea* males than *vice versa*, and the results may be explained by dispersal and geographic distances. This is an interesting aspect since it may be possible that the asymmetry is not a product of female preference or mate choice (i.e. that *capicola* females may prefer *vinacea* males), but a by-product of ecological circumstances. This chapter further shows that molecular analyses are not sufficient to draw firm conclusions, e.g. for mate preferences.

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Chapter three analyses vocalisations and provides playback experiments within and outside the hybrid zone. There was no evidence of a difference in hybrid responses to parental and hybrid vocalisations. Parental species, however, responded differently to con- and heterospecific calls, (as is usually expected) and intermediate to hybrids. Hybrids respond similarly to all stimuli, while parental species discriminate between con- and heterospecific calls. As the vocalisations of hybrids are intermediate between parent species, hybrid males can easier establish territories in the hybrid zone than in the zone of allopatry. This can help to maintain the hybrid zone and to avoid a broadening of it. Also, this fact is new with respect to the discussion of the maintenance of hybrid zones.

As a consequence, chapter four makes an emphasize on signalling theory, and shows that the signals are decoupled in the hybrid zone, and that individuals may learn to whom to respond, another factor that may contribute to the stability of hybrid zones. Although on the population level responses were more or less clear, there was a strong individual variation to the playback stimuli, and response to stimulus and own vocalisation were not always in accordance with each other.

Chapter five presents some kind of validation: hybrids bred in the lab were compared to hybrids in nature – their vocal repertoire is similar. The variation of the vocal repertoire is reached within one generation bred in the lab. Furthermore, the benefit of using doves is to have a vocal repertoire that is inherited genetically and not acquired by learning. This is important because hybrid vocalisation in nature can be formed by genetics or learning (e.g. by false imprinting).

In a synthesis, den Hartog suggests that allopatric *capicola* dispersed into *vinacea* range. By mating heterospecifically (as a result of the absence of a conspecific partner) hybridisation started. However, the ideas about the further development of the hybrid zone remain a bit speculative because DNA-data and vocalisations cannot give a clear answer why females of each species mated heterospecifically. The thesis further suggest that at least in the hybrid zone, F1-hybrids experience no selective disadvantage. Another aspect is that the study is not easy to place within one of the models of hybrid zones, and some further work is needed to assess the fitness of hybrids. However, all these interesting question reach far beyond the work that can be achieved in one single thesis, but this shows that a lot remains to be done in the research in avian hybrid zones.

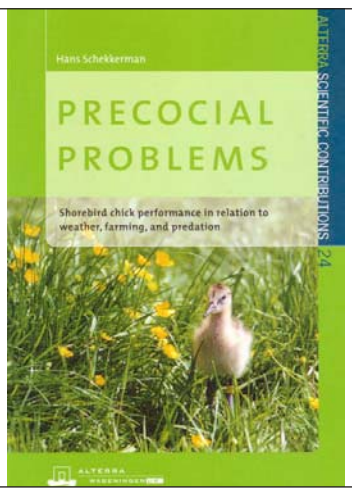
I enjoyed reading the thesis and the thesis makes an important contribution to the field. The strength, again is the methodological approach and also the fact that this study was carried out in doves (with inherited vocal repertoire) and not in songbirds. Until recently, most European work on hybrids was based on songbirds, and the thesis on doves now widens our scope of knowledge. Also, the vocalizations in doves are much more simple compared to most songbirds, rendering the *Streptopelia* an ideal study object.

One final negative point is the horribly long list of acknowledgements that sometimes resembles an Oscar prize show. On the other hand, the list shows how many people are involved in this complex work. Congratulations.

Wirtz P. 1999. Mother species–father species: unidirectional hybridization in animals with female choice. Anim. Behav. 58: 1–12.

*Christoph Randler, Didaktik der Biologie/Zoologie, University of Education, Heidelberg, Im Neuenheimer Feld 561-2, D-69120 Heidelberg, Germany (randler@ph-heidelberg.de)*

**Schekkerman H.** 2008. Precocial problems. Shorebird chick performance in relation to weather, farming and predation. PhD thesis, University of Groningen, The Netherlands.
ISBN 978-90-9022979-9, paperback, 228 pp.




