

Phenology and habitat selection of Black-tailed Godwits (*Limosa limosa limosa*) in south-west Friesland (the Netherlands)



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Abstract

The population of continental Black-tailed Godwits, *Limosa limosa limosa*, has steadily declined since the 1980's. Agri-environment schemes (AES) have been implemented to stop the decline, but have proven ineffective. This study looks at habitat phenology and selection of Black-tailed Godwits during the breeding season in order to understand how agricultural management may affect their reproductive success.

I studied Black-tailed Godwits in the Haanmeer, a small nature reserve in the north of the Netherlands and compared insect density, insect biomass, soil resistance, vegetation structure and earthworm abundance amongst management types. I found that monocultures have a higher soil resistance compared to herb-rich meadows. Differences in insect abundance and biomass were limited, however, with vegetation variables being a better explanation of the differences than weather variables. There was no difference in earthworm abundance between habitat types. Across most variables, differences between individual meadows were much larger than between habitat types. In conclusion, this suggests that soil resistance, and in turn water-levels, and vegetation structure are key characteristics of the habitat of Black-tailed Godwits.

Keywords – *Black-tailed Godwits, Limosa limosa, habitat selection, phenology, agri-environment schemes*

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Introduction

Phenology is the study of periodic events in the life cycle of plants and animals and how climate and other habitat features influence these events. In this study, I measured several features of the breeding habitat of continental Black-tailed Godwits, *Limosa limosa limosa*, throughout the breeding season. By doing so, I hope to understand how these habitat features change during the season and if they influence the habitat selection of godwits.

Godwit habitat selection is influenced by food availability and predator avoidance (T. Johansson, 2001). Godwits tend to avoid trees, since they are used as vantage points by predators (Green et al. 1990). The effect of food availability on habitat selection is complex, since adults and chicks rely on different food sources. Black-tailed Godwits prefer herb-rich meadows with high water tables and foot drains (Groen et al., 2012). These herb-rich meadows are characterized by over ten different herb and several grass species. On the other hand, "monocultures" support only up to three plant species. Schekkerman and Beintema (2007) found that herb-rich meadows harbor more insects than monocultures until they were mown for the first time. Broods hatched in monocultures also moved large distances to these herb-rich meadows after the monocultures were mown, suggesting that insect availability is an important factor influencing habitat selection. Water tables are also important, as they influence soil penetrability, which is critical to the ability of adult godwits to feed on worms and other soil invertebrates (Smart, Gill, Sutherland, & Watkinson, 2006). Adults feed on worms living in the soil, at least in part explaining the importance of soil penetrability and, therefore, water tables.

Soil and vegetation characteristics also influence godwit breeding densities. On the

herb-rich meadows, soils of sandy clay loam and sandy clay were preferred as nesting habitat (Groen et al., 2012). Soil type was not correlated with breeding density on the monocultures. Johansson (2001) also found that plant species surrounding nest-sites were an important predictor of nest placement, as nests were associated with plant species that grow in fertile, mesic habitats. Finally, a study of godwits breeding in Denmark found that godwits preferred meadows with a short growth plant community (Laursen & Hald, 2012).

About 40% of the total European population of Black-tailed Godwits breeds in the Netherlands (Roodbergen, Klok, & Schekkerman, 2008). The Dutch population peaked at 125.000 breeding pairs in 1975 and has decreased rapidly ever since (Schekkerman & Beintema, 2007). In 2004 the population was 62.000 breeding pairs (Schekkerman, Teunissen, & Oosterveld, 2008). In the Netherlands, most breeding pairs are found in monocultures used for dairy farming (Groen & Hemerik, 2002). As highlighted in the sections above, this is not the preferred habitat of Black-tailed Godwits –suggesting a lack of available suitable habitat– and may contribute to the recent population decline.

Several other hypotheses have been put forward to explain the recent decline in the Dutch population. Agricultural intensification is likely one of the main reasons for the population decline. The first mowing of the meadows now occurs earlier in the season than it did 50 years ago, because of increases in spring temperature due to global warming, and changes in agricultural practice (Kruk, Noordervliet, & ter Keurs, 1996). Godwits have adapted to this change in mowing date by arriving earlier at the breeding grounds, but the hatching date has not advanced as much as the mowing date (Kleijn et al., 2010).

Godwit chicks appear to be especially vulnerable to mowing date. Mowing causes mortality and reduces cover, which in turn increases predation, and reduces food availability (Schekkerman & Beintema, 2007; Schekkerman & Boele, 2009). Development is retarded on monocultures when compared to herb-rich meadows (Kentie et al. 2013). In conclusion, mowing is likely having an effect on reproductive success of Dutch godwits.

Other factors likely influence godwit population dynamics as well. For instance disturbance, such as increases in noise levels, can lead to reductions in breeding densities (Gill et al. 2001). Reijnen et al. (1996) highlight that about a third of the area in the north and west of the Netherlands has a noise level above the threshold at which breeding densities decrease. This is also the part of the country that harbors the largest proportion of the godwit population.

Agri-environment schemes (AES) have recently been used as a means to help stop the decline of godwits and other meadowbirds. AES can involve subsidies that compensate farmers for efforts to help nesting meadowbirds: 1) paying farmers per clutch of eggs on their land, 2) postponing mowing until after the completion of the nesting period and 3) mosaic management. Mosaic management can involve nest protection, refuge strips and staggered and delayed mowing (Schekkerman et al., 2008; Verhulst, Kleijn, & Berendse, 2006). Nest protection can consist of marking nests, so farmers can mow around them, and placing nest protectors over nests to stop cattle from trampling them. Refuge strips are uncut strips in early-cut fields that godwits can use to escape from tractors during mowing or as feeding habitat and shelter during brood movement.

