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Identification of Black-tailed Godwit's *Limosa limosa* breeding habitat by botanical and environmental indicators

Karsten Laursen · Anna Bodil Hald

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Abstract Despite concentrated conservation efforts and targeted agri-environmental schemes, breeding wader species have declined in most western European countries during recent decades. Assuming that wader species aggregate in relation to physical and biological features of their breeding habitats, this study aimed to identify botanical and environmental indicators that can be used to identify sites and management regimes to enhance breeding potential for the Black-tailed Godwit *Limosa limosa* as a focal species. We selected 36 fields (mean 7.1 ha) with and without this species in grazed lowland grasslands in the Danish Wadden Sea area. Bird numbers observed during 2007 and 2008 were analysed in relation to environmental and management variables together with presence/absence of plant species in the main body of the fields, the field silt trenches and field edges. Black-tailed Godwits preferred unfertilized fields with a short growth plant community that included the presence of moss-carpet. The plant indicator species for fields with Black-tailed Godwit were besides *Bryopsida* (moss sp.) also *Trifolium pratense* var. *maritimum* (maritime red clover), *Poa trivialis* (rough meadowgrass), *Plantago major* (greater plantain) and *Veronica serpyllifolia* (thyme-leaved speedwell).

Zusammenfassung

Die Bestimmung von Brutgebieten der Uferschnepfe *Limosa limosa* durch botanische und ökologische Indikatoren.

Trotz gezielter Umweltschutzmaßnahmen und agrar-ökologischer Programme haben die in Westeuropa brütenden Watvogelpopulationen in den vergangenen Jahrzehnten größtenteils abgenommen. Unter der Annahme, dass Watvogelarten sich Brutgebiete nach physikalischen und biologischen Faktoren aussuchen, versuchten wir in dieser Studie die botanischen und ökologischen Indikatoren herauszufinden, nach denen potentielle Brutgebiete der Uferschnepfe für Umweltschutzmaßnahmen identifiziert werden könnten. Wir wählten 36 Felder (durchschnittlich 7.1 ha) mit und ohne Brutvorkommen dieser Art im beweideten Tiefland des dänischen Wattenmeerraumes. Die Populationsgrößen zwischen 2007 und 2008 wurden in Bezug auf ökologische Eigenschaften, Management-Maßnahmen und das Vorkommen bestimmter Pflanzen in der Mitte der Felder, in verschlammten Gräben und an Feldrändern untersucht. Uferschnepfen bevorzugten ungedüngte Felder mit niedrigem Bewuchs und Moosdecke. Die Indikatorpflanzen für Uferschnepfen waren neben Bryopsida (Moose) auch *Trifolium pratense* var. *maritimum* (Küsten-Wiesen-Klee), *Poa trivialis* (Gewöhnliches Rispengras), *Plantago major* (Breitwegerich) und *Veronica serpyllifolia* (Quendel-Ehrenpreis).

Keywords Breeding waders · Grassland management · Moss-carpet · Vegetation structure · Wadden Sea

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K. Laursen (✉)
Department of Bioscience, National Environmental Research Institute, Aarhus University, Grenåvej 14, 8410 Rønde, Denmark
e-mail: kl@dmu.dk

A. B. Hald
Nature and Agriculture Aps, Niels Pedersens Allé 2,
8330 Tjele, Denmark
e-mail: natlan@agropark.dk

Introduction

In western Europe, biodiversity is declining in agricultural landscapes (Benton et al. 2002) especially in lowland grasslands, which formerly supported a rich and diverse breeding bird community (Wilson et al. 2004). Generally, intensification of grassland management is associated with adverse effects on avian reproductive output (Donald et al. 2001; Newton 2004; Roodbergen et al. 2008), especially as a result of increased grazing intensity and changes in agricultural practice from grazing to mowing for silage (Beintema and Müskens 1987; Dennis et al. 2007, Roodbergen et al. 2008). In addition, the effects of human disturbance and drainage (Holm and Laursen 2009; Melman et al. 2008), reduced survival of eggs and young and predation by species such as red fox (*Vulpes vulpes*) and raptors, e.g. Buzzards (*Buteo buteo*) (Newton 2004; Schekkerman et al. 2008; Teunissen et al. 2008), all reduce effective breeding areas and recruitment rates. The negative effect of these factors has continued in recent years, and predation rates have even increased (Schekkerman 2008). Together these factors have caused serious declines in breeding bird populations during 1970–1990 in countries which together hold the vast amount of European breeding numbers (Tucker and Heath 1994). The decline since 1980 may be confounded by warmer temperatures that advance plant growth but not breeding times (Kleijn et al. 2010). To reverse the declines in populations of the Black-tailed Godwit *Limosa limosa* and other meadow bird species, several countries in Western Europe have introduced agri-environment schemes (Schekkerman et al. 2008; Breeuwer et al. 2009). Despite such measures, it has proved difficult to reverse the current decline and adverse trends (Schekkerman et al. 2008; Melman et al. 2008; Breeuwer et al. 2009). One reason for the lack of success of the agri-environment schemes could be that their options are too broad to support the specific features of importance to breeding bird species, or that they are applied to sites which lack the necessary ecological features to support such species (Kleijn and van Zuijlen 2004; Melman et al. 2008; Verhulst et al. 2007, but see Breeuwer et al. 2009). As a consequence, some of the financially compensated agricultural areas may not have the potential to function as effective breeding sites for these species. Since breeding bird numbers are still declining (Thorup 2006), it is necessary to focus the financial support on those sites with the highest ecological potential for the species, in order to concentrate the conservation management input most effectively. Evidence-based conservation management options must be based on detailed ecological studies (Sutherland et al. 2004, Buckingham et al. 2004). Such studies should include information on the plant communities, since the vegetation integrates and expresses environmental conditions, including productivity on sites (Ellenberg et al. 1992). However, such information is rarely integrated into bird studies (Breeuwer et al. 2009).

