

A Modern Landscape Ecology of Black-Tailed Godwits: Habitat Selection in Southwest Friesland, The Netherlands

Authors: Groen, Niko M., Kentie, Rosemarie, Goeij, Petra de,
Verheijen, Bram, Hooijmeijer, Jos C.E.W., et al.

Source: Ardea, 100(1) : 19-28

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.100.0105>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A modern landscape ecology of Black-tailed Godwits: habitat selection in southwest Friesland, The Netherlands

Niko M. Groen¹, Rosemarie Kentie^{1,*}, Petra de Goeij^{1,2}, Bram Verheijen¹,
Jos C.E.W. Hooijmeijer¹ & Theunis Piersma^{1,2}



Groen N.M., Kentie R., de Goeij P., Verheijen B., Hooijmeijer J.C.E.W. & Piersma T. 2012. A modern landscape ecology of Black-tailed Godwits: habitat selection in southwest Friesland, The Netherlands. *Ardea* 100: 19–28.

For a long time, agricultural areas had considerable ornithological value, an ecological richness which in The Netherlands was epitomised by the term 'meadow birds'. However, over the last half century, agricultural intensification has negatively affected the quality of meadow bird habitats. Here we provide a quantitative characterization of agricultural habitats and their use by Black-tailed Godwits *Limosa l. limosa* in the south-western part of the province of Friesland, The Netherlands, in 2009, to provide a yardstick to evaluate further change. We used groundwater level, vegetation typology, relief in the landscape, the occurrence of foot drains, land use and soil characteristics such as textures and peat to describe the landscape that comprised 43 polders covering 8480 ha. We used a Principal Component Analysis to summarize landscape characteristics and find that much of the habitat variation is explained by a combination of herb richness of the vegetation, the presence or absence of foot drains and groundwater level. The modern agricultural landscape of southwest Friesland consists of 80% of uniform, intensively managed landscape with herb-poor meadows and low groundwater levels, the remaining 20% being taken by remnants of the former herb-rich meadows. The whole study area was searched weekly and Black-tailed Godwits were mapped between arrival and egg-laying. The positive relationship between godwit density and the first PC axis indicates that Black-tailed Godwits preferred herb-rich polders with high groundwater levels and the presence of foot drains. Soil texture was poorly correlated with godwit breeding densities for intensively managed (herb-poor) parcels, but for herb-rich meadows, soils of sandy clay loam and sandy clay harboured the highest densities of godwits. To protect Black-tailed Godwits, areas should have a herb-rich vegetation, contain foot drains and high groundwater tables should be re-established.

Key words: meadow bird, habitat quality, fragmentation, soil characteristic, PCA, habitat selection, bird conservation

¹Animal Ecology Group, Centre for Ecological and Evolutionary Studies (CEES), Centre for Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands; ²Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands;

*corresponding author (r.kentie@rug.nl)

Changes in agricultural methods initially led to a rise in numbers of grassland breeding birds (Bignal & McCracken 1996), called 'meadow birds' in The Netherlands. However, ongoing industrialization of the agricultural landscape across Europe over the last 60 years has led to widespread declines in many species dependent on farmland (Donald *et al.* 2001, Vickery

et al. 2001, Newton 2004, Wilson *et al.* 2004). Agricultural intensification results in a whole range of changes in land management practices designed to increase the productivity of the land (Harms *et al.* 1987, Donald *et al.* 2001, Newton 2004). In The Netherlands, from 1950 to 1970, the amount of fertilizer applied at Dutch dairy farms grew from 50

kg N/ha/year to 400 kg N/ha/year (Bakker & Berendse 1999), although this amount has dropped since 1990 to 200 kg N/ha in 2010 (CBS 2012). Heavier machinery came to replace man- and horsepower and more recently groundwater levels were lowered by replacing canals and foot drains with belowground drainage pipes. Hereby the bearing of the soil increased and so spring manure application could be advanced. Moreover, the soils warmed earlier, thereby speeding up grass growth and advancing mowing dates by more than a month during the last century (Beintema *et al.* 1985, Kleijn *et al.* 2010). The building of roads and paved farm tracks fragmented polders and caused disturbance from traffic and street lights (van der Vliet *et al.* 2010). Consequently, with agricultural intensification habitat is lost, fragmented, and deteriorated, including habitat of a bird endemic to agricultural Europe, the Black-tailed Godwit *Limosa l. limosa* (Beintema 1983, Hötker *et al.* 1991, Gill *et al.* 2008). The numbers of breeding Black-tailed Godwits in The Netherlands have declined from 120,000 pairs in the 1960s (Mulder 1972) to 45,000 pairs in 2004 (BirdLife International 2004), with numbers continuing to decline by more than 5% per year (van Dijk *et al.* 2010). Numbers have also declined elsewhere due to similar causes (Gill *et al.* 2008), but with more than half of the European breeding population of Black-tailed Godwits within its borders (Thorup 2006), The Netherlands still carries great responsibility for their conservation.

To halt the decline of meadow birds, already in 1975 the Dutch government set up reserves managed especially for meadow birds (Beintema *et al.* 1995). Within these reserves, managers try to maintain or restore the landscape typical of 1950–1960. Additionally, in some well-defined areas outside these reserves, farmers can enter into management agreements (Melman *et al.* 2008), either applying Agri-Environmental Schemes (Kleijn *et al.* 2001, Verhulst *et al.* 2007) or mosaic management (Schekkerman *et al.* 2008, Oosterveld *et al.* 2011), usually consisting of postponed mowing dates and restrictions in agricultural activities to enhance the breeding success of meadow birds.

