General discussion: metapopulation dynamics and conservation applications

Rosemarie Kentie
European landscapes are the results of millennia long human activities, and consequently hardly any untouched wilderness is left (Fuller 2012). Therefore, the definition of nature may be different for European citizens than for citizens of other continents. Especially in the Netherlands, which is one of the most densely populated countries in the world, the vast majority of the landscape is man-made. Yet, the Netherlands is an important stronghold for breeding black-tailed godwits: 85% of the west-Atlantic flyway population (*Limosa limosa limosa*) breeds exclusively on its man-made agricultural grassland. This makes the Dutch greatly responsible for the wellbeing of this species in this flyway. However, in concert with rapid agricultural intensification of these grasslands in the last decades, the population declined and now a quarter of what was breeding here in the 1970s has remained (Box A).

Already in 1903 Jac. P. Thijssen, one of the founders of Dutch ornithology, warned about the danger of early mowing, by hand-held scythes, and the possibility of decapitating late-breeding adults (Thijssen 1903). Later, Haverschmidt (1963) wrote that the improvement of agricultural land may form a threat to the godwits: the transition to mechanically mowing and the advancing mowing dates may become a ‘formidable danger’. For perspective, this was the time when the Dutch godwits were flourishing, and did not show a decline yet. Despite these early warnings, the numerous agri-environmental schemes set up to conserve nature on agricultural land when the population decline became apparent, have not stopped the population decline (Kleijn et al. 2001, Schekkerman et al. 2008, Verhulst et al. 2007).

Our main goal was to investigate and to advance our knowledge on metapopulation dynamics in a fragmented landscape based on empirical data. In this thesis we have examined the role of modern, intensively used agricultural land and the more traditional herb-rich meadows on the metapopulation dynamics at a broad spatial scale. More specific, we wanted to identify whether the population breeding on herb-rich meadows was a source and the population on agricultural monocultures a sink, and whether the population can maintain itself. If not, what can be changed so that godwits can prevail in modern times? In this synthesis we put the focus on conservation.

**ACCURACY OF THE MEASUREMENTS**

Demographic analyses depend greatly on empirical models, most of which are data-hungry. Furthermore, prediction derived from demographic models are only as robust as the data and parameter estimates upon which they are based. Both the number of sample years and the number of individuals used for calculations affect the accuracy of the estimates, but also the possible variance of vital rates caused by environmental variation (Beissinger & Westphal 1998, Doak et al. 2005). How well does our demographic analyses fit reality?

In Chapter 6 we validated predicted population size, based on demographic estimates, with observations of breeding pairs in the field, and although the comparison only involved five years, the correlation coefficient was high for the total population ($r = 0.95$).
However, when comparing estimated and counted numbers, there was an overestimation of the population growth (Fig. 7.1). This can be the result of several factors. First, we counted during the pre-breeding phase and may have left out late arriving individuals, then the prediction is actually more accurate than shown in Fig. 7.1. Secondly, model predictions were based on several assumptions: a) constant dispersal rate over the years, b) apparent survival probabilities approximate true survival probabilities, although apparent survival could only underestimate true survival and therefore would lower predicted counts instead, c) no correlations between vital rates, which would slightly overestimates growth rate (Doak et al. 2005), d) no breeding propensity (all pairs started to breed), which would lower predicted population size, e) habitat quality within monocultures and meadows is homogeneous, f) no immi- and emigrants from and to outside the research area, and g) no density-dependence (which could be positive, negative, or both (Kim et al. 2009)). We simply had to confine ourselves to these assumptions, because we lack in the understanding of most of these processes. At this point we like to note that building too complex models may also lead to unreliable outcomes because of additional uncertainties in parameter values, while simpler models are often easier to use and understand (Beissinger et al. 2006). We think that we included enough realism and that our predictions are of the most accurate as possible, but at the same time we must realize that we might have slightly overestimated population size.