To increase the cost-effectiveness of species management, the aim of this study was to find simple ecological indicators that could facilitate the process of identifying breeding habitat characteristics for wader species, including those grassland bird species identified as having high conservation value under the EU Wild Birds Directive. Successful indicators should be easily identifiable in the fields, e.g. physical features or easily identifiable plant species, so that managers, farmers and administrators can recognise these features or species in the field, and focus their management efforts at sites where they are present to achieve good conditions for breeding wader birds. In this study, we have focused on the Black-tailed Godwit. Since this species is rather faithful to its breeding sites (Buker and Winkelman 1987; Schroeder 2010), the variables underlying the habitat selection can be identified, and we assume (1) that these variables are reflected in the vegetation community, and since the species prefers mowed or grazed pastures and marginal farmland, we also assume (2) that the Black-tailed Godwit prefers sites with a short vegetation structure with little or no fertilizer application (Buker and Groen 1989; Struwe-Juhl 1995).

For this study, we have examined fields with and without breeding Black-tailed Godwits and have gathered data on physical features of the main body of the fields, the field silt trenches and field edges, together with plant species and variables derived from vegetation analyses.

Methods

Study area

The study was conducted in the Danish Wadden Sea, part of the international Wadden Sea area shared with the Netherlands and Germany. It supports large numbers of breeding birds and is one of the most important breeding areas in western Europe (Koffijberg et al. 2006). The Danish part covers a total area of about 1,500 km^2 that comprises saltmarshes and tidal flats outside the sea wall, and large embanked areas with grazed grasslands and arable fields. The area is protected under the EU Wild Birds Directive, the EU Habitat Directive and by terms agreed by the three countries under the Trilateral Wadden Sea Plan (Essink et al. 2005). The Black-tailed Godwit was selected for this study due to its high conservation status and declining numbers as a breeding species in Denmark as in most parts of western Europe (Thorup 2004; Burfield and van Bommel 2004). The Danish Wadden Sea has been a stronghold for this species since the early 1960s, and during 1986–2006 a total of 250–300 pairs bred, with largest densities on the islands and in the Tønder Marsh on the mainland, which constituted 38 % of the total Danish breeding population (Kahlert et al. 2007; Thorup and Laursen 2008).

Species and sites

During 2006, a monitoring programme of breeding coastal and marshland bird species was conducted in the Danish Wadden Sea (Thorup and Laursen 2008), producing a detailed map of all Black-tailed Godwit records. Nine breeding areas were identified that included all observations of the species, and six of these were situated in polders inside the sea walls and three areas outside the sea walls on salt marshes (Fig. 1). Within each of these areas, a number (depending of the size of the breeding area) of specific fields were selected in which at least one Black-tailed Godwit was recorded in the 2006-survey (referred to as 'godwit fields'). Similar fields but without Black-tailed Godwits (referred to as 'non-godwit fields') were selected, where no individuals were recorded during the 2006 survey. The godwit and non-godwit fields were selected in a way that represented similar large-scale physical appearance in each group, e.g. if a field among the godwit fields had a small pond, a low-lying area with humus soil or a channel along the edge, then similar large-scale structures were found in the non-godwit fields. Thus, the analysis focuses on differences in variables at field level. The maximum distance between fields within the nine study area was 3 km. All selected fields were grazed, semi-natural meadows or reseeded grassland fields.

In total 36 fields (18 godwit fields and 18 non-godwit fields) were selected. The total area of all the godwit fields was 125.8 ha (mean = 7.4, SE = 0.26) and for the non-godwit fields 131.1 ha (mean = 6.9, SE = 0.35). In total, 30 of the 36 study fields were reseeded with grass, within at least a 5-year cycle.

Fieldwork

During 2007, all fields were visited twice, and in 2008, three times between 22 April and 28 May to record the Black-tailed Godwit numbers. All observations of the species were mapped.

Environmental and botanical data were gathered in mid-May 2007 and 2008 by walking across the fields along a predefined zigzag route (1.2–1.5 km) with five sampling stations. At each station in 2007, (1) one soil sample was collected and the five samples for each field were pooled before chemical analysis; and (2) the height of the vegetation was measured using a direct measure method (Stewart et al. 2001). In 2008, the plant species dominating in silt trenches and the presence of bare ground in these were recorded. The walking route met each of the four field edges twice, and from these points the field edge biotope was described by management, physical appearance and presence of bare ground and water. In addition, data were collected on the physical structure (i.e. trenches and bare spots) of the main body of the fields (hereafter just mentioned as the fields) (see Appendix 1 in ESM).