The main character of the thesis *Precocial problems* is depicted on the front: a Black-tailed Godwit *Limosa limosa* chick standing in tall green grass. The problems that the chicks of this precocial species will encounter are to find enough food and shelter before fledging. Their main breeding habitat, wet agricultural mead-

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ows, undergoes rapid and strong change by agricultural intensification. Increased use of fertilisers, reseeding with productive grass monocultures, as well as the lowering of the water table and the increase of spring temperatures enable farmers to mow earlier in the season. At the moment, the first cut of the grass is done during the nesting phase and when the chicks are about to hatch. As is shown in this thesis, the food availability of mown grassland is much lower than in unmown grasslands, and shelter from predators is also reduced.

Nevertheless, it is not a thesis on the problems of Black-tailed Godwit chicks solely. The research goal was to understand the energy requirements of self-feeding precocial shorebird chicks in a broader sense. Shorebird chicks feed upon small invertebrates taken from low vegetation and the upper surface of the soil. Invertebrates, however, are sensible to climatic conditions: they are less active on cold windy days and, therefore, harder to find than on warmer days. Additionally, young chicks depend on parental brooding for thermoregulation. During unfavourable weather conditions, they spend more time keeping warm, and less foraging. This might reduce their nutritional condition, which possibly affects their foraging performance and therefore they might end-up into a negative spiral.

Energy expenditure studies on chicks of precocial species are scarce, but for a good reason: their chicks are mobile and cryptic and, therefore, very hard to follow. Nevertheless, in chapter 2 the energy expenditure of Black-tailed Godwit and Northern Lapwing *Vanellus vanellus* chicks was quantified using doubly labelled water. Measurements were obtained in the field and in the lab, and are compared with those of chick of altricial species. The field measurements revealed that their thermoregulation and foraging costs are twice as high compared to the altricial chicks. Moreover, field measurements showed that wild chicks spend twice as much energy on thermoregulation and foraging than chicks reared in the laboratory. Furthermore, they calculated that a small reduction in energy uptake results in a stagnation of growth. Godwit chicks carry just enough extra energy to sustain normal daily energy expenditure for 1.3 days in a period of food shortage. These chicks thus operate within narrow energetic margins, and rely heavily on a predictable food supply.

Despite the high energy requirements of shorebird chicks, there are quite some shorebird species breeding in the Arctic. How do the chicks of Arctic shorebird species cope with the cold climate, and what makes the Arctic such an attractive breeding area for shorebirds? How precocial shorebird chicks growing up in the Arctic challenge this narrow energetic margin, is studied in chapter 3. The hypothesis is tested that in the Arctic a higher invertebrate peek, combined with longer daylight, results in a higher energy uptake. The energy expenditure and time budgets of chicks of Red Knots *Calidris canutus* were compared with that of temperate shorebirds. The chicks seemed to need their rest and did not take full advantage of the prolonged daylight to increase foraging time. However, they were brooded less by their parents than temperate shorebird chicks, and were sooner thermally independent. This increased their available foraging time. The peek in invertebrate abundance was not higher in the Arctic compared to the temperate zone, but the simpler structure of the tundra might result in prey being easier to detect by the chicks which increased intake rates.

The effect of temperature on the growth rate and survival of precocial chicks was further studied in chapter 4. The growth rate of Curlew Sandpiper *Calidris ferruginea* chicks was indeed reduced during cold weather which coincided with reduced availability of their prey. Moreover, the proportion of juvenile Curlew Sandpipers in the 'wintering' areas in southern Africa was also positively correlated with mean temperature in the Arctic breeding area. This suggests that weather condition during the fledgling period explains a large part of the variation in breeding productivity found in this species.