**LOW CHICK SURVIVAL**

First year survival is the key demographic parameter regulating population size (Chapter 6). Variation in first year survival is likely caused by variation in the pre-fledged stage (Chapter 4, Schekkerman et al. 2009). Agricultural monocultures proved to be a bad place.
for a godwit chick to grow up (Schekkerman et al. 2008, Chapter 4): chicks born on monocultures had a 2.5 lower chance to survive until the following year than chicks born on meadows (Chapter 4). They could have died from starvation, taken by a predator, or killed during mowing. Kruk et al. (1997) estimated that in 1990 of all chicks hatched outside a ‘meadowbird reserve’ 5–21% were being killed during mowing. In 1990, median mowing date was around 20 May (Kruk et al. 1996), which coincided with the pre-fledging stage of the chicks (Fig 7.2). However, median mowing dates depend on spring temperature, and have continued to advance over the years (Kleijn et al. 2010).

In our study area median mowing date varied between 4 May in a year with a warm spring (2009) and 30 May in a year with a cold spring (2013). In years with a warm spring, such as 2009, 2011 and 2014, the start of mowing on grassland monocultures occurred before the majority of potential chicks (assuming that every egg will hatch and every chick would fledge 25 days after hatching) would be present (Fig. 7.3). Only in years with a cold spring, such as 2010 and 2013, mowing of monocultures happened during the potential presence of pre-fledged chicks. Nevertheless, the highest measured survival of young hatched on monocultures was in 2010 (Fig 6.1). We could not distinguish differences in return rates for chicks hatched early (< 15 May), halfway (> 15 May and < 25 May) or late (>25 May) on monocultures (Fig. 7.4).

On herb-rich meadows, however, mowing started when between 24% (2009) and 49% (2013) of the chicks had not yet fledged (Fig. 7.3). Thus, in most years chicks on herb-rich meadows faced a higher risk of being killed by mowing machines than chicks on monocultures. This is remarkable, because the majority of herb-rich meadows are especially managed for meadow birds. The return rates of chicks hatched late on meadows, and were in the pre-fledging stage on 15 June when the majority of meadows were mown, were 30% lower than return rates of chicks hatched early or halfway (Fig. 7.4).

Although lower return rates of later hatched chicks could have been caused by mowing fatalities, other factors could not be excluded. For instance, there could be indirect effects of mowing, such as lower food availability and higher predation rates. But it is
Figure 7.3 We used hatching date per nest to calculate presence of pre-fledged chicks on agricultural land (N 2009 - 2014 = 372; 373; 227; 397; 547; 538). We assumed that every egg hatched and that every chick fledged 25 days after hatching. A presence of 0.8 therefore indicates that potentially 80% of the chicks, young and old, were in the pre-fledging stage. Hatching date on meadows was on average 2 days earlier, but the distributions were otherwise alike, and therefore we lumped the two categories together. Chicks could move from monocultures into meadows and the other way around anyways. We checked 43 randomly chosen monocultures and 16 randomly chosen meadows on a daily basis. Because not every year the parcel was mown (it could be grazed or used as arable field), sample size for monocultures were 33, 36, 31, 32, 33, 38 for 2009 to 2014 respectively, and for meadows respectively 12, 15, 14, 13, 16, 16.
also possible that late breeding godwits are of lower quality, because their individual quality is lower (Verhulst et al. 1995), or because they are energetically constrained, and therefore produce lower quality chicks or are worse parents. On the other hand, Kruk et al. (1997) estimated that ~36%, a comparable percentage, of the chicks present on fields about to be mown would be killed when none of them were saved by farmers. In our study area in our time, chicks were sometimes rescued as well (on monocultures and meadows) by farmers who pay attention to wildlife, or by volunteers of local bird organisations which place flags on meadows the day before mowing to scare godwit families away (as described by Kruk et al. 1997). This, however, was not happening at the large scale.