In May 2008, the extent of dry plant material (litter) and a list was made of all plant species recorded in the fields along the zigzag route. Further, the botanical composition of the sward was determined by estimating percentage cover of all plant species present in a plot of 78 m^2 (circle diameter 5 m) located in the middle of each field. During autumn 2008, the farmers were interviewed for information about previous and present management of each field (see Appendix 2 in ESM). All environmental biotic and abiotic variables—measured and calculated—were grouped into eight functional data groups (A–H) (see Appendix 1 in ESM).

In the statistical analyses, we also used variables based upon the specific assemblage of plant species observed, e.g. Ellenberg F for moisture, Ellenberg N for production value and Ellenberg S for salt-indicating species were calculated (Ellenberg et al. 1992). Also, the number of plant species in the vegetation with high and low potential for green height, i.e. midsummer height if unmanaged, was calculated using the methods and data of Grime et al. (1988) and Hansen (1981). Finally, the nature quality index of the site as fresh water meadow and salt meadow was calculated using the species scores developed by Fredshavn and Ejrnæs (2007).

Data analysis

Since no relationship was found between number of Black-tailed Godwits and field size (parameter estimate = −0.026; $r^2 = 0.010$; $T = -0.40$; $P = 0.692$; $n = 18$; linear regression analysis), we did not use densities but total number of Black-tailed Godwits observed in each field in 2007 and 2008. To analyse relationships between the Black-tailed Godwit and environmental variables, we used an ANOVA Mixed models analysis (SAS Enterprise Guide 4 2006) with the total number of Black-tailed Godwits as the dependent variable, and the biotic and abiotic variables as independent variables.

The relatively small number of fields in the study ($n_1 = 36$) compared to the large number of variables ($n_2 = 51$) increases the risk of obtaining statistical significant results at the 5 % level by chance. Thus, we conducted the statistical tests in three steps to reduce the number of variables in the final test, and further, we raised the significance level to 1 % in the final test. In step (1) of the statistical tests, we analysed the variables from each of

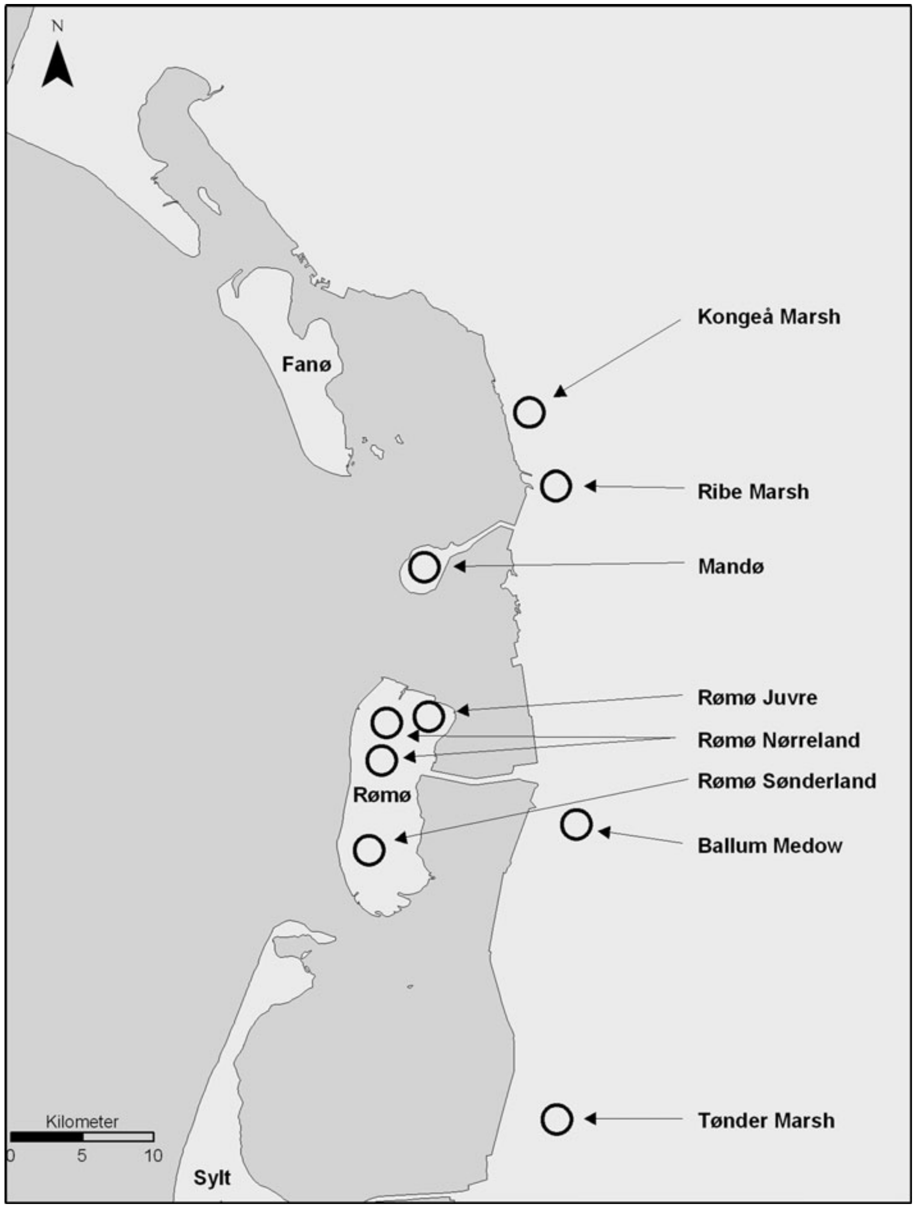

Fig. 1 The Danish Wadden Sea area with the nine studied Black-tailed Godwit *Limosa limosa* breeding sites. Sites at Rømø Nørreland and Rømø Sønderland are situated outside the sea walls. The study area is grouped into three regions: Mandø (8 fields), Rømø (16 fields) and the Mainland (12 fields)