Assessments of changes in both landscape and birds usually suffer from a lack of quantitative landmarks. Our ambition here is to provide such a landmark by quantifying the agricultural landscape in relation to the abundance of Black-tailed Godwits in southwest Friesland, in 2009. This northern part of The Netherlands is well known for the high numbers of breeding godwits. Additional to assessments of future change (see Smart *et al.* 2008 for an example), it can also be

used to help define areas outside of Friesland that have potential to be restored for Black-tailed Godwits.

We used a principal component analyses (PCA) to integrate characteristics that summarize variation in habitat best. As the result of glacial events, the impact of several rivers and, later, the creation of artificial dikes (van Eerden *et al.* 2010), The Netherlands contains various soil types. Soil texture influences earthworm abundance (Lapied *et al.* 2009), the main prey for adult godwits in the breeding period, and affects penetrability of the soil (Green 1988), hence prey availability. Therefore, we also incorporated soil type and texture in our analysis. Next, we investigated habitat selection of Black-tailed Godwits by correlating the density of godwits during arrival and breeding with the PC axes and with soil characteristics.

METHODS

Study area

The study area covers 10,700 ha including villages, canals and open water. The agricultural land covers 8480 ha (79.3%) and stretches from the villages of Makkum (53°03.18'N, 05°25.48'E) in the north, to Laaksum (52°50.59'N, 05°25.16'E) in the south. It borders Lake IJsselmeer in the west and south and consists of 43 separate polders. A polder is a tract of land originally enclosed by embankments known as dikes, forming a hydrological entity. A polder has no connection with outside water other than through water pumps or an artificial water inlet. Water levels and soil textures are not uniform for the whole polder. Parcels are the basic units in a polder and separated from each other by ditches or fences. The studied polders vary in size from 3.3 ha to 248.9 ha with an average of 196.9 ha. The polders include 2284 unique parcels (range 1–158 parcels per polder) measuring on average 7.8 ha (range 1.6–61.0 ha).

Landscape characteristics

We selected seven landscape characteristics to describe habitats in our study area. Four of these were measured in the field by visiting all parcels in the study area in spring and early summer. *Juncus effusus* presence and presence of drainage were scored in 2007, land use and vegetation typology in 2009. These are:

1. Land use. MEADOWS: parcels with predominantly grasses, ARABLE LAND: ploughed parcel for growing maize, tulips, potatoes or other annual crops, or MARSH/WATER: shallow pools in polders and land outside the summer dike (embankment to hold back water).

2. Vegetation typology. Meadows were classified into four categories. HERB-POOR: generally reseeded 'artificial' meadows, 1 to 3 plant species, dominated by high-productive ryegrasses *Lolium* spec., some dandelions *Taraxacum* spec. and stichwort *Stellaria* spec. or arable land with monocultures of corn, potatoes or tulips. MODERATE HERB-RICH: meadows with 4 to 10 species, dominated by different grasses and herbs such as buttercup *Ranunculus* spec., Cuckoo Flower *Cardamine pratensis* and Daisy *Bellis perennis*. HERB-RICH: over 10 species of herbs and several grasses such as Sweet Vernal Grass *Anthoxanthum odoratum*, Crested Dog's-tail *Cynosurus cristatus* and typical herbs for this class such as Ragged Robin *Lychnus flos-cuculi*, Yellow Rattle *Rhinanthus angustifolius* and Water Forget-me-not *Myosotis scorpioides*. BOTANICALLY VALUABLE: species like Marsh Thistle *Cirsium palustre*, orchids and all species from herb-rich meadows. They are in general managed by a nature conservation organisation. To minimize observer bias, data on vegetation typology for this analysis is gathered by one observer (BV).

3. Presence of *Juncus effusus* (Soft Rush). Because it is believed that *J. effusus* alters plant species diversity and species richness (Ervin & Wetzel 2002) and anecdotal evidence suggests that *J. effusus* cover negatively affects the suitability for breeding meadow birds.

4. Type of drainage is determined because it affects potential wetness of a parcel and heterogeneity of the field. Intensively used agricultural parcels have water drained by pipes 50–70 cm under the ground, while these parcels originally drained surface water by foot drains; small channels which are 10–30 cm deep. We scored the presence of foot drains per parcel. The underground drainage system was not always visible, only where drainpipes discharge the water into the ditch, however we believe that all parcels without foot drains were drained by a belowground drainage system.

5. Groundwater levels were obtained from Wetterskip Fryslân. They provided the mean highest groundwater level (MHGL) and the mean lowest groundwater level (MLGL) in the form of a GIS database with a resolution of 25 m, of which we calculated the mean spring groundwater level (MSGL) with the formula: $MSGL = 0.83 \text{ MHGL} + 0.19 \text{ MLGL} + 5.4 \text{ cm}$ (Runhaar *et al.* 1997). We averaged MLGL per parcel.

6. Relief. Variability of the groundwater level per parcel provides information on the presence or absence of relief, the little dips or pools or gradually sloping, old creeks and gullies characterizing these parcels. We calculated relief from the groundwater level map: parcels contained relief if at least 10% of the field

differed more than 50 cm in groundwater level from the rest of the field.

7. Soil types. Data on soil texture was obtained from a 1:50,000 soil texture map (WUR-Alterra 2006). We distinguished seven soils in the study area: (1) loam, (2) silty clay, (3) clay, (4) peat, (5) sand, (6) sandy clay loam and (7) sandy loam. The spatial distribution of the landscape characteristics is shown in Figure 1.

Mapping of Black-tailed Godwits

In 2009, we counted individual Black-tailed Godwits across all parcels twice during the arrival period (16–29 March) and once during early breeding (13–20 April). After 20 April we would have missed the birds that started to incubate. For the arrival period we averaged the counts. We did not count around noon, because during this time of the day most godwits were resting on roost sites. The two weekly counts in the arrival phase were averaged. Densities were calculated per polder and parcel, and expressed as godwits per 100 ha.