The results of AES have been mixed however and in some cases they do not appear to have been effective. For instance, mosaic management did increase productivity of Black-tailed Godwits, but not enough to ensure long-term population viability (Schekkerman et al., 2008). Furthermore, this AES was very sensitive to the prevailing weather, since rainfall forced farmers to postpone mowing on both AES and non-AES fields and led to a very similar timing of the first cut in both habitats. Similarly, Kentie et al. (2013) also found that chick development was slower in monocultures, despite the application of AES. Kentie et al. even suggest that AES might be counterproductive: They found that godwits often chose the wrong habitat, potentially suggesting the existence of an 'ecological trap' when cues for habitat selection (food availability) are decoupled from reproductive success (Kleijn et al. 2001). Meadows with AES did have slightly higher densities of breeding waders in another study (Verhulst et al., 2006). These results were probably caused by changes in the water table and not by AES, itself, though. AES might also be too broad in their aim, as failing to target specific species, which might reduce the effectiveness (Laursen & Hald, 2012). Not all AES have been ineffective though. In Scotland, the application of limited grazing and agricultural operations during the breeding seasons limited the decline of breeding waders. The decline was even reversed in some cases (O'Brien & Wilson, 2011). Interestingly, in this study, a higher water table did not prove beneficial, which contradicts the findings of Verhulst et al. (2006). This suggests that local conditions are very important and that an AES that is beneficial in one location, may not be effective everywhere.

Previous studies have shown that Dutch godwits prefer to breed in herb-rich meadows, but the cues they use to choose between monocultures and herb-rich meadows are not well understood. In this study, I explored the habitat phenology and habitat selection of Black-tailed Godwits. I measured several habitat features in monocultures and herb-rich meadows – insect abundance, soil penetrability, earthworm abundance and vegetation structure – that may affect godwit habitat selection. The densities of breeding godwits were used as an approximation of habitat selection.

I attempted to answer four specific questions:

- How do insect abundance and biomass differ between the two habitats and are they correlated with weather, vegetation structure or other variables?
- How does earthworm abundance differ between the two habitats?
- How does soil penetrability differ between the two habitats?
- Which habitat supports the most godwit nests?

My predictions are:

- Insect biomass is higher in herb-rich meadows and insects are less abundant when it is cold and wet (Schekkerman & Beintema, 2007; Senner & Sandercock, in review).
- Earthworm abundance does not differ between the habitat types (Verhulst et al., 2006).
- Soil penetrability is higher in the herb-rich meadows (Laursen & Hald, 2012).
- More nests will be found in the herb-rich meadows (Kentie et al., 2010).

Materials and methods

Black-tailed Godwits

The Black-tailed Godwit (*Limosa limosa*) is a species of migratory bird. They migrate north from their wintering grounds in Africa to arrive at their breeding grounds in early spring (Groen & Hemerik, 2002). Multiple disjunctively breeding subspecies of godwits exist. The subspecies *L. l. limosa* largely breeds in the Netherlands (Kentie et al., 2013). Dutch-breeding godwits form pairs after their arrival at the breeding grounds. These pairs then find and defend a breeding territory. (Green et al., 1990; Groen & Hemerik, 2002). Between years, godwits are faithful to their former partner and to their nest-site (Groen & Hemerik, 2002; Kentie et al., 2010). Egg laying usually starts in April (Groen & Hemerik, 2002). The average clutch size is four eggs, which both parents incubate (T. Johansson, 2001). The average incubation period is 23 days (Groen & Hemerik, 2002). Black-tailed Godwit chicks are precocial and feed mainly on insects (Schroeder, 2010). Adult godwit southward migration starts at the end of June, with juvenile migration continuing until August (Groen & Hemerik, 2002).

Study site

I carried out my research on a 10000 ha study site situated in south-west Friesland, The Netherlands (see Fig. 1). The site stretches from Makkum in the north to Laaksum in the south and from the IJselmeer in the west to the Frisian lakes in the east (See Kentie et al. 2010 for more details). The area consists mainly of monocultures managed for dairy cattle (Groen et al., 2012). Meadows in these areas often have a low abundance of herb species and are mainly used for grass production in order to support dairy cattle. Some parcels are also used for grazing by livestock, the production of maize, as bulb fields or for other purposes.

A smaller part of the study site consists of more extensively used meadows. Meadows in these areas generally have a higher abundance of herb species. They are managed by nature organizations, such as It Fryske Gea and Staatsbosbeheer. Some farmers also use (part of) their lands less intensively to support meadow birds.

