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Coastal grassland wader abundance in relation to breeding habitat characteristics in Matsalu Bay, Estonia

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Wader populations have been declining worldwide, providing a fundamental question as to which environmental factors limit population growth. Many studies have focused on the effects of habitat change on wader populations as a result of climate change, agricultural intensification or abandonment of arable land. However, there are few studies investigating the relationship between wader distribution/abundance and prey abundance. This study focused on the relationship between breeding wader abundance, habitat characteristics and prey abundance on different types of coastal and floodplain grasslands. The study was carried out in the Matsalu Bay area, Western Estonia between 2001 and 2005. Results showed that most wader species were strongly related to habitat flooding type but not to plant species richness or evenness or mean vegetation coverage. Abundance of epigeic earthworms at a site was positively correlated with wader species diversity and abundance, as well as at the individual species level for abundance of Northern Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa* and Redshank *Tringa totanus*. Endogeic earthworm abundance was not significantly related to total wader abundance, although for some species there was a weak negative relationship. We conclude that epigeic earthworms are an important food source for most wader species on Matsalu grasslands and endogeic earthworms are not likely to be utilised as a prey source. Wader abundance was most strongly related to flooding as a determinate factor for breeding habitat characteristics and with epigeic earthworms as a food source. These factors are important environmental variables influencing local abundance and distribution of coastal waders.

1. Introduction

Wader populations have suffered recent declines worldwide (Delany *et al*. 2009). This decrease in numbers and the fragmentation of breeding ranges of shorebirds is of particular concern throughout Europe. Many authors have shown that several wader populations that utilise short-grass habitats on the Baltic Sea coast for breeding have declined during the second half of the 20th century (Kumari 1958, Kuresoo & Mägi 2004, Rönkä *et al*. 2006, Delany *et al*. 2009, Kuresoo 2010).

In Estonia, as with the whole Baltic Sea region, considerable changes in wader populations have been taking place. Species such as Ruff *Philomachus pugnax*, Great Snipe *Gallinago media*, Great Ringed Plover (hereafter Ringed Plover) *Charadrius hiaticula*; Baltic Dunlin (hereafter Dunlin) *Calidris alpina schinzii* and Black-tailed Godwit *Limosa limosa* have suffered substantial population declines over the last forty years (Elts *et al*. 2013). Conversely, some species such as Northern Lapwing *Vanellus vanellus* have increased, or maintained stable populations, i.e., Common Snipe *Gallinago gallinago*, in recent decades (Kuresoo 2010, Elts *et al*. 2013). Due to the critical population sizes and continued population declines, both Ruff and Dunlin have been listed as endangered, category I protected species in Estonia, and action plans for their protection were implemented in 2010 (Mägi & Pehlak 2008, Erit *et al*. 2008).

Previous studies have shown that changes in land management cause a reduction in habitat quality and availability, which significantly affects local abundance of waders (Durant *et al*. 2008, Zwarts *et al*. 2009, Groen *et al*. 2012, Verkuil *et al.* 2012). Water level, flooding, micro-topography, vegetation and food availability are all factors that can significantly influence the abundance and diversity of wader communities (van de Kam *et a*l. 2004, Huntley *et al*. 2007, Delany *et al*. 2009, Møller *et al*. 2010, Verkuil *et al*. 2012). Relatively few studies have investigated the abundance of breeding waders in relation to prey abundance as a possible limiting factor (Högstedt 1974, Beintema *et al*. 1991, Schekkerman & Beintema 2007). In addition to environmental factors, increased human disturbance and associated nest and chick predation have also been found to negatively impact local abundance of waders (van de Kam *et a*l. 2004, Møller *et al*. 2010, van der Vliet *et al*. 2010).

The aim of this study is to assess the relationship between grassland wader abundance, breeding habitat characteristics and prey abundance, in order to identify the primary factors influencing, and potentially limiting, local population size. For this purpose we used the Matsalu Bay area where waders have been monitored almost continuously since the 1960s, providing a long term dataset of population trends in this area