The last 4 research chapters focus on temperate agricultural grasslands, where growing precocial shorebird chicks face challenges caused by the intensive land management. Chapter 5 reports of the foraging behaviour of godwit chicks. For this purpose, enclosures of 0.4–0.6 ha were built around the nests which kept the chicks inside after hatching, but allowed the parents to move freely in and out. Up until 8–10 days old, parental brooding forms a large part of the daily routine. Thereafter, foraging time increased to 70–90% of the daylight period.

In chapter 6, the difference between foraging success of godwit chicks and the abundance of invertebrates between a meadow bird reserve and an intensively managed dairy farm was compared. Before the first cut of grass of the intensively managed agricultural land, there was only a slight difference in abundances of invertebrates. However, after mowing, the abundance was much higher in meadow bird reserves. This coincided with the time the chicks were just hatched. In a foraging experiment, captive chicks ingested 31% less prey on a cut meadow than on uncut meadows in meadow bird reserves. This is a large enough difference to expect substantial negative effects on growth and survival. Thus, postponing mowing dates until after the

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fledging period of the chicks will have beneficial effects on breeding success of this species.

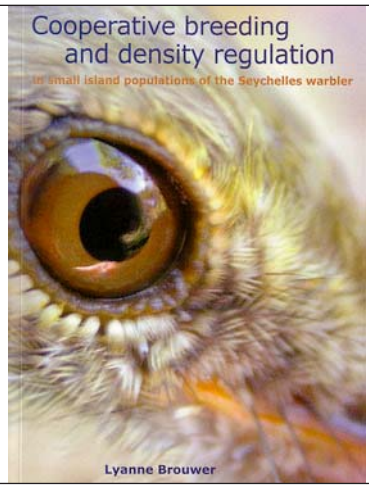
In response to this conclusion, Dutch conservation organisations developed a new agri-environmental scheme: 'mosaic management'. Mosaic management includes uncut 'chickgrass' to provide sufficient foraging habitat for chicks. In chapter 7, the effect of this mosaic management on the reproductive output of Black-tailed Godwits has been researched and described. Chick survival was indeed higher when more uncut grass was available, however, the reproductive output stayed below the required level for a self-sustaining population. A comparison with previous studies revealed that the reproductive outcome has declined considerable over recent decades, and is the major driver of this species' population decline.

Chapter 8 deals with the mortality of godwit and lapwing chicks. This has been studied by tracking radio-tagged chicks. The aim was to quantify different mortality factors, such as predators and agricultural management. The tags did not have an effect on the condition and survival chance of godwit chicks, but it had an effect on the body-condition of the smaller lapwing chicks. Predators were the main cause of death, with Grey Herron *Ardea cinerea*, Stoat *Mustela erminea*/Least Weasel *Mustela nivalis*, Common Buzzard *Buteo buteo* and Carrion Crow *Corvus corone* as the most common predator species. However, 5–10% of the chicks were mowing-victims. The role of agricultural practice is even higher, because the predation hazard of godwit chicks on recently cut and grazed fields was higher than in tall vegetation.

All the aspects treated in this thesis are nicely brought together in the synthesis: from energetic requirements of chicks on the tundra, to that of chicks in the intensively managed agricultural landscape. A very important effect of this thesis was the discussion that it initiated in The Netherlands on meadow bird conservation. The protection of single nests and postponing of mowing alone are not sufficient to maintain the Black-tailed Godwit population. An approach on a broader scale is necessary, where conservation measures should be carried out on a landscape level. Schekkerman suggests to concentrate conservation efforts in those areas with favourable preconditions and applying rigorous measures there. In such a way the chance that the required reproductive outcome for a self-sustaining population will be reached is larger.

*Rosemarie Kentie, Animal Ecology Group, University of Groningen, P.O. Box 14, 9715 AA Haren, The Netherlands (r.kentie@rug.nl)*

**Brouwer L.** 2007. Cooperative breeding and density regulation in small island populations of the Seychelles warbler. PhD thesis, University of Groningen, The Netherlands. ISBN 978-90-367-3166-9, paperback, 155 pp.
Available at http://irs.ub.rug.nl/ppn/304968013.