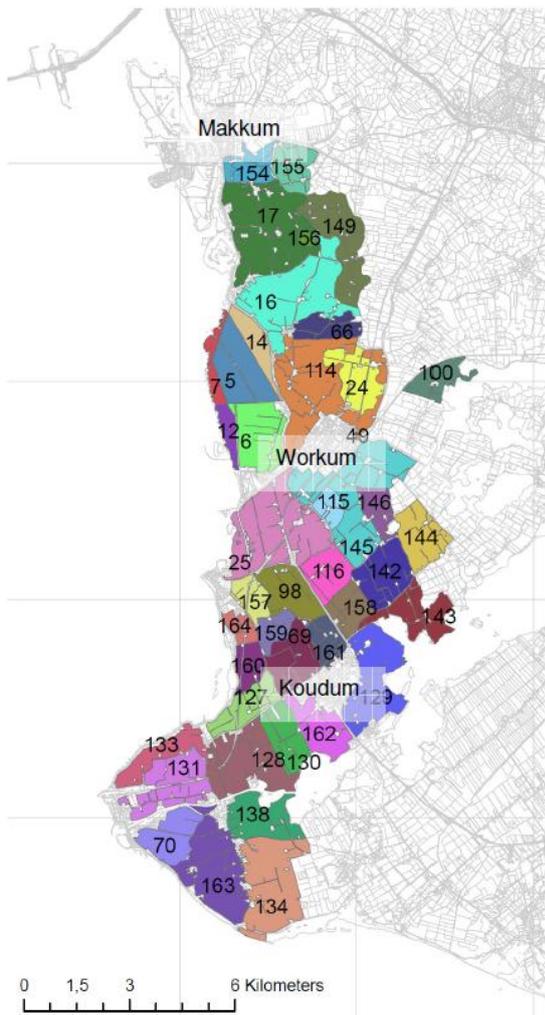


Figure 1: Map of the study site. The Haanmeer is situated at number 69 (Kentie et al., 2010).

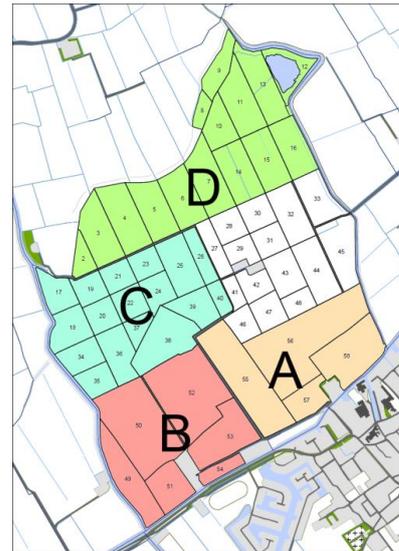


Figure 2: Division of Haanmeer into sectors.

The research area includes several polders, which are subdivided into parcels by farmers. The majority of my research was performed in the Haanmeer, a polder north of Koudum. The central coordinates are 52.92N, 5.44E. This polder consists both of monocultures and herb-rich meadows managed by Staatsbosbeheer as a meadowbird reserve. I divided the Haanmeer into four sectors (see Fig. 2). Two sectors were in the intensively used part of the Haanmeer (sectors A & B), while the other two were in the extensively used part (sectors C & D).

Earthworm density

I measured earthworm density in the Haanmeer. Samples were taken along nine transects. These transects were set out from north to south. A soil sample was taken every 100 meters and was 20x20x20 cm large. The sample was then cut, in the field, into four layers, each 5 cm thick. Layers were immediately placed in plastic bags for subsequent analysis. The length and weight of the worms was measured. The two deepest layers were not used in my analysis, since godwits cannot access worms at these depths.

Earthworm density was measured twice, first in early March, when Black-tailed Godwits were arriving in the study area, and again at the beginning of May, when most godwits had started incubating. However, this second sample was not included in my analyses, since godwits had already chosen their nest sites by this time.

Insect abundance & biomass

I measured the insect abundance along four transects in the Haanmeer. Each transect was comprised of five traps, placed 15 meters apart. Two transects were placed in both monocultures and herb-rich meadows.

Insects were caught using modified pitfall traps, as described by Brown, Lanctot, Liebezeit, Smith and Gates (2013). The traps consist of both below (container) and above (net) ground components. The container was filled with a mixture of water and propylene glycol to preserve insects between visits.

Insects were collected from the traps every day, from mid-March until the end of June. Collection was only interrupted by mowing, when traps were temporarily removed.

Insects were identified to order. The length of the insects was also measured to the nearest mm. This measurement was used to estimate biomass using the formulas given by Benke et al. (2013), Ganihar (1997) and Rogers et al. (1977).

Godwit chicks rarely forage on prey from the ground, such as haplotaxida and julida and thus these taxa were excluded from my analysis (Schekkerman & Boele, 2009). Unfortunately, I was not able to convert neuroptera to biomass due to lacking the correct formula; however, only three neuroptera were caught in total. Furthermore, insects smaller than 2 mm or larger than 9 mm were left out. These insects are either too small or too large to be considered prey items

for godwit chicks (Schekkerman & Boele, 2009).

Soil resistance

Soil resistance was assessed using a penetrometer, which measures the force (in Newtons) needed to push a metal rod into the ground. Measurements were taken every day in the Haanmeer, along the same transects used for sampling insect abundance. I measured penetrability every 5 m along each transect, resulting in 14-15 measurements per transect. Sampling started at the end of March and continued until the end of May.

Vegetation structure

The vegetation structure in the Haanmeer was analyzed along four transects. These were the same transects as used for measuring insect abundance. Five measurements were taken 15 meters apart. A measurement was taken every other day, starting 3 April until 28 June.

A one-meter tall stick was placed a couple of meters from each insect trap. The vegetation was analyzed within a circle with radius 50 cm around each stick. Vegetation height was divided into percentages per range of 5 cm, including bare ground. All plants higher than 50 cm were grouped together (Stewart, Bourn, & Thomas, 2001).

The sticks were marked every 5 cm. Vegetation density was estimated by looking down the sticks and determining which mark, starting from the ground, was the lowest that could be seen.

Nest density

All of the meadows in the Haanmeer were intensively searched for nests. Nest density was calculated for each meadow, based on the number of nests and the size of the meadow. I calculated averages for each sector as well.

Weather data

Weather data were obtained from a weather station of the Royal Dutch Meteorological Institute (KNMI) in Stavoren, about 6 kilometers from the study site. I used average daily temperature, average wind speed and total daily precipitation in my analyses.