2. Methods

2.1. Study area

This study took place in 11 meadow parcels located on the south and east sides of Matsalu Bay. Matsalu Bay is situated on the west coast of Estonia (between 58°49’ N, 23°26’ E and 58°42’ N, 23°48’ E) (Fig. 1) and is part of BirdLife International’s Väinameri Important Bird Area (IBA) and a Ramsar Site. The coastal grasslands located there are maintained using a combination of low intensity grazing/mowing regime to create an open sward, and are included in the Natura 2000 habitat type “Boreal Baltic archipelago, coastal and land upheaval areas, Boreal Baltic coastal meadows”, code 16 (Sundseth 2009). Matsalu floodplain grasslands are situated around the Kasari River delta and are included in Natura 2000 habitat type “Semi-natural tall-herb humid meadows, northern boreal alluvial meadows”, code 64 (Eriksson 2008). According to Ivask *et al*. (2006, 2007), four broad vegetation types of grasslands have been

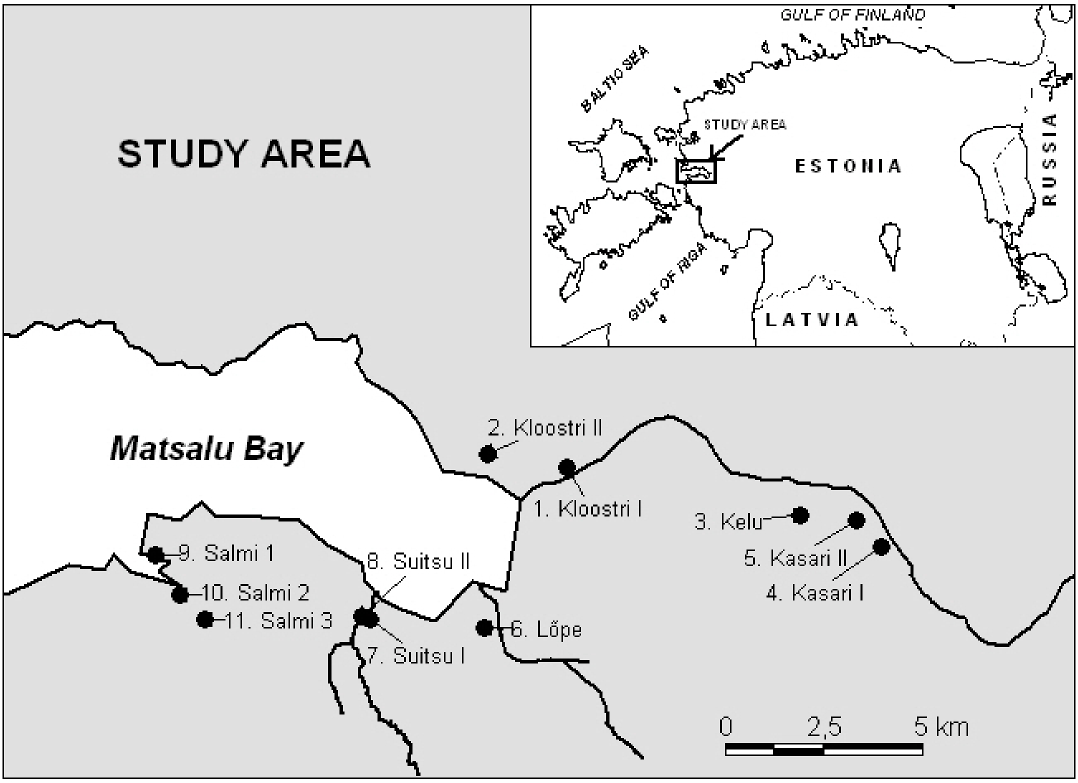

Fig. 1. Location of the study area and study sites in 2001–2005. Habitat characteristics of the study sites are presented in Appendices 1 and 3.

identified in the study area on the basis of the moisture regime and salinity gradient: coastal, transient, fresh and wet floodplain grasslands (Fig. 1, Appendix 1).

2.2. Bird censuses

Within Matsalu Bay, wader abundance has been monitored almost continuously along the south coast of the bay since 1960 and on the River Kasari floodplain since 1983. Censuses on the coastal grasslands were interrupted between 1975–1981 and 1988–1991 (Kuresoo & Mägi 2004). The survey method, used since 1960, consisted of one observer walking along fixed census transects who recorded all territorial birds in a survey belt of unlimited width. The observer counted territorial birds or pairs, and a common census unit of breeding pairs per kilometre (pairs km^{-1}) was derived. Censuses were carried out twice during the breeding season, in the second half of May and the first half of June, between sunrise and midday. Onno (1963) estimated the accuracy of this method to be 30–80% dependent on species.