Statistics

With agricultural intensification, a whole suite of landscape characteristics is modified. Because these landscape characteristics will be highly correlated, data describing parcel characteristics were combined using principal component analysis (PCA). The purpose of a PCA is to reduce the number of redundant variables to a few uncorrelated principal components. At the parcel level, many of our variables were categorical, while underlying data for a PCA should be continuous. We therefore ran the PCA at the polder level, calculating the percentage of the area per polder of meadows (opposed to arable fields), herb-rich (including botanical valuable) vegetation, parcels with foot drains, parcels with relief and parcels with *J. effusus*. Analysing at the polder level also reduced spatial pseudoreplication. Percentages were arcsine transformed. The mean spring groundwater level (MSGL) was averaged per polder. Because soil is a categorical variable with more than two categories, we could not include soil in the PCA. Two polders were managed as grassy marshlands and one (small) polder was not examined, which left 40 polders for the PCA analyses. Only principal components with an eigenvalue greater than one were further examined. We correlated the density of godwits in the arrival and breeding phase with the PC axes. After log-transformation, densities of godwits were normally distributed. We then used a variable that best described agricultural management (herb richness) to test relationships between soil types, agricultural management

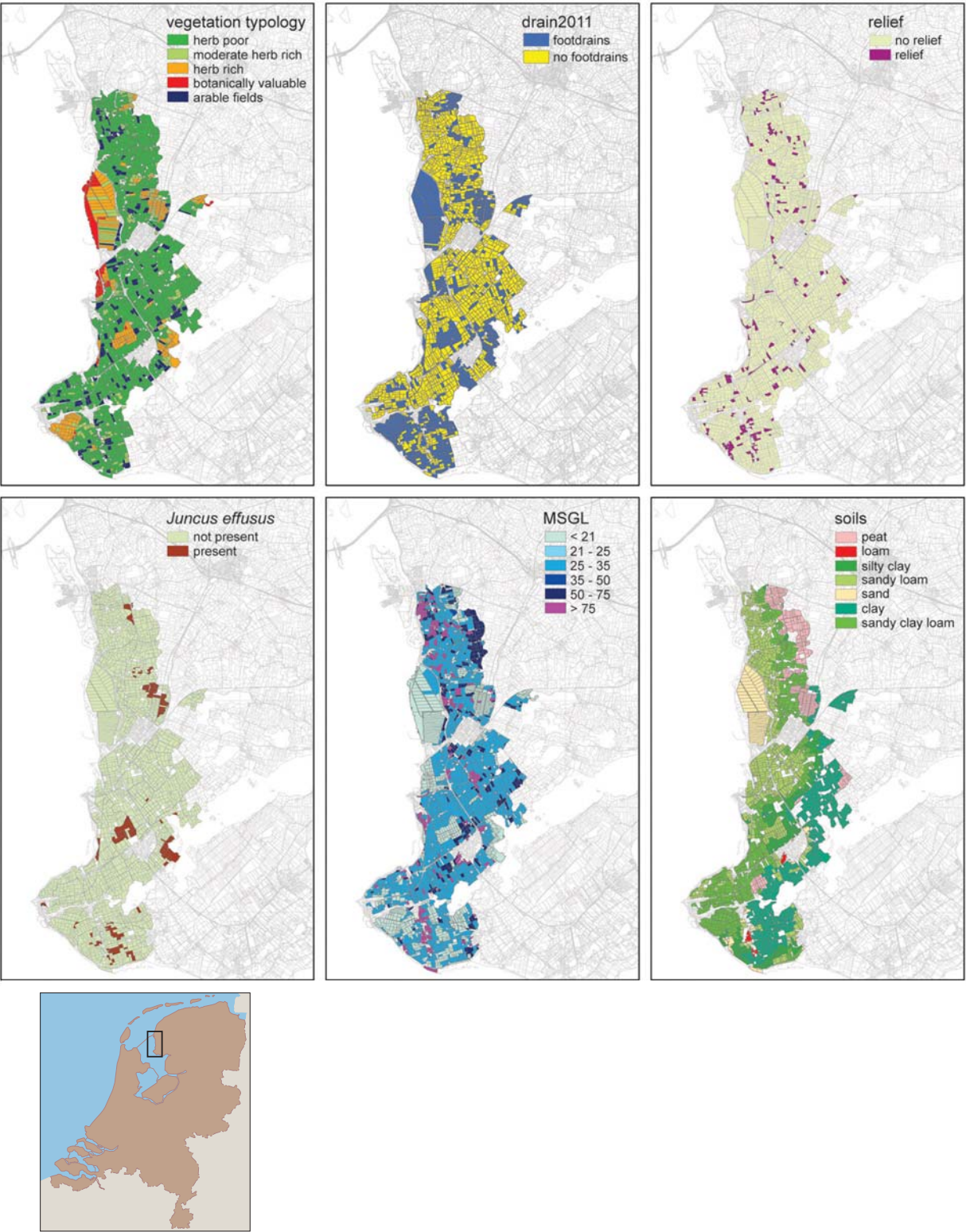


Figure 1. The spatial occurrence of the measured habitat characteristics in the study area.

and densities of godwits in the arrival and breeding phase. With a χ^2 test we tested if the different soil types were equally distributed over the agricultural management types, and also if the density of arriving and breeding godwits differed per soil type in the different agricultural management regimes.

We used R.2.13.0 (R Development Core Team 2008) for statistics. PCA was performed with the function `prcomp`, using a correlation matrix. We tested linear relationships using linear regression.