eight functional data groups (A–H) separately (see Appendix 1 in ESM): (A) field soil samples; (B) structure and vegetation of silt trenches in the fields; (C) field general physical structure; (D) field general vegetation; (E) field plot vegetation; (F) field edge vegetation; (G) field edge physical structure; and (H) field management (farmer interviews). The variable 'region' (Mandø, Rømø and the Mainland) was included in all functional data groups to analyse for regional differences (Fig. 1). For each data group (A–H), we identified the variables that together showed the highest explanatory power (the highest statistical significance level in the Type 3 tests) in relation to the recorded Black-tailed Godwit numbers. For each functional group, we conducted the analyses by entering all group variables into the ANOVA Mixed model and stepwise removed variables with the lowest explanatory power until a final model was obtained, i.e. a model showing the highest possible significance level for the remaining variables. In step (2) of the analysis, the variables in the first step that were statistically significant in the Type 3 tests ($P < 0.05$) were allocated into two groups: field variables (data groups A–E) and field edges/management variables (data groups F–H). For each of these two groups the variables were entered an ANOVA Mixed models analysis by using the same procedure as in step (1). In step (3), the final statistical analysis, the statistical significant variables from step (2) were entered the ANOVA Mixed models analysis using the same procedure as in step (1). Data values were expressed as log ($n + 1$) and proportions were arcsine transformed.

To identify plant species that occurred more frequently in fields with Black-tailed Godwits than in fields without this species, we conducted an indicator plant species analysis using the statistical program PCORD that estimates a correlation coefficient and a corresponding P value for the statistical significance (Dufrene and Legendre 1997).

Results

Vegetation and plant indicator species

In total 102 plant species were recorded from the 36 fields. On average, 21 species were observed in each field and 10 species inside the field plots (Table 1). Few rush and sedge species (2 for fields and 0.6 for plots), and cultivated species were recorded (2 and 1.5). The mean nature quality values for both salt meadow and the fresh water meadow were 2.0 and 1.7, respectively, for the field plots. The field plant species communities had a mean Ellenberg moisture value of 6.1 and a mean Ellenberg productivity value of 5.3. The measured vegetation height in the fields in mid--May varied from 1.2 to 28.8 cm, and the potential vegetation height (canopy height) in midsummer ranged between 10 and 60 cm (Table 1).

The nine most frequent species in all field plots were in descending order: white clover (*Trifolium repens*), marsh foxtail (*Alopecurus geniculatus*), creeping bent (*Agrostis stolonifera*), common mouseear (*Cerastium caespitosum*), meadow buttercup (*Ranunculus acris*), annual meadowgrass (*Poa annua*), rough meadowgrass (*P. trivialis*), creeping buttercup (*R. repens*), and common silverweed (*Potentilla anserina*). All these species had a total field frequency of exceeding 64 %.

The five indicator plant species with the highest score in godwit fields were greater plantain (*Plantago major,* $P = 0.012$), red clover (*Trifolium pratense* var. *maritimum,* $P = 0.019$), moss-carpet (mostly *Pleurocarpe* moss species, $P = 0.022$), thyme-leaved speedwell (*Veronica serpyllifolia,* $P = 0.028$) and rough meadowgrass (*P. trivialis,* $P = 0.078$). The six best indicator plant species for non-godwit fields were long-bracted sedge (*Carex extensa,* $P = 0.028$), common mouseear (*C. caespitosum,* $P = 0.034$), thrift (*Armeria maritima,* $P = 0.058$), Danish scurvygrass (*Cochlearia danica,* $P = 0.016$), buck's-horn plantain (*Plantago coronopus,* $P = 0.032$) and procumbent pearlwort (*Sagina procumbens,* $P = 0.071$). The three last-mentioned species were primarily found on anthills. All other species had $P \geq 0.08$.

Table 1 Botanical description of study fields (mean size of 7.1 ha) based on all plant species recorded during a zig-zag walk (fields walk) and on a detailed analysis (field plots)

Variable	Field walk[a] Equal weight to all species: mean (range)	Field plots (78 m^2)[b] Dominating species given double weight: mean (range)
Total number of species	21.1 (9–34)	10 (2–16)
Number of grass species	5.7 (2–10)	3.5 (1–6)
Number of broadleaved herb species	11.2 (1–20)	4.6 (0–9)
Number of rush and sedge species	2.0 (0–9)	0.6 (0–4)
Number of cultural species	2.0 (1–5)	1.5 (0–4)
Nature quality for salt meadow	2.1 (0.9–3.8)	2.0 (0.7–4.1)
Nature quality for fresh water meadow	2.1 (0.4–3.8)	1.7 (−0.1–4.1)
Ellenberg moisture value (EF)	6.1 (5.2–6.9)	6.0 (5.3–7.3)
Ellenberg productivity value (EN)	5.3 (4.1–6.0)	5.6 (4.5–6.3)
Ellenbergs salinity value (ES)	0.8 (0.3–2.5)	0.9 (0.1–2.9)
Grime canopy height (2 = 101–299 mm; 3 = 300–599 mm)	–	1.8 (1.3–3.0)
Vegetation height in spring (cm)	8.9 (1.2–28.8)	–