Besides being an excellent piece of work, this thesis should be best considered as a fine illustration on how to combine conservation management with fundamental science. Brouwer's main topic concentrates on one of the most essential questions in population ecology and examines the factors that determine the number of individuals within populations and the processes involved in the regulation of these numbers over time. She thereby focuses on density dependent factors in population regulation. What makes this thesis unique, however, is the fact that she explores density regulation processes by using the well-monitored rescue-program of the Seychelles Warbler *Acrocephalus sechellensis*. The species is endemic to just a few islands in the Indian Ocean and has been intensively studied since 1985 (Komdeur, Richardson) with almost every individual of the species being individually colour-marked. The species went through a severe bottleneck in the 1960s during which the population was restricted to c. 30 birds on Cousin Island. Due to restoration of the original habitat the warbler population has recovered and is now saturated with approximately 320 individuals. Three additional populations were successfully founded through translocation of birds to the nearby islands of Aride (1988) and Cousine (1990) and Denis (2004). Especially the data available on the translocations of individuals to create new populations on nearby islands created unique opportunities for exploring causality of density dependent processes.

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Besides the opportunity to use the translocation of individuals as a natural experiment, this study also has some major advantages compared to studies of population dynamics on the mainland. While the dispersal of individuals outside the study population is often the cause of serious biases in survival and demographic estimates, dispersal from islands does not occur in this species. What makes this study also different from other work on population dynamics is that Seychelles warbler are a cooperative breeding species, with group sizes varying between one to seven birds per territory, making this one of the first studies linking group-living to density dependent processes. Altogether Brouwer has synthesized several aspects of this unique study-system in her thesis with an emphasis on density-dependent processes integrated with the behavioural ecology of a cooperative breeder. All patterns are thoroughly explored by the extensive use of capture-mark-recapture models throughout the thesis.

Chapter 1 provides some general background information on the study system and a general outline of the research topics. In the following two chapters, which I consider as being outstanding, she examines the role of density dependent and independent processes in population regulation. Chapter 2 analyses patterns of adult and juvenile survival over a 19-year period on Cousin Island and relates this to both natural variation in population density as well as the experimental reduction of the population density by the removal of birds from the population for translocation purposes in 1988 and 1990. Despite significant variation in survival between years, no associations were found with changes in either natural or experimental changes in population size or density, nor could this variation be explained by environmental factors such as rainfall or temperature. It is mentioned that two extreme weather-events (drought in 1986 and flooding in 1997) did have a great impact on survival, which however, illustrates the population's vulnerability to adverse weather conditions rather than a population regulation effect of weather. In fact, the population size has remained remarkably stable over the last 20 years with survival rates of both adults and juveniles being extremely high (84% and 61%, respectively), even for a tropical species. So, if the environmental conditions are relatively stable, while survival of individuals is high and no dispersal is occurring out of the system, how come the population size remained stable? To answers this question the data was further analysed at a scale at which competition between individuals takes place. This revealed an interesting negative effect of density dependence. In contrast to previous findings by Komdeur (1992, Nature 358: 493–495), showing positive effects of territory quality on survival, Brouwer's results were in fact showing the opposite with territory quality affecting survival negatively. Further analyses revealed that these contradictory results were attributable to group size effects and not territory quality itself (e.g. due to food availability, not taken into account by Komdeur). In high quality territories, the groups of subordinates were larger, which probably increased the competition for food within territories, thereby eventually reducing survival. Brouwer clearly illustrates the complexity of density regulation in cooperative breeding systems. Her study is also one of the few studies, showing that density dependence may only be detectable at the level of the individual and not at the population level (cf. Both & Visser 2000, J. Anim. Ecol. 69: 1021–1030).