RESULTS

Landscape characteristics

Meadows (parcels vegetated primarily by grass) made up for 88.5% of the study area, arable land 11.0% and marshland or pools 0.5%. Of the arable land, 90% was cultivated with maize and the rest with potatoes or tulips. The PCA of the six habitat characteristics resulted in two components with eigenvalues greater than one, accounting for 48% and 19% of the variance. Five out of six habitat characteristics had a correlation coefficient greater than 0.5 with PC1: percentage of area containing meadows, percentage of area containing parcels with herb-rich vegetation, presence of foot drains and of *J. effusus* and mean spring groundwater level (MSGSL). Percentage of relief showed a negative, and MSGSL a positive correlation with PC2 (Table 1, Figure 2). PC1 represents agricultural management intensity, with the more positive values for less intense management. Percentage of herb richness and occurrence of foot drains within a polder has the strongest positive correlation with PC1, indicating that they are a good predictor for the intensity of agricultural management. PC2 represents relief, and in lesser extent ground wetness.

Table 1. Coefficients of the correlations between habitat characteristics and the first two principal components. MSGSL stands for mean spring groundwater level.

	PC1	PC2
Meadows	0.56	-0.43
Herb-rich	0.90	0.00
Foot drains	0.91	-0.04
<i>J. effusus</i>	0.55	0.25
Relief	0.29	-0.79
MSGSL	0.71	0.52

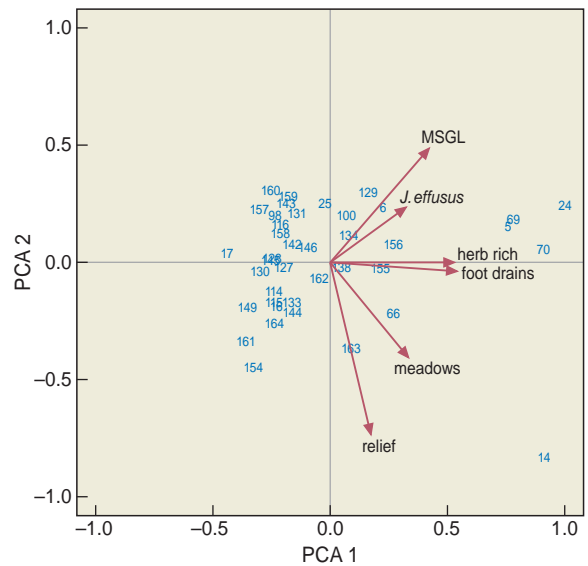


Figure 2. Biplot of PCA results. The arrows indicate the direction of the habitat characteristics, the blue numbers are the identifying numbers of individual polders.

Habitat selection by Black-tailed Godwits

In the arrival period, we counted 1523 Black-tailed Godwits, and in the breeding period 2110. Godwits were not randomly distributed over the study area and the highest densities of godwits were found in polders with high PC1 values (arrival: $F_{1,38} = 17.65$, $R^2 = 0.32$, $P < 0.001$, breeding: $F_{1,38} = 23.6$, $R^2 = 0.38$, $P < 0.001$; Figure 3). The density of godwits showed no relationship with PC2 (arrival: $F_{1,38} = 0.06$, $R^2 < 0.01$, $P > 0.5$, breeding: $F_{1,38} = 0.36$, $R^2 = 0.01$, $P > 0.5$).

Soil types

Herb-rich meadows were not equally distributed over the available soils ($\chi^2_6 = 2343$, $P < 0.001$). Although sandy soils made up only 9% of the total area, 38% of all the herb-rich wet meadow area was found on sand (Figure 4). The most dominant top soils were sandy clay loam (25%), sandy loam (24%) and clay (23%), and on each of these soils circa 15% of the area were herb-rich wet meadows. Peat soils made up 10% of the total area and 14% of all herb-rich meadows was found on peat. On the other soils, less than 2% of the area were herb-rich meadows (Figure 4). On both intensively managed land and herb-rich meadows, densities of arriving and breeding godwits were different between soil types (arrival: herb-poor $\chi^2_6 = 18$, $P = 0.005$, herb-rich $\chi^2_5 = 92$, $P < 0.001$, breeding: herb-poor

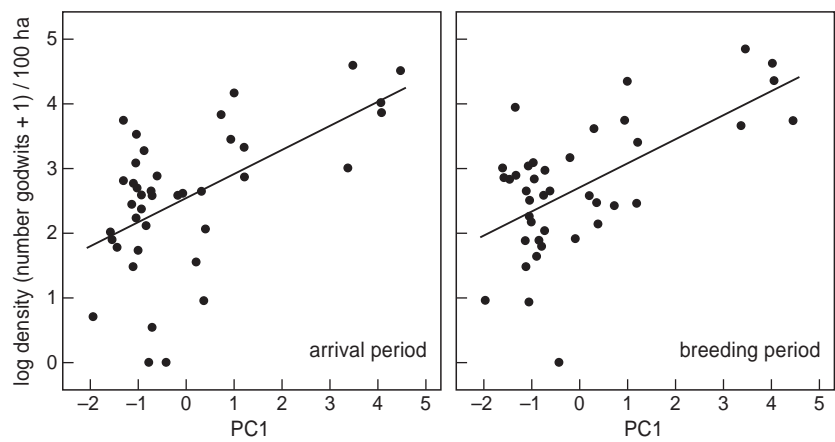
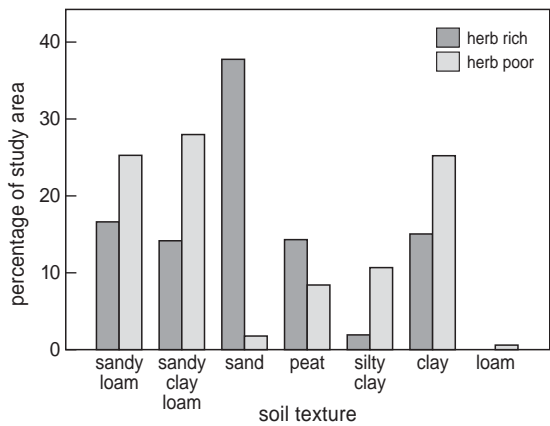


Figure 3. Relationship between the ¹⁰log density of godwits with the PC1 value per polder, separately for the arrival period and the breeding period.