The Ellenberg value for moisture (EF), productivity (EN) and salinity (ES) was calculated from the recorded plant list giving a score to each species for the three environmental variables. Grime canopy height (calculated from the recorded plant species) is the average height the green plant parts of the vegetation can obtain at midsummer without management

[a] See Appendix 1 in ESM group D for further explanations of variables

[b] See Appendix 1 in ESM group E for further explanations of variables

Black-tailed Godwit occurrence

Of the 18 godwit fields, i.e. fields that a priori are expected to hold Black-tailed Godwits; the species was recorded both years in nine fields and in only one year in three fields, i.e. 67 % of godwit fields supported the species in at least one year. On the other hand, in the 18 ‘non-godwit fields’, the species was absent from 13 fields in both years (72 %), but it was observed in six fields (33 %) in at least one year.

In step (1) of the statistical analyses, soil dry matter was correlated with the Black-tailed Godwit numbers (Table 2). Among the variables of the field trenches, bare ground was positively related and Ellenberg moisture value negatively correlated to the Black-tailed Godwit numbers (a high Ellenberg moisture value for silt trenches indicates plant species growing in permanently wet soil, which are often taller and dense-growing species). Among the variables of physical structure in the fields, the presence of anthills was related negatively and bare ground positively with Black-tailed Godwit numbers. Variables derived from the field’s general vegetation data showed negative correlation with both number of plant species with a high potential green height and the actual measured vegetation height. Among variables derived from the field plot vegetation, both presences of moss-carpet and buttercup species (*Ranunculus* sp.) was positively related to Black-tailed Godwit numbers, but a negative correlation was found for the total number of plant species recorded in the plots. For the field edges, the presence in two or more of the four edges of grazed meadow vegetation of tall, nutrient richness-indicating species vegetation and of ungrazed rush were all negatively related with Black-tailed Godwit numbers. For the physical structures in the field edges (data group G), none of the variables was statistical significant. Among the management variables, farmer’s use of fertilizer was negatively related with Black-tailed Godwit numbers.

In step (2) of the statistical analyses, the number of plant species on the field with a high potential green height was negatively correlated with Black-tailed Godwit numbers, and both presences of moss-carpet and of bare ground in silt trenches showed a positive relationship (Table 2). For the field edges and management variables, both presence of grazed meadow vegetation (along more than two edges) and farmer’s use of fertilizer in the field were negatively related to Black-tailed Godwit numbers.

In step (3), the final statistical analysis, the presence of moss-carpet in the fields showed a positive relation to Black-tailed Godwit numbers, and number of plant species with potential green plant height $\geq$60 cm together with farmer’s use of fertilizer showed negative correlations (Table 3; Fig. 2).

Discussion

General vegetation structure

The study fields had few plant species and scored low mean botanical quality values for both the salt meadow and the fresh water meadows (Fredshavn et al. 2009) (Table 1). The mean Ellenberg moisture value indicated relatively dry conditions. The Ellenberg productivity value indicated a low nutrient demand—although not nutrient-poor conditions (Ellenberg et al. 1992). The structure of the fields varied much as indicated by the range (1.2–28.8 cm) in measured vegetation height in spring (see Table 1). Although 30 of the 36 fields are reseeded at intervals, our results indicate that they represent less intensively managed fields. Thus, the vegetation was influenced by white clover, naturally occurring grasses and buttercup species and not species such as perennial ryegrass, which is a commonly sown species in intensive managed Danish grasslands.

Black-tailed Godwit and plant species

The plant species that indicate the presence of Black-tailed Godwit were red clover var. *maritimum* which inhabit well-grazed coastal semi-natural meadows (i.e. low vegetation structure), and rough meadowgrass, which is a short-lived semi-rosette perennial grass species commonly occurring on grassland in open swards temporarily covered with fresh water (Grime et al. 1988). The other positive indicator species, moss-carpet, greater plantain and thyme-leaved speedwell, are all common on low productivity cultivated grassland several years after the last reseeding and with light open vegetation. The indicator plant species for non-godwit fields were all species from high nature quality coastal meadows with anthills, excluding common mouseear (*Cerastium caespitosum*) (for plant species defining high quality costal meadows, see Fredshavn and Ejrnæs 2007). This is in agreement with the negative relationship found between Black-tailed Godwit numbers and the presence of anthills. In this study, the anthills were present on some of the natural costal meadows that were undergrazed and had a lot of litter, partly caused by sea couch (*Elytrigia pungens*). Such sites were obviously not suitable for Black-tailed Godwits.