In Chapter 3, Brouwer continues to disentangle the mechanism of population regulation, this time by making use of the translocations of birds to nearby islands as a natural experiment. She analyses survival and reproduction in relation to the change in numbers during the process of saturation. Density dependence in population size was shown by both the fast recovery of the numbers in the founding population of Cousin and the fast increase in numbers in the newly created populations, which reached a plateau within several years. Population growth in the new created populations also evolved in a classical way for cooperative breeders. With increasing densities the territory sizes of new established pairs decreased, while reproductive strategy shifted from pair-breeding to cooperative breeding. In both newly created populations, an increase in density negatively affected reproduction, but not survival, providing convincing evidence for population regulation via density dependent reproduction. Based on differences in insect densities between islands Brouwer hypothesizes that competition for food may be the main mechanism behind the observed decrease in overall reproduction with increasing densities. The most convincing arguments for this idea are based on the observations that at low densities the growth rate was higher for the population with the highest insect densities and that the islands with the lowest insect densities also had the lowest asymptotic population density. It is clearly stated that experiments are needed to test this hypothesis. Overall, these two chapters show that the population densities are regulated on the population level by density dependent reproduction and at the local scale by density dependent survival.

Chapter 4 further examines the relative effects of territory and parental quality and the rearing environmental (i.e. groups size, nest mates, number of helpers)

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on individual fitness and, more specifically, offspring fitness. To separate the quality effects from environment effects she performed a cross-fostering experiment of nestlings. In Chapter 2 and 3 it was shown that territory quality itself apparently did not directly affect survival or reproduction, but that group size differences may have major fitness consequences for all members of the group. An increase in group size in high quality territories may counterbalance the positive effects of territory quality on reproductive success and even result in a lower adult survival due to competition for food. This is intriguing given that negative effects of group-living in cooperative breeders have rarely been reported. The experiment confirmed that territory quality indeed has no affect on offspring survival, but perhaps more surprisingly, neither did group size. Again, it turned out to be more complicated. Despite having groups sizes of up to seven birds per territory, the number of individuals that were actual helping was found to be never more than two. However, even a differences of just one helper between groups had significant positive effects on offspring survival. Furthermore, the effect appeared to be a long term as the number of helpers also increased subsequent adult survival.

Chapter 5 differs from the rest of the story in the sense that it focuses on the physiological aspects of group-living rather than its relation to fitness variation and population ecology. The chapter describes a neat experiment in which subordinate males are promoted to primary males in order to investigates the proximate mechanisms underlying cooperative helping. It is first shown that primary males differ from subordinate males in having higher levels of circulating testosterone and larger cloacal protuberance sizes (indicating the storage of more sperm); in both cases most evident during the females fertile period. Subordinate males on the other hand were shown to be either physiological suppressed or of general lower quality (as shown by have a lower residual body mass and higher buffy-coat values (a measure of immuno-competence). After experimentally removing the primary males, the new promote males became more similar to the original primary males except for testosterone levels. Although this suggests that subordinates are physiologically suppressed rather than of being of low quality, more information is needed to reveal how such suppression would work and to understand why testosterone levels did not increase.

Chapter 6 focuses again on population regulation and fitness variation by studying the genetic effects on survival. The population went through a severe bottleneck in the 1960s and genome-wide inbreeding effects are likely to play an important role in Seychelles Warblers. Brouwer investigated the effects of heterozygosity (measured at 14 microsatellite loci) on individual survival and the parental heterozygosity effects on offspring survival. To separate between direct genetic and social genetic effects (e.g. heterozygosity of helpers) a cross-fostering was performed. No effects of multilocus heterozygosity on individual survival was found, suggesting that inbreeding depression was very weak.

All in all, this thesis is great piece of work. Brouwer has combined both large and small scale experiments, giving insights in causality of factors involved in density regulation and enhancing our knowledge of the population ecology of cooperative breeders in general. She used both field data and molecular techniques to explain fitness variation on both the population and individual level, thoroughly analyzed using capture-mark-recapture models. Given that many ecosystems around the world are currently under severe pressure due to the ever increasing impact of the human population, this study's contribution to the understanding of population dynamics of an island species may provide a welcome contribution to better protection of our environment. As Lyanne Brouwer stated in the first paragraph of this thesis "understanding the factors that influence the number of individuals and determine how we can manipulate such factors is one of the main challenges ecologists now face". Brouwer faced the challenge and greatly succeeded.

