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.

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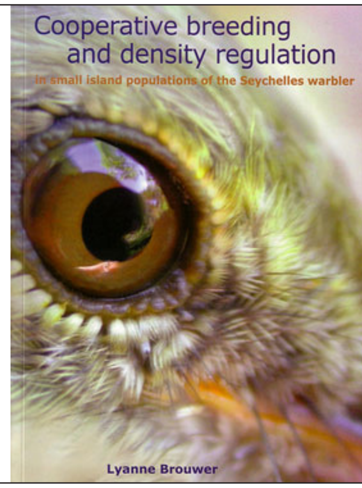

Besides being an excellent piece of work, this thesis should be best considered as a fine illustration on how to combine conservation management with fundamental science. Brouwer's main topic concentrates on one of the most essential questions in population ecology and examines the factors that determine 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.

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) 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.

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