Most studies of breeding wader give only general descriptions of the habitat type as, e.g. low or wet grassland and fens or peat bogs, and do not include the vegetation in general nor the plant species as variable in the analyses. However, in the Netherlands, field preference studies show that Black-tailed Godwit is found in heterogeneous fields, i.e. fields with flowering forbs (*Ranunculus, Rumex* or *Taraxacum*), grasses other than *Lolium perenne* and a high

Table 2 Final model of the step 1 and step 2 analyses of the ANOVA mixed model showing relationships between the Black-tailed Godwit *Limosa limosa* numbers and the biotic and abiotic variable measured in the fields

Fields	Solution for fixed effects					Type 3 tests of fixed effects	
	Estimate	*df*	*SE*	*t* value	*P*	*F* value	*P*
Step 1 analyses							
A. Soil samples							
Intercept	−3.7135	33	1.6525	−2.25	0.0314		
Dry matter	2.0085	33	8.8180	2.46	0.0195	6.03	0.0195
B. Silt trenches							
Intercept	−0.0136	33	0.2773	−0.05	0.9612		
Bare spots in trenches	0.6457	33	0.2164	2.98	0.0053	8.91	0.0053
Ellenberg F (moisture) value	−0.1256	33	0.0539	−2.33	0.0262	5.42	0.0262
C. Physical field structure							
Intercept	−0.0604	32	0.1006	1.76	0.0880		
Anthill index	−0.5714	32	0.2016	−2.83	0.0079	8.03	0.0079
Bare spots in field	0.3267	32	0.1464	2.32	0.0328	4.98	0.0328
D. General field vegetation							
Intercept	1.0529	33	0.1649	6.38	0.0001		
Indication of species height	−1.0858	33	0.2824	−3.85	0.0005	14.78	0.0005
Measured vegetation height	−0.0203	33	0.0092	−2.20	0.0346	4.86	0.0346
E. Field vegetation in plots							
Intercept	−0.0296	31	0.4427	−0.07	0.9472		
Moss index	0.6834	31	0.1860	3.67	0.0009	13.50	0.0009
Buttercup index	0.5822	31	0.2454	2.37	0.0241	5.63	0.0241
Number of plant species	−0.8098	31	0.4033	−2.01	0.0534	5.22	0.0293
Field edges							
F. Vegetation							
Intercept	0.7957	32	0.1214	6.55	0.0001		
Grassed meadow vegetation	−0.5999	32	0.1567	−3.83	0.0006	14.65	0.0006
Tall, nutrient indicating species	−0.5552	32	0.1821	−3.05	0.0046	9.29	0.0046
Un-grassed rush	−0.5363	32	0.2527	−2.12	0.0417	4.50	0.0417
G. Physical structure							
H. Management							
Intercept	0.7270	33	0.1630	4.46	0.0001		
Fertilizing	−0.3610	33	0.1546	−2.33	0.0258	5.45	0.0258
Step 2 analyses							
Fields (groups A–E)							
Intercept	−0.0795	32	0.2018	−0.39	0.6961		
Indication of species height	−1.0637	32	0.2169	−4.90	0.0001	24.04	0.0001
Moss index	0.5767	32	0.1655	3.48	0.0015	12.14	0.0015
Bare spots in silt trenches	0.4182	32	0.1807	2.31	0.0272	5.36	0.0272
Field edges and management (groups F–H)							
Intercept	0.8035	32	0.1171	6.86	0.0001		
Grazed meadow vegetation	−0.5393	32	0.1447	−3.73	0.0007	13.89	0.0007
Fertilizing	−0.3420	32	0.1386	−2.47	0.0192	6.09	0.0192
Tall, nutrient indicating species	−0.3492	32	0.1722	−2.03	0.0509	4.11	0.0509

All statistical significant variables ($P < 0.05$ in the Type 3 analyses) are allocated into eight structural and functional groups (A–H) in the step 1 analyses. These variables entered the step 2 analyses. In group G, physical structure in field edges, no variables were statistical significant. Concerning variables in the different groups, see Appendix 1 in ESM

Table 3 Final model of the step 3 analysis of the ANOVA mixed model showing relationships between the Black-tailed Godwits number and significant ($P < 0.01$) biotic and abiotic variables from the step 2 analyses (see Table 2)

Step 3 analyses	Solution for fixed effects					Type 3 tests for fixed effects	
	Estimate	*df*	*S E*	*t* value	*P*	*F* value	*P*
Intercept	0.4618	31	0.1891	2.44	0.0205		
Fields, indication of species height	−0.9461	31	0.2124	−4.45	0.0001	19.85	0.0001
Fields, moss index	0.6254	31	0.1469	4.26	0.0002	18.12	0.0002
Management, fertilization	−0.2853	31	0.1011	−2.82	0.0083	7.96	0.0083

variability of sward height (Verhulst et al. 2011). A plant list of dominating species from conventional fields and 'reserve' fields is presented by Schekkerman and Beintema (2007) showing that *Lolium perenne* and *Poa trivialis* dominated in conventionally managed agricultural fields, and, similarly, *Holcus lanatus, Alopecurus pratensis* and *Anthoxanthum odoratum* in 'reserve' fields. Among these five grass species, *Poa trivialis* was a positive indicator species for Black-tailed Godwit in our study. Dominance of species from drier grassland in this Dutch study indicates differences in plant community between the two studies. From British marshlands, only a general description of plant species are given, and among these are marsh foxtail and creeping bent (Eglington 2008). These two species were among the dominating species in our study indicating their general appearance in moist to wet grasslands, but they were not indicators for godwit fields. Creeping bent is a stoloniferous perennial species, which makes a dense sward in permanently wet areas, without open vegetation with moss-carpet and spots of bare ground. Furthermore, if not heavily grazed, this species produces large amounts of litter. The use of plant species as indicators for breeding waders has also been used for nest sites descriptions, important in relation to predation risk (Whittingham et al. 2002; Thyen and Exo 2005).