*Thijs van Overveld, Evolutionary Ecology Group, University of Antwerp, Department of Biology, Groenenborgerlaan 171, B-2020 Antwerp, Belgium (thijs.vanoverveld@ua.ac.be)*

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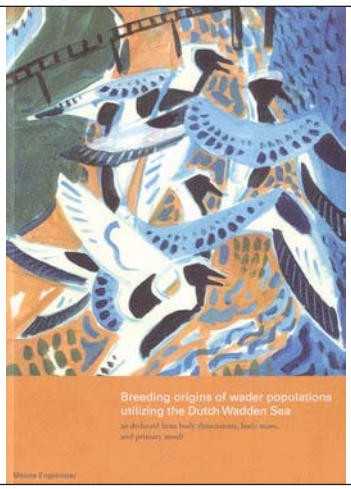
**Engelmoer M.** 2008. Breeding origins of wader populations utilizing the Dutch Wadden Sea as deduced from body dimensions, body mass, and primary moult. PhD thesis, University of Groningen, The Netherlands. Fryske Akademy, Leeuwarden, The Netherlands. ISBN 978-90-367-3309-0, paperback, 226 pp. Available at http://irs.ub.rug.nl/ppn/306073528.




The breeding origins of waders stopping over and wintering in the Dutch Wadden Sea has puzzled wader enthusiasts ever since the start of field studies in the 1970s. The subsequent recoveries of marked waders helped to define the East Atlantic Flyway: the coastal area between NE Canada in the west, Taimyr peninsula in the east and Table Mountain in the south with the Wadden Sea as a major hub in its centre. Although the ringing activities on Vlieland and Schiermonnikoog were initiated by professionals, much of the work carried out later and in other areas were almost exclusively supported by volunteers. Now, 30 years and 30 000 captured waders later, Meinte Engelmoer made an attempt to make quantitative statements about the geographical breeding origins of waders wintering and staging in one of the most important wetlands in the world, the Wadden Sea. These statements are simply based on the basic measurements of size: bill and wing length and weight. Thirty years later, a wide spectrum of techniques is available to pin down the origin of migratory birds with ever increasing accuracy but against increasing costs: molecular information, trace elements, stable isotopes, GPS-loggers and satellite transmitters. This thesis explores the value of simple measurements routinely taken in monitoring trapping schemes. It complements one of the first milestone publications about the significance of the Dutch Wadden Sea for waders: its function as a moulting area (Boere 1976, Ardea 64: 210–291). A comprehensive survey of all museum specimens of wader species collected during breeding was published earlier (Engelmoer & Roselaar 1998, Kluwer Academic Publishers).

The author, however, was not satisfied with a detailed analysis of the biometrical variation in twelve wader species alone and extended his studies to temporal and spatial variation in moult patterns, age ratios and numbers. The bigger pattern which emerges from this work of monumental proportions is that all populations of the twelve wader species involved have their own, very specific migration strategy and, consequently, unique long-term population trends. Perhaps not surprising considering the large, interspecific differences in their feeding ecology.

Chapters 2 to 3 introduce the basic methods used for trapping and counting, correcting for mass loss during captivity and the choice of method to standardize body mass for structural size differences. Chapter 4 describes the bivariate statistical method (POSCON) applied to estimate the proportions of wader populations staging and wintering in the Wadden Sea if these populations are characterized by differences in wing and bill length. The wing and bill measurements of each captured individual are confronted with the bivariate distribution of birds of known breeding origin (usually measurements of museum specimens corrected for shrinkage). POSCON estimated confidence intervals of posterior probabilities, in case of waders, without knowledge of the prior probabilities, the 'typicality probabilities'. That is, how typical an individual wader is for one or more populations or subspecies of interest. Because the aim of the author is to estimate the relative proportions of populations staging in the Wadden Sea, an optimization procedure of a maximum likelihood function is applied. Although this method also provides estimates of the reliability of the relative population proportions, these estimates are not presented, simply because they are relatively large.