$\chi^2_6 = 34, P < 0.001$, herb-rich $\chi^2_5 = 50, P < 0.001$, see Figure 5). In the arrival period, the highest godwit densities were found on herb-rich peat (84 godwits/100 ha) and herb-rich sandy loam (63 godwits/100 ha). Densities on herb-poor parcels were lower and more uniform. During the breeding period the highest godwit densities were found on herb-rich sandy loam and sandy clay loam (88 and 86 godwits/100 ha, respectively). Numbers on herb-poor soils were overall lower, with the highest densities occurring on sandy clay loam (21 godwits/100 ha).

Figure 4. Occurrence of soil textures and peat in our study area. The dark grey bars show the percentage of area per soil texture and peat in intensively managed agricultural land (herb-poor areas without foot drains) and the light grey bars represents the percentage of area with herb-rich meadows and foot drains.

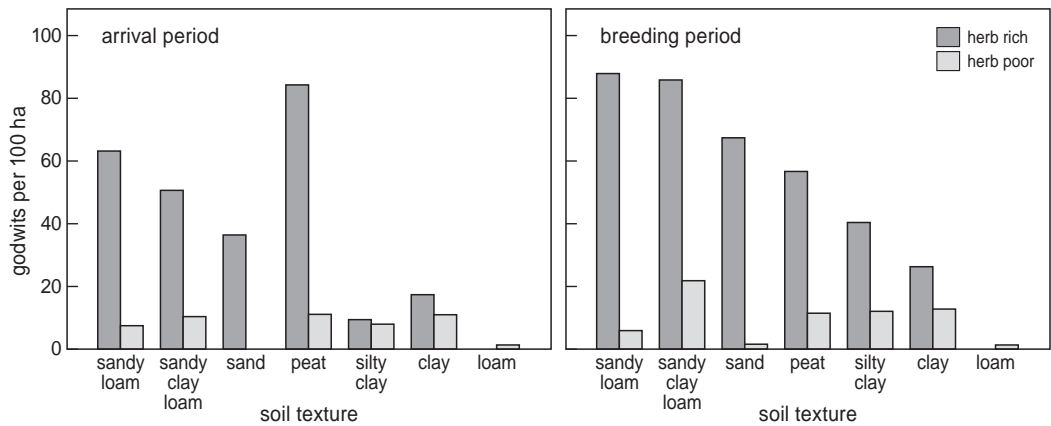


Figure 5. Density of Black-tailed Godwits in the arrival period and the breeding period on different soil types, separate for herb-rich meadows and herb-poor fields.

DISCUSSION

The modern landscape

The modern agricultural landscape and how it relates to the distribution of a meadow bird of high conservation concern can be characterized with a few simple variables, which are highly correlated with each other. The first principal component is best described by vegetation typology (herb richness) and the occurrence of foot drains, followed by the percentage of meadows, groundwater level and presence of *J. effusus*. Intensively managed agricultural land is reseeded with fast growing ryegrasses and foot drains are replaced by a belowground drainage system, indicating that PC1 summarises the intensity of agricultural management. However, we recently noticed a trend that farmers make foot drains on land with an underground drainage system, to prevent flooding from heavy downpours. These parcels with modern foot drains are very scarce in our research area and have no effect on the results. *J. effusus* is related to high phosphate levels and therefore often found on agricultural land where management changed from intensive with high fertilizer input to less intensive (Smolders *et al.* 2008).

The second principal component seems to describe relief. Relief is one of the relicts of the historical landscape and the result of salt-marsh dynamics (northern part of study area) and glaciation events (southern part of study area) that influenced the landscape before the creation of dikes (1200 AD) and the closure of part of the North Sea, the Zuiderzee, with the Afsluitdijk in 1932 (van Eerden *et al.* 2010). Relief showed no correlation with PC1 and seems to have no relationship with agricultural management. MSGL also correlated, in the opposite direction of relief, with PC2. Because of the variability in height of parcels with relief, it makes sense that these parcels, at least partially, have a low groundwater level.

Habitat selection in the modern landscape

During the arrival period, non-territorial groups can consist of more than 150 godwits which are often a mixture of local breeding birds, non-local breeding birds and godwits of the *islandica* subspecies that stage in the Dutch meadows (Alves *et al.* 2012). Higher densities of godwits during both the arrival and the early breeding phases occurred in herb-rich polders with high groundwater levels and foot drains. These polders are often especially managed for meadow birds, and resemble the meadows from the years when the godwit population was thriving, i.e. 1950–1970. Godwits that breed on herb-rich meadows have higher

breeding success than godwits breeding on intensively used agricultural parcels (Kentie *et al.* 2011). Because godwits show highest site-faithfulness when they successfully hatch their eggs (Groen 1993), higher densities are expected in the herb-rich polders with high groundwater levels and foot drains. Other waders, such as Snipe *Gallinago gallinago*, Curlew *Numenius arquata* and Redshank *Tringa totanus*, also prefer ‘unimproved’ agricultural land (Baines 1988, Smart *et al.* 2006).

Adult godwits feed mainly on earthworms, which they catch by probing in the soil with their long bill. Although the total number of earthworms may be higher in herb-poor meadows where fertilizers are used more frequently (Curry *et al.* 2008), the availability of worms in the top layer is usually higher in herb-rich meadows (J. Onrust *et al.*, unpubl. obs.), and wet soils are easier to probe for worms (Green 1988, Green *et al.* 1990, Kleijn *et al.* 2011). Soil organic matter and texture might also influence food availability of adults, either through their effect on soil penetrability, because some soils have better potential in retaining water (Holmstrup *et al.* 2011), and through the number of earthworms (Didden 2001). This might explain part of the relationship between soils and godwit densities on herb-rich wet meadows. However, on herb-poor meadows, groundwater level might have a stronger effect on food availability than soil texture, possibly explaining the less pronounced differences in godwit densities in that habitat.