Statistical analysis

All statistical analyses were performed using the R statistical program, version 3.0.1 (R Core Team, 2013). Quality of models was judged based on their Akaike Information Criterion score (AIC). Variables were excluded if their omission improved the quality of the model. ANOVA's were used to analyze possible differences between groups. Tukey-HSD test were used as a follow-up test, if there were any significant effects. I used several libraries within the R core program, namely *MBESS*, *arm*, *car*, *lme4*, *MuMIn* and *LanguageR* (Baayen, 2011; Fox & Weisberg, 2011; Kelley & Lai, 2012; Barton, 2013; Bates et al. 2013; Gelman & Su, 2013;).

To analyse earthworm abundance across habitat types, I calculated the number of prey items per field and used an ANOVA to test if there was an effect of sector on earthworm abundance coupled with a Tukey-HSD test to identify which sectors significantly differed.

I used linear model averaging to examine the effect of different variables on the insect abundance and biomass. The independent variables included in the models were sector, mean wind speed, mean daily temperature, total precipitation, vegetation density, percentage of bare ground, percentage of the vegetation above 30 cm and the mean highest height category of the vegetation. All possible combinations of these variables were considered. I averaged amongst all models with a delta AIC ≤ 2 . The importance of each variable was calculated as the sum of Akaike weights over all models including the

explanatory variable. Furthermore, I used a type II ANOVA to examine the effect of each factor.

I also checked the quality of models that just included the weather variables (wind, rain, temperature) or vegetation variables (height, percentage of vegetation > 30 cm, percentage bare ground and average highest vegetation category). I did this to test them as different hypotheses that could explain differences in insect abundance and biomass in the different habitats. I compared the AIC of these models to the AIC of the global-best model.

I used a linear mixed-effect model to analyze the relationship between soil resistance, sector, date, precipitation and nest density. I again used an ANOVA to differentiate amongst categorical fixed effects when the overarching categorical variable was identified as significant in the linear mixed-effect model. I used a Tukey-HSD test as a follow-up test to examine the differences between sectors.

I used linear model averaging in the analysis of the nest densities to test which combination of variables best explained the measured nest densities. Using all models with a delta AIC ≤ 2 , I used model averaging to choose amongst sector, insect biomass and abundance, earthworm abundance, meadow size, percentage of bare ground, the vegetation density, percentage of vegetation above 30 cm and the mean highest height category. I used an ANOVA in combination with a Tukey HSD test to test whether there was a difference between the sectors.

Results

Earthworm density

Sectors differed significantly in their earthworm density ($F = 2.888$, $p = 0.0393$, $df_1 = 3$, $df_2 = 101$). A Tukey-HSD test indicated significant differences between sectors C and D ($p = 0.040$). The mean \pm SE was 3.88 ± 0.71 for sector C and 12.5 ± 3.36 for sector D. Figure 3 shows the density of earthworms in each meadow.

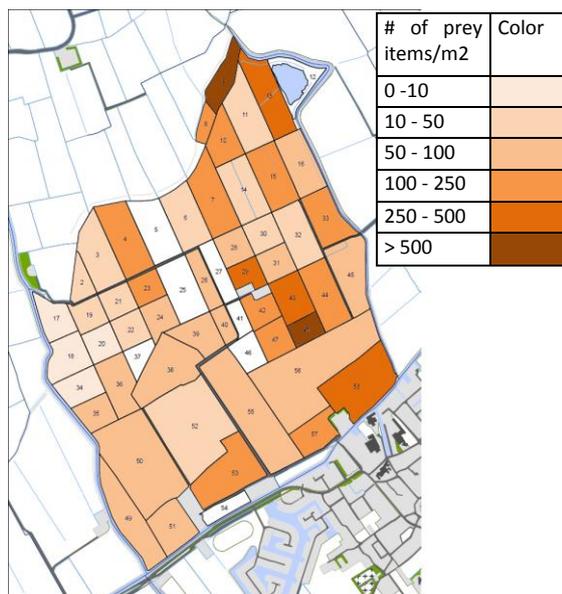


Figure 3: Earthworm abundance in different meadows of the Haanmeer, The Netherlands.

Insect abundance & biomass

Average wind speed, vegetation density, date and percentage of the vegetation above 30 cm were excluded in the final model of insect abundance. Sectors C and D significantly influenced insect abundance, with lower abundances found in these sectors. Average highest vegetation category and average temperature were positively correlated to insect abundance.

The correlation between all variables was smaller than 0.30. Temperature, sector and average highest vegetation category were the most important variables (table 1). The AIC-score of the best model was 760.2. The model just consisting of weather variables had a delta AIC = 1219.5 compared to this model and thus was a much poorer fit. The model that consisted only of the vegetation variables was a much better fit, with a delta AIC of 9.29. The type II ANOVA also showed the significant influence of sector and vegetation height (table 2).

All initial variables were preserved in the final model of insect biomass. Sector C, sector D and date were significantly negatively correlated with biomass. Vegetation height and average temperature were positively related to biomass. All other variables were not significant (Table 3). Date, vegetation height and average temperature were the most important variables (table 3). The AIC score of the best model was 513.9. The model that consisted of weather variables had a delta AIC of 823.52. The model that consisted of the vegetation variables had a delta AIC of 18.92.

The mean \pm SE for each sector were: (A) 2.12 ± 0.21 ; (B) 1.69 ± 0.14 ; (C) 2.04 ± 0.12 ; (D) 1.59 ± 0.11 . A regression of temperature against mean insect biomass over all sectors showed an increase in biomass of 0.08 per degree Celsius ($R^2 = 0.15$). A regression of highest vegetation height against biomass showed an increase in biomass of 0.05 per cm for sectors A and B ($R^2 = 0.22$) and a decrease in biomass of 0.02 for sectors C and D ($R^2 = 0.12$).