The trend analysis of wintering waders in Chapter 5 shows that the wintering number of most species have increased over the last three decades in reaction to milder winters. A surprisingly simple result considering the recent, supposedly man-induced, changes in the Wadden Sea. The seasonal changes in numbers, however, show that peak number of most waders occur in August–September. Chapters 6 and 7 show that in this period most juveniles stop-over in annually varying proportions and virtually all twelve species are in primary moult. Starting dates of this time and energy demanding physiological process are (again) different for most populations of the twelve species considered and

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probably related to the specific migration constraints of each population. The absence of any correlation between productivity and wintering numbers is remarkable but perhaps not surprising as the author showed that these numbers are highly correlated with winter temperature.

One of the most intriguing results in this thesis is the observation that in most populations and species (except Redshank *Tringa totanus*) the proportion of primary moulting birds with relatively low weights and large gaps (Grey Plover *Pluvialis squatarola*) is much higher on the islands ('moult resorts'). The coastal sites are characterized by heavier birds preparing for departure to West Africa and smaller proportions of birds in primary moult ('highway'). It would be interesting to see if this pattern can be extended to juveniles who do not moult their primaries and mainly stopover to prepare for further migration. Lower proportions of juveniles would be predicted for the island 'moulting resorts' and higher proportions for the mainland 'highway' as has been found in Dunlin *Calidris alpina* (van der Have *et al.* 1984, in: Evans *et al.*, Cambridge University Press, pp. 160–176). Chapter 8 shows that, indeed, juveniles of most species build up sizeable energy reserves in autumn. Body mass patterns in adult waders again show considerable variation among species, which is primarily determined by the timing of primary moult in autumn and departure in spring.

Chapter 9 presents the composition of wader populations according to their presumed breeding origin as estimated with POSCON. The results generally confirm previous ideas about the populations present in the Dutch Wadden Sea based on recoveries and timing of migration. It is encouraging that 25 out of 34 birds with known breeding origin (five species) were assigned to the right subspecies.

Frustrating perhaps for policy makers, but good scientists generate more questions than they resolve, as is the case with this thesis. How can we understand what causes waders migration strategies to be so different among all populations and species using the Wadden Sea? Is it mainly an adaption to the spatial and temporal constraints induced by breeding locality? Or predominantly shaped and influenced by interspecific competition in habitats like the Wadden Sea during post-breeding periods when densities are high? Evidently, the study of migration strategies is currently hot among behavioural and evolutionary ecologists. On the other hand, increasing human use of intertidal habitats of the Wadden Sea area makes an ecosystem approach more urgent, which lacks scientific attention in recent years.

Two major, hidden assumptions of the biometrical analysis of wader populations are apparent in this thesis: size variation in each considered population is (a) stable over the thirty year study period and (b) it is not related to the individual choice by staging waders of spatial and temporal characteristics of the intertidal Wadden Sea. Both assumptions are likely to be not true and challenge some of the conclusions of this thesis. For example, it is concluded that the estimated proportion of nominate Dunlin has decreased, while the proportion of the subspecies *centralis* has increased over three decades. An alternative explanation could be that the Dunlin population staging in the Wadden Sea has become bigger due to some unknown selection pressure. I would welcome further integration of monitoring temporal and spatial information of numbers, moult, body condition and size variation of all wader populations involved. As recommended by Meinte Engelmoer, these studies would be much helped by simple molecular techniques to sex waders during capture increasing the accuracy and precision of the bivariate methods as presented in this thesis. The fact that wader monitoring (trapping and counting) in one of the most important wetlands in the world is after thirty years still predominantly a volunteer affair clearly illustrates 'institutional failure' in governing the Wadden Sea (Lawton 2007, J. Appl. Ecol. 44: 465–474). Meinte Engelmoer's thesis is another landmark publication in our understanding of the Dutch Wadden Sea. It provides a standard how to utilize simple size measurements in monitoring programs and generates a wealth of questions about the function and importance of the Wadden Sea for waders.

*Tom van der Have, Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB Wageningen, The Netherlands*
*(Tom.vanderHave@wur.nl)*

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