Besides food availability for adults, food availability for chicks – insects living in the vegetation – might also play a role in selecting a breeding location. Herb-rich wet meadows provide higher food availability for the nidifugous and precocial godwit chicks (Schekkerman & Beintema 2007, Kleijn *et al.* 2010), especially if water is let in during dry periods (Eglington *et al.* 2010). Foot drains increase micro habitat variation and heterogeneity on the field surface. Even within intensively managed agricultural fields, godwits select the more heterogeneous fields (Verhulst *et al.* 2011). As most of the intensively managed meadows are mowed during the nesting period, this reduces vegetation cover for chicks which therefore experience higher predation rates (Schekkerman *et al.* 2009). The selection for herb-rich wet meadows might thus be due to a combination of better food availability for adults and chicks and improved chances of chick survival.

It is often believed that high densities of *J. effusus* have detrimental effects on the habitat quality of meadow birds (see for instance van 't Veer *et al.* 2008). However, some meadow birds, such as Lapwings

Vanellus vanellus, show no relationship (Baines 1988), or a positive relationships in the case of Snipe (Baines 1988) and Redshank (Smart *et al.* 2006). Whether these are direct responses, or indirect responses, because *J. effusus* indicates wetter soils, is often unclear. In our study, the density of godwits was higher in polders with more parcels with *J. effusus*, but it is not possible to conclude whether godwits actively selected for these parcels, or that they preferred other habitat characteristics, such as herb richness and foot drains that were associated with it. Moreover, it is possible that in our study area the densities of *J. effusus* were not high enough to cause detrimental effects.

Conservation issues

Agri-environmental schemes (AES) have been developed to preserve breeding bird populations in modern agricultural landscapes, and 87% of the national budget (€ 31 million) was invested in meadow bird protection (Schekkerman *et al.* 2008). However, these schemes, which often only include postponed mowing and per-clutch payment while farming practices are otherwise unrestricted, have meanwhile been shown not to be effective for meadow bird conservation (Kleijn *et al.* 2001, Verhulst *et al.* 2007). Here we observed once more that the highest breeding densities of godwits occurred in herb-rich wet meadows, mostly (87%) managed by nature conservation organisations or implemented with the most meadow bird friendly management. In our study area, management by nature conservation organizations thus seems to be successful. The modern ways of farming does not sustain godwits: the birds are unable to cope with the intensification. For instance, godwits advanced their laying date parallel with the first mowing date of the meadows up to 1980, but thereafter mowing dates kept on advancing while laying dates did not (Kleijn *et al.* 2010, Schroeder *et al.* in press). Godwits still breed in intensively managed meadows, although at lower densities. If breeding success is lower than necessary for population stability, these areas would act as population sinks (Levins 1969). If such sinks nevertheless attract breeding birds, these meadows would be an ecological trap (Battin 2004). Because godwits live long, it is possible that the changes of the landscape happened too rapidly for the species to have adapted to altered habitat cues.

Historically, herb-rich wet meadows were the most common type of agricultural land in The Netherlands. Now they are the rarest. In our study area, only 20% of the agricultural area consists of herb-rich meadows. A large percentage of herb-rich meadows is found on the atypical sandy soils of recently established polders

Table 2. Habitat quality for breeding Black-tailed Godwits in relation to habitat characteristics. Dark grey blocks represents good-quality habitat, light grey areas with a plus are moderate quality habitat, but only in combination with each other. Middle grey blocks are combinations of habitat characteristics that did not occur in our study area.

Vegetation typology	Foot drains		Groundwater level		
	yes	no	0–30	30–50	>50
Botanically valuable					
Herb rich					
Moderate herb rich	+		+		
Herb-poor					

bordering Lake IJsselmeer. Nevertheless, we think that this study is relevant for other potential meadow bird areas, because soil type only had a small effect on godwit densities compared to agricultural management.

Clearly, conservation of meadow birds, a key ornithological value of The Netherlands, necessitates the care for enough high-quality habitat. In these areas, the vegetation should be herb-rich and not mowed during the breeding and chick rearing periods, and water levels should be high. Moreover, foot drains might provide water in periods of drought and irrigate the excess in wet periods (see Eglington *et al.* 2010), but also serve as cover and as ‘run(a)ways’ if the grass is growing denser late in spring. Table 2 summarizes the vital habitat characteristics, in conjunction with each other, of a good-quality habitat for Black-tailed Godwits.

ACKNOWLEDGEMENTS

NG and RK contributed equally to the manuscript. We thank our fellow members of the successive ‘grutto-teams’ of the University of Groningen that contributed to this study: Valentijn van den Brink, Ysbrand Galama, Job ten Horn, Pedro Lourenço, Rinkje van der Zee, Krijn Trimbos, and the many students and volunteers. Nature conservancy organisations (It Fryske Gea and Staatsbosbeheer) and private landowners gracefully issued permission to access their properties. This work started off in 2006 with a grant from the Prins Bernhard Cultuurfonds administered by It Fryske Gea. Financial support was also received through the ‘Kenniskring weidevogels’ of the former Ministry of Agriculture, Nature Management and Food Safety. We thank Eelke Folmer for writing the R-script to derive soil texture and water level per parcel, and Jennifer Smart and an anonymous reviewer for constructive feedback. The Stichting Huib Kluijver Fonds made it possible to print the maps in colour.