The type II ANOVA indicated significant effects of date, average temperature and vegetation height (Table 4). Other factors were not significant in this test.

Coefficient	Importance	Estimate	Std. Error	Adjusted SE	z-value	P-value ≤
Intercept		-0.372	1.417	1.425	0.261	0.794
Sector B	1.00	0.051	0.753	0.758	0.067	0.947
Sector C	1.00	-6.223	0.899	0.906	6.873	0.001 ***
Sector D	1.00	-4.773	0.833	0.839	5.692	0.001 ***
% Bare ground	0.31	0.035	0.031	0.031	1.118	0.264
Mean highest vegetation category	1.00	0.157	0.030	0.031	5.103	0.001 ***
Total precipitation	0.81	-0.162	0.085	0.086	1.886	0.059
Mean temperature	1.00	0.174	0.073	0.074	2.365	0.018 *

Table 1: Average linear model coefficients for factors explaining insect abundance at the Haanmeer-polder, the Netherlands, 2013.

Coefficient	Sum of squares	Df	F-value	P-value ≤
Sector	259.59	3	11.0250	0.001 ***
% Bare ground	7.32	1	0.9331	0.336
Mean highest vegetation category	139.09	1	17.7218	0.001 ***
% of vegetation > 30 cm	0.00	1	0.0004	0.984
Vegetation density	0.05	1	0.0063	0.937
Total precipitation	24.54	1	3.1264	0.079
Mean temperature	25.58	1	3.2591	0.073
Mean wind speed	0.23	1	0.0292	0.864
Date	0.01	1	0.0014	0.970
Residuals	1114.50	142		

Table 2: Type 2 ANOVA results for factors explaining insect abundance at the Haanmeer-polder, the Netherlands, 2013.

Coefficient	Importance	Estimate	Std. Error	Adjusted SE	z-value	P-value
Intercept		546.67	133.162	134.211	4.073	0.001 ***
Sector B	0.58	0.135	0.342	0.345	0.392	0.695
Sector C	0.58	-0.885	0.409	0.412	2.148	0.031 *
Sector D	0.58	-0.862	0.373	0.376	2.291	0.022 *
% Bare ground	0.61	0.024	0.013	0.014	1.740	0.082
Mean highest vegetation category	1.00	0.048	0.016	0.016	2.983	0.003 **
% of vegetation > 30 cm	0.07	-0.011	0.009	0.009	1.214	0.225
Vegetation density	0.25	0.068	0.046	0.046	1.470	0.141
Total precipitation	0.08	-0.030	0.038	0.039	0.79	0.442
Mean temperature	1.00	0.152	0.044	0.044	3.465	0.001 ***
Mean wind speed	0.64	-0.082	-0.049	0.050	1.654	0.098
Date	1.00	-0.030	0.007	0.007	4.065	0.001 ***

Table 3: Average linear model coefficients for factors explaining insect biomass at the Haanmeer-polder, the Netherlands, 2013.

Coefficient	Sum of squares	Df	F-value	P-value ≤
Sector	5.575	3	1.1980	0.313
% Bare ground	2.690	1	1.7346	0.190
Mean highest vegetation category	16.327	1	10.5264	0.002 **
% of vegetation > 30 cm	0.596	1	0.384	0.536
Vegetation density	1.089	1	0.702	0.404
Total precipitation	0.515	1	0.332	0.565
Mean temperature	18.701	1	12.057	0.001 ***
Mean wind speed	4.328	1	2.790	0.097
Date	23.622	1	15.230	0.001 ***
Residuals	220.25	142		

Table 4: Type 2 ANOVA results for factors explaining insect biomass at the Haanmeer-polder, the Netherlands, 2013.