In most of the recent years, on monocultures mowing machines may pose less of a direct threat for pre-fledged chicks than they did 20 years ago. Yet, indirect effects of mowing may have influenced survival probabilities on monocultures. Food availability is lower on mown fields than on fields where grass is available (Schekkerman & Beintema 2007), and, on fields with regrown grass, insect abundance may be high but insect size is smaller compared to herb-rich meadows (Kleijn et al. 2010). Older chicks are dependent on larger prey (Schekkerman & Boele 2009) and may therefore experience too low an energy intake. In Chapter 4 we indeed showed that chicks born on monocultures had a lower growth rate than chicks on meadows, but due to low sample sizes we could not distinguish between years. In 2013 and 2014 we recaptured enough chicks on monocultures to compare growth in these two years, where 2013 had a cold spring and fields were mown late, and 2014 had a warm spring and fields were mown early (Fig. 7.3). If indirect

![Figure 7.4](image-url)
effects of mowing would be present, we expect that the surviving chicks would grow less
well on monocultures in the year with early mowing (2014), than in the year of late
mowing (2013). We compared the condition index (observed age-dependent mass /
expected age-dependent mass derived from Beintema & Visser (1989)) for chicks recaptured
on monocultures and meadows. As expected, we found that the condition index of
chicks caught on monocultures in 2014 was lower compared to chicks caught on
meadows in 2014, and from chicks caught on monocultures in 2013. In contrast, the
condition index of chicks caught on monocultures and meadows in 2013 was similar (Fig.
7.5). Foraging conditions, which consists of food availability and time spend foraging,
seemed thus only inferior on monocultures in 2014, of which most were mown during the
chick rearing period. The similar growth rate in 2013 suggests that food conditions on
unmown monocultures may either be comparable to herb-rich meadows, or the slow
growth in this particularly cold spring may have increased herb richness and structure in the field, which in turn positively affected food conditions.

Chick predation (Schekkerman et al. 2009) and harsh weather conditions
(Schekkerman & Boele 2009) are other factors affecting chick survival. Both may interact
with a lower body condition: hungry chicks may take more risks (Swennen 1989) and
chicks in an already low condition may suffer more from harsh weather. Moreover, chicks
on mown fields lack sufficient cover, making them more vulnerable for predators. Thus, in
order to increase chick survival rate, mowing must be postponed further. Especially fields
that are being subsidized for meadow bird conservation should be mown at least after 1
July. However, in years with a warm spring, grass on intensely fertilized monocultures
and meadows often grows so dense that chicks are unable to walk through it, and instead
they walk on top of it (pers. obs.). This will increase predation rate, and probably also
lowers intake rate. The lower part of the grass starts to decompose, and this grass
becomes economically unprofitable when delaying mowing. A solution would be to lower
fertilizer input.

Figure 7.5 The condition index, which is the observed age-dependent mass divided by the
expected age-dependent mass (from Beintema & Visser 1989), for chicks recaptured on monocul-
tures and meadows in 2013 and 2014. Identical letters (a and b) indicate non-significant differ-
ences between groups (ANOVA, Tukey post-hoc

test, p < 0.05). Sample sizes are in 2013 respec-
tively 27 and 42 for monocultures and meadows
respectively, and in 2014 35 and 13 for monoco-
tures and meadows, respectively.
PREDICTED POPULATION TRENDS

With the estimated demographic parameters it is possible to predict future population size. In a study on Orchids it was possible to make a reasonable long-term prediction, which was eight lifespans ahead (Schödelbauerová et al. 2010), however, the environment was more or less stable in the 13 study years. In another study on the Montserrat Oriole (Icterus oberi), where demographic rates were correlated with environmental factors, such as rainfall, the future prediction of population size became highly uncertain (Oppel et al. 2014). Yet, these predictions helped to evaluate possible scenarios of the strength of decline, how urgent action should be taken, and about the relative merits of various conservation options (Beissinger & Westphal 1998).

We predicted likely scenarios of population trends for the next 100 years using the estimations from our detailed demographic rates presented in Chapter 6 with a stochastic variance model. We included yearly variation caused by environmental and demographic stochasticity, by using for each year a randomly chosen set of estimates drawn from the parameter distributions based on mean and SE. Sample error was included by calculating 500 trajectories. With the estimated vital rates, the godwit population will slowly decrease (Fig. 7.6A). This outlook is less grim than the previously predicted extinction within 100 years based on a smaller set of demographic traits within the same study population (Schroeder et al. 2009). However, there are concerns on how effective demographic stochastic population models can predict extinction (Beissinger & Westphal 1998). Although our measurements may be accurate, we might have missed important demographic rates and relationships. For instance, we have not included breeding propensity, the probability that each individual will actual breed in a given year. Skipping a year is apparent in many species, especially in longer lived species (Bruinzeel 2006, Frick et al. 2010, Kendall et al. 2003, Reed et al. 2004). We therefore included breeding propensity to assess the effect on growth rate (Fig. 7.6B). With a breeding propensity of 90%, the population size would actually decrease much faster.