REFERENCES

- Alves J.A., Gunnarsson T.G., Potts P.M., Gélinaud G., Sutherland W.J. & Gill J.A. 2012 Overtaking on migration: does longer distance migration always incur a penalty? *Oikos* 121: 464–470.
- Baines D. 1988. The effect of improvement of upland marginal grasslands on the distribution and density of breeding wader birds (Charadriiformes) in Northern England. *Biol. Conserv.* 45: 221–236.
- Bakker J.P. & Berendse F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14: 63–68.
- Battin J. 2004. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Conserv. Biol.* 18: 1482–1491.
- Beintema A.J. 1983. Meadow birds as indicators. *Environ. Monit. Assess.* 3: 391–398.
- Beintema A.J., Beintema-Hietbrink R.J. & Müskens G.J.D.M. 1985. A shift in the timing of breeding in meadow birds. *Ardea* 73: 83–89.
- Beintema A.J., Moedt O. & Ellinger D. 1995. Ecologische atlas van de Nederlandse Weidevogels. Schuyt & Co, Haarlem, The Netherlands.
- Bignal E.M. & McCracken D.I. 1996. Low-intensity farming systems in the conservation of the countryside. *J. Appl. Ecol.* 33: 413–424.
- BirdLife International 2004. Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge, UK. BirdLife International Series No. 12.
- CBS 2012. Centraal Bureau voor de Statistiek (CBS). www.cbs.nl
- Curry J.P., Doherty P., Purvis G. & Schmidt O. 2008. Relationships between earthworm populations and management intensity in cattle-grazed pastures in Ireland. *Appl. Soil Ecol.* 39: 58–64.
- Didden W.A.M. 2001. Earthworm communities in grasslands and horticultural soils. *Biol. Fert. Soils* 33: 111–117.
- Donald P.F., Green R.E. & Heath M.F. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. B* 268: 25–29.
- Eglington S.M., Bolton M., Smart M.A., Sutherland W.J., Watkinson A.R. & Gill J.A. 2010. Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *J. Appl. Ecol.* 47: 451–458.
- Ervin G. & Wetzel R. 2002. Influence of a dominant macrophyte, *Juncus effusus*, on wetland plant species richness, diversity, and community composition. *Oecologia* 130: 626–636.
- Gill J.A., Langston R.H.W., Alves J.A., Atkinson P.W., Bocher P., Cidraes Vieira N., Crockford N.J., Gélinaud G., Groen N., Gunnarsson T.G., Hayhow B., Hooijmeijer J., Kentie R., Kleijn D., Lourenço P.M., Masero J.A., Meunier F., Potts P.M., Roodbergen M., Schekkerman H., Schröder J., Wymenga E. & Piersma T. 2008. Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. *Wader Study Group Bull.* 114: 43–50.
- Green R.E. 1988. Effects of environmental factors on the timing and success of breeding of common snipe *Gallinago gallinago* (Aves: Scolopacidae). *J. Appl. Ecol.* 25: 79–93.
- Green R.E., Hirons G.J.M. & Cresswell B.H. 1990. Foraging habits of female Common Snipe *Gallinago gallinago* during the incubation period. *J. Appl. Ecol.* 27: 325–335.
- Groen N.M. 1993. Breeding site tenacity and natal philopatry in the Black-tailed Godwit *Limosa l. limosa*. *Ardea* 81: 107–113.
- Harms W.B., Stortelder A.H.F. & Vos W. 1987. Effects of intensification of agriculture on nature and landscape in the Netherlands. In: Wolman M.G. & Fournier F.G.A. (eds). Land transformation in agriculture. John Wiley & Sons, New York, pp. 357–379.
- Holmstrup M., Lamande M., Torp S.B., Greve M.H., Labouriau R. & Heckrath G. 2011. Associations between soil texture, soil water characteristics and earthworm populations in grassland. *Acta Agr. Scand. B-S P.* 61: 583–592.
- Hötker H., Davidson N.C. & Fleet M. 1991. Waders breeding on wet grasslands. *Wader Study Group Bull.* 61, Suppl.
- Kentie R., Hooijmeijer J., Both C. & Piersma T. 2011. Grutto's in ruimte en tijd 2007–2010, eindrapport. Directie Kennis, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag.
- Kleijn D., Berendse F., Smit R. & Gilissen N. 2001. Agri-environmental schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413: 723–725.
- Kleijn D., Schekkerman H., Dimmers W.J., van Kats R.J.M., Melman D. & Teunissen W.A. 2010. Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in The Netherlands. *Ibis* 152: 475–486.
- Kleijn D., Lammertsma D. & Müskens G. 2011. Het belang van waterpeil en bemesting voor de voedselbeschikbaarheid van weidevogels. In: Teunissen W.A. & Wymenga E. (eds). Factoren die van invloed zijn op de ontwikkeling van weidevogelpopulaties. SOVON Vogelonderzoek Nederland, Nijmegen; Bureau Altenberg & Wymenga, Veenwouden; Alterra, Wageningen.
- Lapié E., Nahmani J. & Rousseau G.X. 2009. Influence of texture and amendments on soil properties and earthworm communities. *Appl. Soil Ecol.* 43: 241–249.
- Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15: 237–240.
- Melman T.C.P., Schotman A., Hunink S. & de Snoo G.R. 2008. Evaluation of meadow bird management, especially Black-tailed Godwit (*Limosa limosa* L.), in the Netherlands. *J. Nat. Conserv.* 16: 88–95.
- Mulder T. 1972. De Grutto (*Limosa limosa* (L.)) in Nederland: aantallen, verspreiding, terreinkeuze, trek en overwintering. KNNV, Hoogwoud, The Netherlands.
- Newton I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146: 579–600.
- Oosterveld E.B., Nijland F., Musters C.J.M. & de Snoo G.R. 2011. Effectiveness of spatial mosaic management for grassland breeding shorebirds. *J. Ornithol.* 152: 161–170.
- R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org
- Runhaar H., Witte F. & Verburg P. 1997. Ground-water level, moisture supply, and vegetation in the Netherlands. *Wetlands* 17: 528–538.