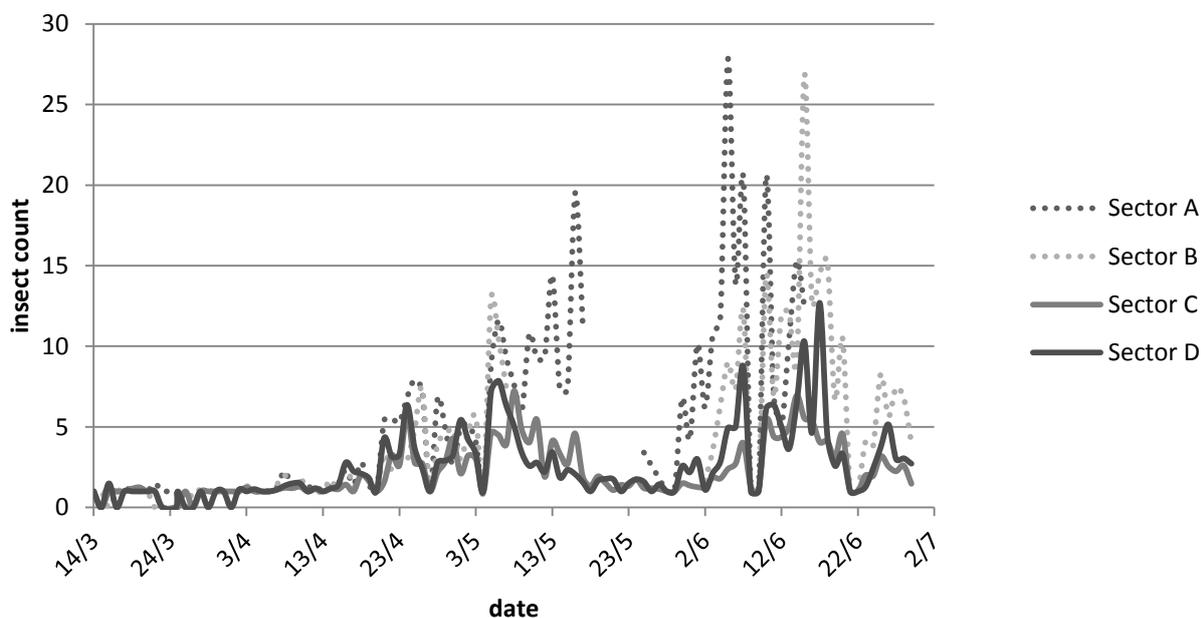


Figure 4: Insect abundance for each sector from half March until the end of June in the Haanmeer-polder, the Netherlands 2013. Gaps are caused by mowing activities in the agricultural meadows.

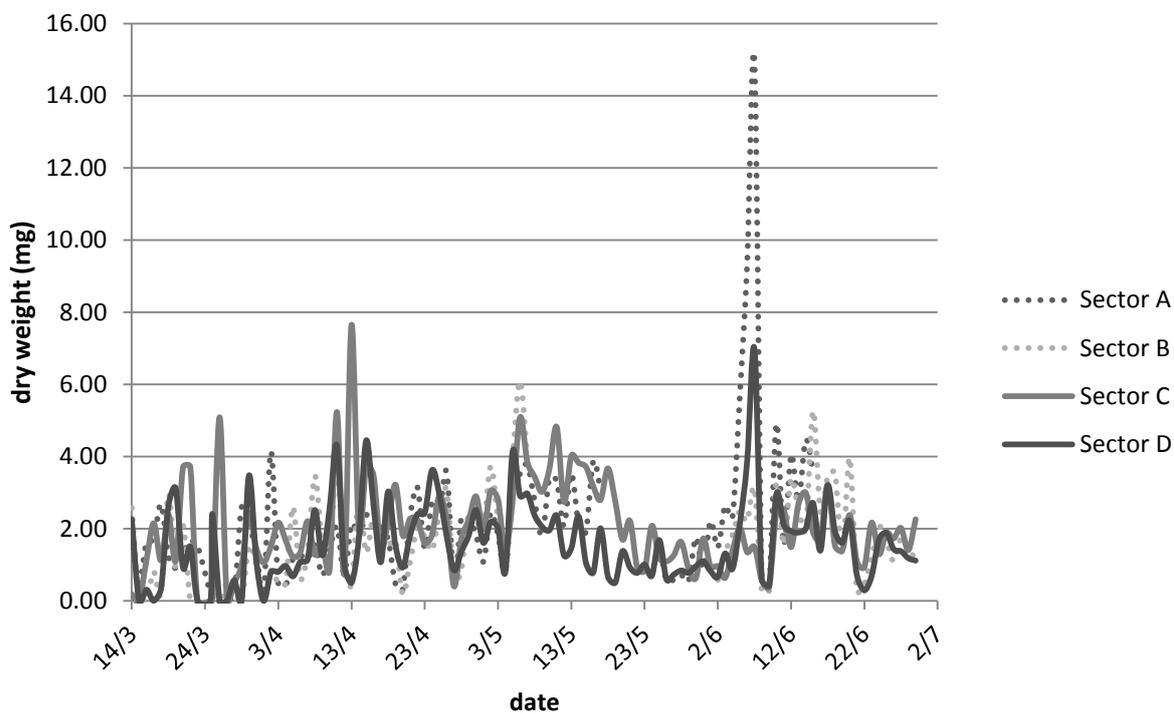


Figure 5: Insect biomass for each sector from half March until the end of June in the Haanmeer-polder, the Netherlands 2013. Gaps are caused by mowing activities in the agricultural meadows.

Soil resistance

Sector, date and precipitation were included in the final model as independent variables. Sectors A, C and D showed significant effects, as well as date. The multiple R^2 for this model was 0.51 (Table 5). As can be seen in figure 6, the soil resistance is lower in sectors C and D. The high values in the beginning can be explained by the fact that much of the ground was still frozen at the time.

The ANOVA indicated that the variable sector had a significant effect on soil resistance ($F = 73.276$, $p < 0.001$, $df_1 = 3$, $df_2 = 159$). Date also significantly influenced the soil resistance. ($F = 5.700$, $p = 0.018$, $df_1 = 63$, $df_2 = 159$). Precipitation did not have a significant effect. The Tukey-HSD test showed that sectors A and B did not differ significantly, nor did sectors C

and D. Sectors A and B did differ from sectors C and D ($p < 0.001$). The linear mixed model indicates the significant effects of sectors A, C, D, date and precipitation. The effect of sample is limited (Table 6).

Nest density

Three factors significantly influence nest density after model-averaging. These were the percentage of bare ground, the soil resistance and the average highest height category. The highest height category was a more important variable (0.43) than soil resistance (0.32) and the percentage of bare ground (0.25) (Table 7). The ANOVA showed a significant effect of the sectors. ($F = 4.469$, $p = 0.009$) The Tukey HSD test showed only a significant difference between sectors B and C ($p = 0.018$).