Black-tailed Godwits and environmental variables

The highest Black-tailed Godwit numbers were found in unfertilized fields with short vegetation and the presence of moss-carpet. In the Netherlands, it was also found that Black-tailed Godwit preferred fields with little or no fertilizer use, and that the parents led their chicks to these fields where the mean invertebrate size was larger and chick growth and survival higher, compared to conventionally managed fields that were often mowed earlier due to the use of largers amount of fertilizer being applied (Beintema et al. 1985; Schekkerman and Beintema 2007; Breeuwer et al. 2009). Wader chicks in British grazed grasslands preferred a sward height of 2–10 cm (range 0–30 cm) (Eglington et al. 2008), which is within the same height as found for the godwit fields in our study, although 1 month later in the growing season. Open swards and vegetation structure were also favoured by feeding godwit young and associated with higher survival in the Netherlands (Breeuwer et al. 2009; Kleijn et al. 2010). Moss-carpet as an indicator for breeding Black-tailed Godwits has not been described before, but its significance emerged from two different statistical analyses (the plant and the environmental analyse), which suggests that the relationship is a robust one. Moss-carpet indicates the importance of open and low-growing plant communities undisturbed for a long period of years.

The significance of water was shown by a positive effect of silt trenches with bare ground (significant at the step 2 level of the statistical analysis) and occurrence of the indicator species, rough meadowgrass (see above). However, precipitation was low during spring in both 2007 and 2008 (Danish Metrological Institute data), and the presence of rough meadowgrass and of bare ground in silt trenches indicated the presence of open water prior to the breeding season, and probably also during the initial phase of the breeding season in years with normal precipitation conditions. Our findings are supported by results from British lowland grasslands, where silt trenches and foot drains together with associated bare ground were found to be important for adult Black-tailed Godwits and their chicks (Eglington et al. 2008) and for Redshanks *Tringa totanus* (Smart et al. 2006). In the Netherlands, Black-tailed Godwit chick survival also increased with raised ground water (Breeuwer et al. 2009).

However, the breeding habitat and Black-tailed Godwits cannot be considered as static. Previously, the species bred in poorly drained pastures, waterlogged marginal farmland or grasslands managed as meadows, and especially areas grazed in spring and flooded during winter, that results in bare muddy patches (Cramp and Simmons 1983). In the beginning of the last century, it started to breed in cultivated land and numbers increased (Schroeder 2010). By 1960, the species was mainly found on grassland and few remained on peat bogs and fens. However, the increased

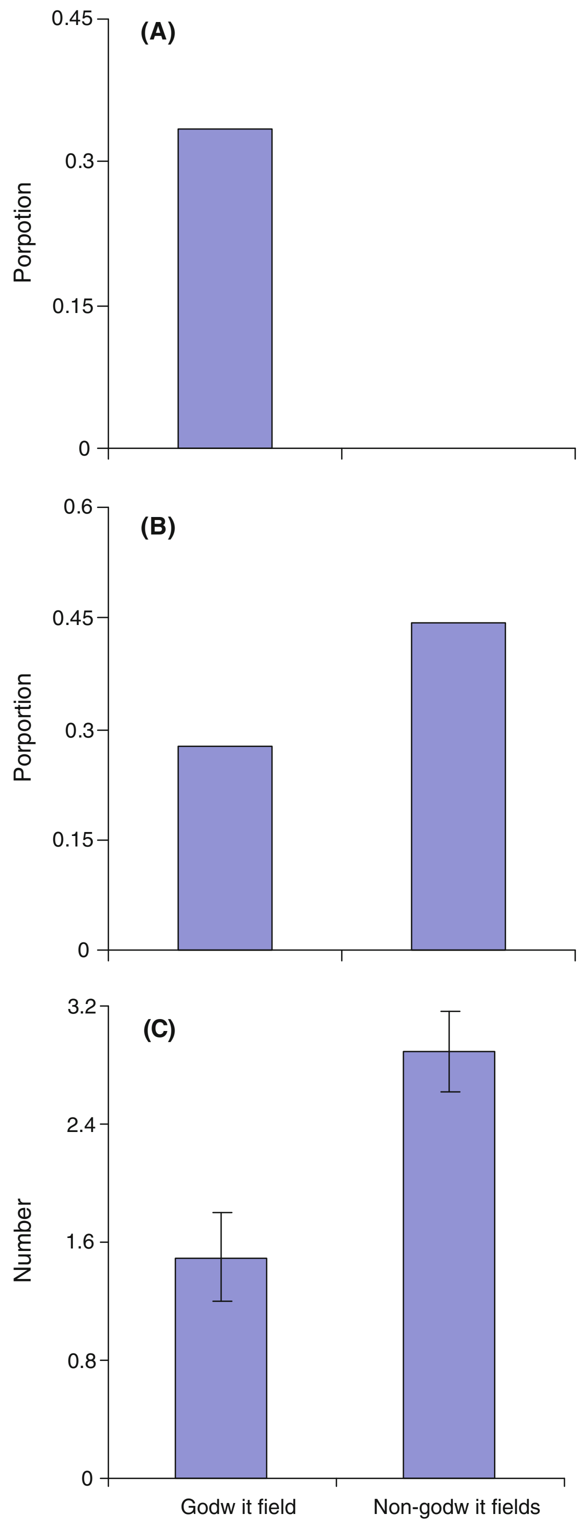

Fig. 2 Proportion of fields with **a** moss-carpet and **b** use of fertilizer together with the **c** number (mean ± SE) of plant species with potential vegetation height ≥60 cm in godwit fields and in non-godwit fields. The three variables show statistical significant correlations with the Black-tailed Godwit numbers ($P < 0.01$; see (Table 3)