From our population study we could investigate the success of different management actions for stabilizing population sizes, or to achieve a certain level of population growth. In Chapter 6 we have shown that chick survival explained most of the variation in population growth rates. Therefore we focussed on measures affecting productivity, and thus measures which can be taken in the breeding area, although many more scenarios should and could be investigated. A logical measure would be to postpone mowing on herb-rich meadows from 15 June to 1 July, as most of these meadows are often already managed for breeding birds. We assumed that direct or indirect mortality rate of pre-fledged chicks due to mowing is 35%, based on the above analysis of return rates and on the findings of Kruk et al. (1997). We used the average rate of 38% of chicks that had not fledged at 15 June (Fig. 7.3). Moreover, we assumed that chicks did not leave the habitat type on which they hatched. When mowing is postponed, the total population will grow until the carrying capacity is reached (Fig. 7.6C). Because we have not included density-dependent effects, there is no limit of godwit pairs. This is likely to kick in at some point. Still, this
The exercise illustrates that postponing mowing on herb-rich meadows would likely be an effective management strategy, given that mowing indeed kills a great proportion of pre-fledged chicks.

In Chapter 6 we have shown that dispersal caused a ‘leakage’ of godwits from sources to sinks. Closing this leak would be another way to stop the decrease in population size. With an increase of 20% of dispersal from monocultures to meadows and a similar decrease of dispersal from meadows to monocultures, the population would be stable (Fig. 7.6D). One way to reach this is to make monoculture grasslands less attractive. Stopping protecting nests would probably not help, as we could not find a relationship with nest success and dispersal (Chapter 5). Instead, increasing the area of herb-rich meadows may help, or a different, perhaps more fine-grained, spatial arrangement of the

**Figure 7.6** Predicted future population size where the thin lines represent 50 stochastic population trajectories. The bold line is the averages based on 500 population trajectories. (A) shows the prediction based on the known demographic parameters (Chapter 6), (B) shows the prediction when including a breeding propensity of 90%, (C) shows the prediction when mowing in herb-rich meadows is postponed until 1July, assuming that mowing kills 30% of the present pre-fledged chicks, and (D) shows the prediction when dispersal from monocultures to meadows increases with 20% and from meadows to monocultures decreases with a similar amount.
herb-rich meadows within the monoculture so that dispersing individuals from meadows would easier settle in another meadow area. However, this needs further investigation and we have made a start in 2013 when we included the Skriezekrite Idzegea as part of our long-term demographic study area (Chapter 4).

Our models lacked any density-dependent feedback loops that either diminish declines in smaller populations or prevent unlimited growth in large populations (Lack 1954), or in case of an Allee effect, accelerate declines at low population sizes (Courchamp et al. 1999). Although density dependence must be important in almost any population where the carrying capacity does not fluctuate drastically, long time series are needed to find support for this (as in Lok et al. 2013b), and we were unable to consider it in our limited time series. Density dependence can affect survival (e.g. Lok et al. 2013b), reproduction (e.g. Bretagnolle et al. 2008), and/or dispersal (e.g. Kim et al. 2009). It is still an open question whether densities in the meadows at the moment are high enough for negative competitive effects to operate. For some individuals, dispersal from meadows to monocultures could be the best of a bad job, if they would have performed even worse when attempting to breed in meadows. We do not consider this likely, as we found that young birds, the ones with the highest dispersal rates, were equally able as older birds to select high-density breeding areas (Chapter 5), but then this raises the challenging question why individuals do still disperse from the high to the low quality habitat. Is this just a matter of maladaptive habitat choice? Could there be an inborn tendency to disperse to lower density areas, when food densities at the time of settlement do not differ too strongly? And would there be a lower density at which this dispersal to the low quality habitat stops naturally, and thereby allowing the population in the high quality to grow again? These are questions that need to be addressed to even better predict how populations in such a fragmented landscape can be managed.