Coefficient	Estimate	Std. Error	t-value	P-value	
Intercept	$-1.41 \cdot 10^4$	$6.07 \cdot 10^3$	-2.33	0.021	*
Sector B	$-7.03 \cdot 10^0$	$1.98 \cdot 10^1$	-0.36	0.723	
Sector C	$-1.97 \cdot 10^2$	$1.74 \cdot 10^1$	-11.30	<0.001	*
Sector D	$-1.95 \cdot 10^2$	$1.74 \cdot 10^1$	-11.20	<0.001	*
Date	$9.16 \cdot 10^{-1}$	$3.84 \cdot 10^{-1}$	-2.39	0.018	*
precipitation	$-4.79 \cdot 10^0$	$2.61 \cdot 10^0$	-1.83	0.068	

Table 5: Linear model coefficients for factors explaining soil resistance at the Haanmeer-polder, the Netherlands, 2013.

Random Effects				Fixed Effects				
Parameters	Variable	Variance	SE	Variable	Estimate	SE	t-value	$P \leq$
Sample	Ind.	$2.81 \cdot 10^{-5}$	$5.30 \cdot 10^{-3}$	Intercept	$-1.47 \cdot 10^2$	$1.97 \cdot 10^3$	-7.47	0.01
	Residual	$1.41 \cdot 10^4$	$1.19 \cdot 10^2$	Sector B	$6.37 \cdot 10^0$	$6.34 \cdot 10^0$	-1.06	
				Sector C	$-1.97 \cdot 10^2$	$5.60 \cdot 10^0$	-35.18	0.01
				Sector D	$-1.95 \cdot 10^2$	$5.69 \cdot 10^0$	-34.28	0.01
				Date	$9.54 \cdot 10^{-1}$	$1.25 \cdot 10^{-1}$	7.66	0.01
				Precipitation	$-4.87 \cdot 10^0$	$8.50 \cdot 10^{-1}$	-5.73	0.01

Table 6: Linear mixed model coefficients for factors explaining soil resistance at the Haanmeer-polder, the Netherlands, 2013.

Coefficient	Estimate	Std. Error	Adjusted SE	z-value	P-value \leq	
Intercept	0.381	1.242	1.246	0.305	0.76	
Mean highest vegetation height	0.042	0.012	0.012	3.476	0.001	***
Soil resistance	-0.005	0.001	0.001	3.372	0.001	***
% Bare ground	-0.037	0.011	0.011	3.286	0.001	**

Table 7: Average linear model coefficients for factors explaining nest density at the Haanmeer-polder, the Netherlands, 2013.

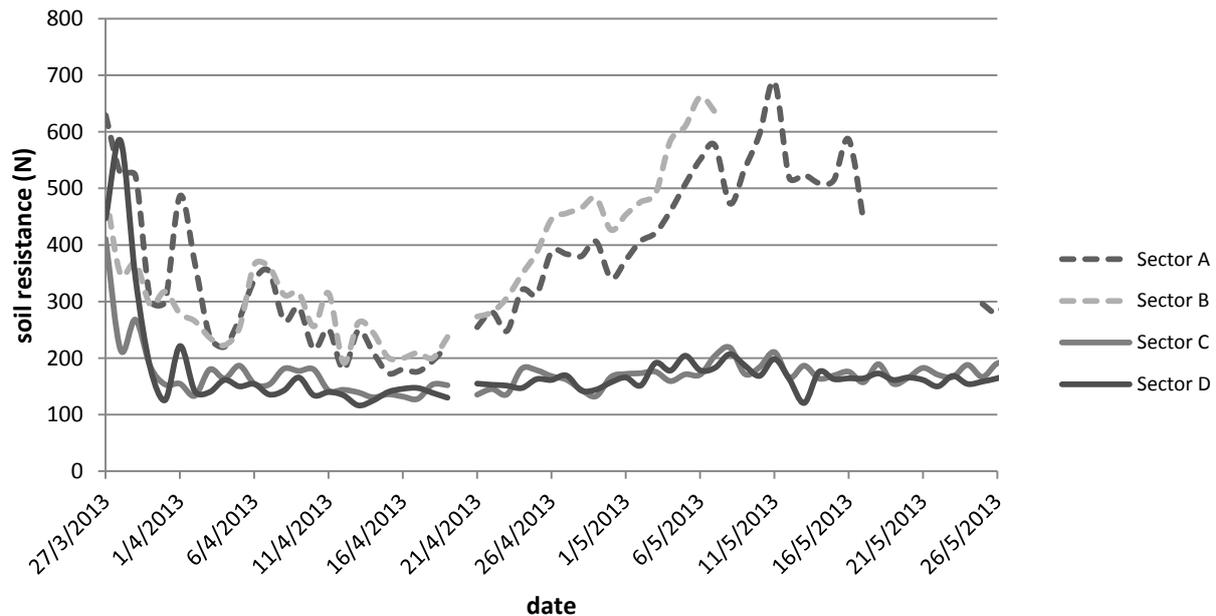


Figure 6: Soil resistance for each sector and precipitation from late March until late May in the Haanmeerpolder, the Netherlands 2013. Gaps are caused by mowing activities in the agricultural meadows

Discussion

My results show that more godwits breed in the nature reserve, compared to the intensified agricultural areas. The main difference between the two habitat types is the soil resistance. This is probably due to a higher water table in the nature reserve. The differences in insect abundance and biomass are limited, although the average size of insects is a bit larger in the nature reserve. Vegetation variables explain more of the differences in insect abundance and biomass than weather variables. The difference in earthworm abundance is much bigger between samples than between the habitat types. It is possible that soil type could explain at least some of the differences in earthworm abundance. From my research, I can conclude that earthworm abundance is not an explanation for the higher density of breeding godwits in the nature reserve.