application of fertilizers and intensified agriculture management (water drainage, fast-growing plants) reduced plant and insect diversity, affecting bird reproduction and numbers (Breeuwer et al. 2009; Schroeder 2010). The phenotype of male Black-tailed Godwits has apparently changed (males have become paler) since c.1840, associated with the shift from natural and semi-natural habitats to cultivated fields (Schroeder 2010). Thus, selection may potentially have favoured less aggressive males as breeding areas changed and the species increasingly associated with human activity and agricultural management.

Site fidelity of Black-tailed Godwit

Site faithfulness is common amongst migrating shorebirds and helps them to settle rapidly (Schroeder 2010). Breeding Black-tailed Godwits and other meadow bird species demonstrate a high degree of site fidelity and often breed in the same fields during successive years (Buker and Winkelman 1987). This attribute is positively correlated with breeding success whilst habitat quality is constant (Thomson and Hale 1989; Groen 1993; Roodbergen et al. 2008). These studies suggest that some conditions in the selected fields are stable over several years and that Black-tailed Godwits prefer fields which experience more or less constant environmental conditions year after year. The site selection process studied by colour-marked birds show that all birds are observed near their previous year's nest-site, and that a decision to move is only made after considerable time investment there, which indicates that site faithfulness is conditional on experiences after return to the nesting area (Schroeder 2010). The most frequent reason to change nest site seem to be changes in vegetation height and defence against predators (assemblage in semi-colonies). We also found indications of site fidelity, since 67 % of the selected godwit fields were used by the species in at least 1 of 2 years. However, out of the 18 non-godwit fields, we observed Black-tailed Godwits in six fields (33 %). On the other hand, selection of these fields in the first place was only based on 1 year's monitoring and therefore their initial status is uncertain. Despite between-year changes in the distribution of bird species, it is generally accepted that individuals select the most optimal sites as their first choice (Sutherland 1983; Gunnarsson et al. 2006), and that these choices have a positive influence on the species' survival rate (Gill et al. 2001). Since we found a high degree of site fidelity, we assume that optimal fields for the species breeding are within the selected field sample. On the other hand, habitats obviously looking suitable during settlement can function as ecological traps with no or low breeding success.

Proximate versus direct variables for management

We have used proximate variables, i.e. botanical and environmental variables, in this study, and have identified indicator plant species, structures and management methods that reflect Black-tailed Godwit occupancy and can focus future management efforts (see Appendix 2 in ESM). Other studies have shown strong links between farming management and more direct variables related to survival, i.e. arthropod density (Benton et al. 2002). It is shown that traditional, grazed grassland has three to four times the arthropod biomass compared to conventional (rotational) arable land (Eglington et al. 2010), and also that high bird density correlates with arthropod density (Southerwood and Cross 1969). Furthermore, relationships exist between areas with high arthropod density and higher survival of wader chicks (Johansson and Blomquist 1996; Blomquist and Johansson 1995; Schekkerman and Beintema 2007; Eglington et al. 2010). Studies show that increasing wetness in dry grasslands raises the arthropod density, and that wader chicks during their first weeks after hatching have higher survival rates in those parts of the marshes that have small water-logged areas or high groundwater levels compared to drier parts (Schekkerman and Beintema 2007; Eglington et al. 2010). These results are supported by studies in Danish marshlands showing that sub-surface-drained dry grasslands together with dry fields in yearly rotation were not attractive to breeding wader species compared to undrained, semi-natural grazed grasslands (Kahlert et al. 2007). The introduction of agri-environmental schemes (AES; i.e. reduced fertilizer and retaining of surface water) to dry grasslands failed to change bird densities at these sites. However, the density of waders increased on semi-natural grassland never subjected to sub-surface draining when run-off was retained in field trenches (Kahlert et al. 2007). The importance of silt trenches was also found in south-west England for Redshanks and Lapwings *Vanellus vanellus* breeding in larger densities in fields with a dense pattern of these ditches, which were used by feeding birds (Milsom et al. 2002). Late winter high groundwater levels are obviously important for breeding meadow birds for a number of reasons: (1) they retard sward development and delay agricultural activities such as mowing and grazing (Beintema et al. 1997), (2) they keep the upper soil level moist and soft, facilitating birds probing for prey, and (3) they increase the accessible food biomass for breeding waders, i.e. macro-invertebrates, especially leatherjacket larvae *Tipulidae* sp. and earthworms (Ausden et al. 2001; Kleijn and van Zuijlen 2004). Thus, several studies show strong connections between botanical and environmental indicators suggesting the high value of extensively managed fields for Black-tailed Godwits as found in this study and the value of such fields for waders' feeding condition, breeding results and survival.

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