- Schekkerman H. & Beintema A.J. 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. *Ardea* 95: 39–54.
- Schekkerman H., Teunissen W. & Oosterveld E. 2008. The effect of mosaic management on the demography of black-tailed godwit *Limosa limosa* on farmland. *J. Appl. Ecol.* 45: 1067–1075.
- Schekkerman H., Teunissen W. & Oosterveld E. 2009. Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. *J. Ornithol.* 150: 133–145.
- Schroeder J., Piersma T., Groen N.M., Hooijmeijer J.C.E.W., Kentie R., Lourenco P.M., Schekkerman H. & Both C. In press. Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *J. Ornithol.* doi: 10.1007/s10336-011-0747-5.
- Smart J., Gill J.A., Sutherland W.J. & Watkinson A.R. 2006. Grassland-breeding waders: identifying key habitat requirements for management. *J. Appl. Ecol.* 43: 454–463.
- Smart J., Amar A., O'Brien M., Grice P. & Smith K. 2008. Changing land management of lowland wet grasslands of the UK: impacts on snipe abundance and habitat quality. *Anim. Conserv.* 11: 339–351.
- Smolders A.J.P., Lucassen E.C.H.E.T., van der Aalst M., Lamers L.P.M. & Roelofs J.G.M. 2008. Decreasing the abundance of *Juncus effusus* on former agricultural lands with noncalcareous sandy soils: possible effects of liming and soil removal. *Restor. Ecol.* 16: 240–248.
- Thorup O. 2006. Breeding waders in Europe 2000. International Wader Studies 14. International Wader Study Group, UK.
- van 't Veer R., Sierdsema H., Musters C.J.M. & Groen N.M. 2008. Gebiedsgerichte analyse van historische datasets. Directie Kennis, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Den Haag.
- van der Vliet R.E., van Dijk J. & Wassen M.J. 2010. How different landscape elements limit the breeding habitat of meadow bird species. *Ardea* 98: 203–209.
- van Dijk A.J., Boele A.J., Hustings F., Koffijberg K. & Plate C.L. 2010. Broedvogels in Nederland in 2008. SOVON Vogelonderzoek Nederland, Beek-Ubbergen.
- van Eerden M.R., Lenselink G. & Zijlstra M. 2010. Long-term changes in wetland area and composition in The Netherlands affecting the carrying capacity for wintering waterbirds. *Ardea* 98: 265–282.
- Verhulst J., Kleijn D. & Berendse F. 2007. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. *J. Appl. Ecol.* 44: 70–80.
- Verhulst J., Kleijn D., Loonen W., Berendse F. & Smit C. 2011. Seasonal distribution of meadow birds in relation to in-field heterogeneity and management. *Agr. Ecosyst. Environ.* 142: 161–166.
- Vickery J.A., Tallowin J.R., Feber R.E., Asteraki E.J., Atkinson P.W., Fuller R.J. & Brown V.K. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *J. Appl. Ecol.* 38: 647–664.
- Wilson A.M., Ausden M. & Milsom T.P. 2004. Changes in breeding wader population on lowland wet grasslands in England and Wales: causes and potential solutions. *Ibis* 146 (Suppl. 2): 32–40.
- WUR-Alterra 2006. Dataset grondsoortenkaart van Nederland 2006. Wageningen, The Netherlands.

SAMENVATTING

Het agrarische landschap in Nederland heeft lange tijd een aanzienlijke ornithologische waarde gehad. De laatste vijftig jaar heeft de intensivering in de landbouw echter een negatief effect gehad op de kwaliteit van het habitat van de weidevogels. In 2009 hebben wij in het zuidwesten van Friesland een kwantitatieve karakterisering gemaakt van het agrarische habitat en het gebruik hiervan door Grutto's *Limosa l. limosa*. Hiermee willen we een ijkpunt bieden om veranderingen in het landschap en het gebruik door Grutto's in de toekomst te kunnen evalueren. Met een 'Principal Component Analysis' (PCA) hebben wij het landschap in 43 polders met een oppervlakte van 8.480 ha beschreven op basis van grondwaterstand, vegetatietypologie, het reliëf in het landschap, de aanwezigheid van greppels, het landgebruik en de structuur van de grondsoort. De grootste variatie in het landschap wordt verklaard door kruidenrijkdom, het voorkomen van greppels en de grondwaterstand. Het moderne agrarische landschap in het zuidwesten van Friesland bestaat voor 80% uit een uniform, intensief beheerd agrarisch land met kruidenarme weilanden, zonder greppels en met een lage grondwaterstand. De overige 20% bestaat uit overblijfselen van het vroegere kruidenrijke land met greppels en een hoge grondwaterstand. De Grutto's prefereerden na aankomst en in de broedtijd deze kruidenrijke, extensief beheerde weilanden. De hoogste dichtheden aan broedende Grutto's werden gevonden op zavelgronden. Op de zand- en veenbodems waren de dichtheden lager, al lagen de meeste extensief beheerde gronden juist op deze twee bodemsoorten. De beschermingsmaatregelen op intensief beheerd agrarisch land blijken niet succesvol genoeg om de Grutto tegen uitsterven te beschermen. Wij pleiten daarom voor meer en grotere arealen met kruidenrijke, natte weilanden. In tabel 2 geven wij aan hoe een gruttogebied van hoge kwaliteit er wat betreft landschapkenmerken uit zou moeten zien.

Corresponding editor: Popko Wiersma

Received 22 December 2011; accepted 14 March 2012