A few comments about the methods can be made. It should be noted that insects were not collected directly after each cut of the meadow. Other research shows that insect

abundance drops directly after the grass in a meadow is cut (Scheckerman & Beintema, 2007). Because I was unable to measure insect immediately after the meadows were mown, I cannot make statements about the cause of the decline in insect abundance after the cut, although it is probably caused by the cut. The fact that the herb-rich meadows are not cut until mid June could also be one of the reasons why godwits prefer these meadows. The monocultures are cut far earlier in the season. This could mean that food availability is not as reliable in monocultures as in herb-rich meadows. There is some evidence that supports the hypothesis that reliability of food sources is important for habitat selection (Monsarrat et al., 2013).

Furthermore, insect biomass was estimated based on insect length and order. It might be more accurate to take the width of the insect into account as well. Insects of the same order can be of equal length, but not mass. Other methods estimate insect biomass based on head-width (Benke et al., 2013). Benke et al.

show differences in biomass estimate between and within insect orders based on head width. Insect head-width should be included to increase the accuracy of the analysis. Another way to increase the accuracy is to identify insects on family instead of order. Benke et al. (2013) show differences in insect biomass estimates within orders. I am unable to say if changing the method for estimating insect biomass would have affected my results.

Predation is another factor that might limit reproductive success of godwits. Mowing increases the risk of predation, since high vegetation offers cover from predators (Schekkerman et al. 2005; Whittingham & Evans, 2004). The delayed mowing of the nature reserve thus likely decreases the risk of predation. This might also be one of the reasons why godwits prefer this habitat. A study on several shorebird species in Canada highlights the importance of predation (Allen, Gilchrist, Smith, & Smith, 2007). It showed that shorebirds did not prefer habitats where food availability was highest. Instead, predation had the highest effect on reproductive success. Furthermore, Black-tailed Godwits share their nesting habitat with several other bird species, such as the Common Redshank (*Tringa totanus*) and Northern Lapwings (*Vanellus vanellus*). If this coexistence results in higher cumulative nest densities, the predation risk could increase (Martin, 1993). Some meadow birds are able to produce multiple clutches of eggs per breeding season. This also indicates the importance of predation, since high nest predation is associated with an increase in the number of broods (Martin, 1995). Teunissen et al. 2006 investigated chick survival of meadow birds in the Netherlands and found that 60-80% of chicks were lost due to predation. These studies highlight the

potentially significant effect of nest predation on reproductive success.

The importance of predation can be related to my finding that vegetation height was a good predictor of habitat selection of godwits. The increased vegetation height offers cover from predators to godwit chicks. Adult godwits that select meadows with a higher vegetation height might have an advantage, since their chicks are less vulnerable to predation. Therefore, high predation pressure could explain why godwits prefer nesting in areas with a high vegetation height.

Soil penetrability, which is related to groundwater levels, seems to be one of the characteristics of a habitat suitable for Black-tailed Godwits. It is unclear, however, whether raising water tables is beneficial to meadow birds. Schekkerman and Beintema (2007) argue that higher water tables lead to delayed mowing, which is beneficial to meadow birds. Kleijn et al. (2010) add that raising groundwater levels will create open, accessible vegetation for chicks to feed in. In contrast, O'Brien and Wilson (2011) do not find a positive effect of increasing water levels on wader breeding densities, but just of limiting grazing and agricultural operations during the breeding season. They argue that this could be caused by a difference in agricultural management by farmers. The fields on which the water table is raised might be less productive to start with and suffer from gradual reduction of agricultural production, leaving the vegetation on these fields less attractive to waders. The fields on which grazing and other agricultural operations are limited during the breeding season might be more productive and used more intensively outside of the breeding season, creating a more favorable vegetation.

Appropriate timing of mowing practices is undeniably important for reproductive success of meadow birds. The effect of mowing on insect abundance was not accurately measured during this study, but other research shows a decline of insect abundance directly after each cut (Schekkerman & Beintema, 2007). Nowadays, godwit chicks often hatch after mowing practices have already begun, leaving the chicks vulnerable to predation and without their preferred habitat (Kleijn et al., 2010). Postponing mowing on monocultures does not seem to be effective at raising chick survival, since the sward density in these fields becomes too high to allow for efficient foraging by chicks (Kentie et al., 2013). Still, postponement of mowing reduces direct mortality and gives chicks an opportunity to move to more favorable meadows in the area. Postponing mowing could be effective at raising chick survival if there are meadows with a good vegetation structure in the area to which the chicks can move. Johansson and Blomqvist (1996) also highlight the importance of vegetation height in their study on Northern Lapwings, finding that Northern Lapwing chicks foraged more often in areas with a low vegetation height. They add that the agricultural landscape should be varied to accommodate the different habitat needs of wader species during different phases of the breeding season. Kruk et al. (1996) argue that it might be possible to 'fine tune' agricultural management to the peak of hatching. They

were able to predict the peak of hatching based on spring temperatures. They add that postponed mowing on just those fields rich in meadow birds should not be very expensive for the farmer.

The role of vegetation height and structure in wader reproductive success appears to be very complex. On the one hand, high vegetation height offers protection from predators and insect abundance is higher. On the other hand, high vegetation might limit the foraging rates of chicks. It seems that the optimal vegetation should be high enough to offer protection from predators, but, at the same time, open enough for chicks to forage in. How agricultural management can be used to obtain the ideal vegetation characteristics is currently unclear.

In summary, I found that monocultures have a higher soil resistance compared to herb-rich meadows. Differences in insect abundance and biomass were limited, however, with vegetation variables being a better explanation of the differences than weather variables. There was no difference in earthworm abundance between habitat types. Across most variables, differences between individual meadows were much larger than between habitat types. In conclusion, my research suggests that soil resistance, and in turn water-levels, and vegetation structure are key characteristics of the habitat of Black-tailed Godwits.

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