In contrast to our study population, the Icelandic black-tailed godwit, Limosa limosa islandica, mainly breeding on Iceland, increased in population size: from ~2,500 individuals around 1900 to ~75,000 individuals at present (Gill et al. 2007). The growing population expanded into breeding and wintering habitat of poorer quality (Gunnarsson et al. 2005), which suggests that density-dependent effects are operating in this population. It might therefore be interesting to investigate density-dependent effects on dispersal decisions and vital rates, and compare these with the similar rates of the declining Dutch population. Moreover, it would help to predict the course of the population growth, may future Dutch godwit conservation turn effective.

**MANAGEMENT IMPLICATIONS**

In Chapter 6 we showed that populations breeding on herb-rich meadows were in most years a source. Nonetheless, the results presented in this thesis demonstrate that we urgently have to change currently accepted conservation strategies. With our estimates of the most important demographic rates, we expect that the future godwit population would continue to decline (Fig. 7.6A), especially when considering that we would most
likely overestimated population growth (Fig. 7.1). When we predict future population size under different scenarios, it becomes apparent that postponing mowing on herb-rich meadows until 1 July will produce positive effects (Fig. 7.3). However, if chick food availability and profitability are decreasing during the season, the positive effects of later mowing will be reduced. Especially if seasonal food peaks advances with global climate change (Both & Visser 2001), and this needs further investigation. However, because the majority of herb-rich meadows are already part of a high-level conservation scheme, and particularly managed for breeding birds such as godwits, postponing mowing seems to be a feasible, and also logical, step.

Recently, the Dutch government formulated plans to focus conservation of meadow birds in core areas, with the idea that concentrating efforts on a limited area is more effective than dilute efforts over a large area (Melman et al. 2011). Indeed, it seems quite illogical to spend conservation money in areas where no birds are breeding. The proposed set-up of core areas is to assign existing good quality areas which have a minimal size of 100 ha, with a surrounding buffer zone of a kilometre wide where less strict management rules are applied (Melman et al. 2011, Teunissen et al. 2012). However, the fact that dispersal distances of young godwits are in general larger, and, especially young, birds may not start to breed in the designated areas, should not be overlooked (Chapter 5). Moreover, when production of offspring in these core areas will be comparable to the production of offspring in herb-rich areas in our study, would result that abandoning all protection measures outside the core areas may even harm the metapopulation more. We need to invest in a better knowledge on settlement decisions of young and adult godwits to be able to prevent leakage to sink areas, and thus to assure the success of the core area management plan.

When individuals select poor quality habitats over high quality habitats, a phenomenon which primarily happens in human-altered landscapes (Battin 2004), assessing habitat quality by local densities or population trends overestimates habitat quality of sinks and underestimates habitat quality of sources (Chapter 6). Only monitoring population trends might lead to wrong conclusions, we therefore must monitor demographic rates, even though this means a lot of effort. Previous agri-environmental schemes, which has cost billions of euros of subsidies (Kleijn et al. 2011b), were not successful in halting the population decline. To assess the success of the ‘core area’ conservation plan of the government, vital rates should be monitored, and the conservation plan should be adjusted when these vital rates prove to remain insufficient.

Black-tailed godwits also use agricultural land outside the breeding area: rice fields in Iberia (Lourenço et al. 2010, Márquez-Ferrando et al. 2014) and in West-Africa (Hooijmeijer et al. 2013). Due to the political interest of agricultural land, and the need to feed the growing human population, it is likely that the agricultural environment will continue to change. Any changes agricultural practices in these wintering and staging areas may influence adult survival, the second most important vital rate explaining population growth, and possibly also post-fledging survival. Consequently, to be able to notice changes in vital rates, and to predict the effects it may have on the metapopulation size, we must continue to monitor the godwit population.