Censuses of breeding waders were conducted at all study sites (Fig. 1) in 2001, 2002 and 2003, using the same census method employed since 1960. Transect length varied in different study sites from 0.6 to 2.7 km and the total length of transects in all sites was 16.5 km (Appendix 2). Three-year average numbers of birds were calculated for analysis. The main criterion for study site and transect selection was that they should include all four types of grassland in the Matsalu area (Ivask *et al.* 2006) and that the length of census transects should be proportional to the total area of different habitats.

2.3. Habitat characteristics and prey fauna

A study was conducted in 2003 at each of the sites (Fig. 1) to identify land management, vegetation, and soil characteristics. In addition, abundance of earthworms and epigeic macroinvertebrate fauna were assessed. Spring flooding in 2003 and 2004 hindered the bird censuses and made completion of the field studies impossible; these were delayed until 2005. In the analyses, an assumption was made that land use, vegetation and invertebrate fauna parameters of 2005 were representative of the period 2001–2003, as previous studies have shown little change in vegetation and invertebrate fauna over this time scale (Ivask *et al.* 2006, 2007).

A survey of habitat characteristics (vegetation, edaphic factors and invertebrates) was conducted at all sites in July 2005 (Appendix 2). The habitat assessment consisted of recording a series of 1 m^2 plots (5 to 7 dependent on vegetation heterogeneity, total 57 plots) along a 100 m long transect and recording all plant species, percentage cover of each species, mean vegetation height and height class, and within-site plant species evenness. Vegetation within-site evenness was calculated using the Shannon index of evenness: $J' = H' / \ln(S)$, where H' is the Shannon-Wiener diversity index and S is species number (Pielou 1969). Within each 1 m^2 plot, relevant soil ecological parameters for each plant community were assessed indirectly using Ellenberg's plant species indicators values from 1 to 6 (Lindacher 1995) (Table 1, Appendix 1).

Soil characterisation was conducted by randomly examining five soil blocks (50 cm × 50 cm × 40 cm) at each study site. Within each soil block, soil moisture content (105°C), pH, organic matter (loss on ignition at 360°C), nitrogen concentration (Kjeldahl method), soluble phosphorus concentration (lactate extractable method), K and Na concentration (flame photometry) and the hydrolytic activity of the microbial community were measured. Total activity of the microbial community was measured by the fluorescein diacetate method, which estimates the activity of dehydrogenase enzymes in a composite sample (Schnürer & Roswall 1982). Edaphic parameters were measured in order to identify explanatory variables for the soil environment and reduce the number of variables by applying generalized linear models (GLMs) to analyse relationships between the abundance of waders and habitat characteristics.

Flood characteristics were not measured between 2001 and 2005. In November 2012, automatic sensors Solinst Levelloger Junior 3001 were installed at the study sites. Using these sensor data, spring flood level and duration in 2013 were recorded (Appendix 1). Unfortunately these first measurements of flood duration could not be used in the analysis to establish the actual impact and relative importance of this potential factor on wader abundance. However, these data characterize flooding duration in the different grassland types studied.

Being an important food source for several wader species (Blotzheim *et al.* 1975, Rhymer *et al.* 2010) earthworm abundance within the soil samples was measured. This was undertaken by combining two methods: (i) hand sorting of live earthworms from soil blocks (Meyer 1996), and (ii) where hand sorting was impracticable due to high water table, overly wet soil or unfavourable soil texture, a 15% solution of mustard was used as a vermifuge (Gunn 1992). Live earthworms were washed, kept in the refrigerator for 48 hours, counted and weighed. All individuals were identified to species level and the mean number of individuals per 1m^2 of soil surface were calculated (Appendix 3). Epigeic invertebrate fauna, defined in this study as ground dwelling macro-invertebrates, were captured using pitfall traps. Pitfall traps (0.07 m diameter plastic containers) were located at 10 m intervals along the 100 m transect at each site. Trap containers were quarter filled with a 20% salt (NaCl) solution and covered with a raised cap to prevent rainwater diluting the salt solution. Traps were emptied after 5 days and all individuals identified to species (*Carabidae*) or family (all other taxonomic groups) level. At study site 10, several characteristics were not recorded due to unsuitable weather conditions.

2.4. Statistical analysis

Spearman's rank correlation was used (R) to estimate general relationships between the abundance and number of wader species and habitat characteristics (vegetation type, flooding type, utilization type and characteristics, basic vegetation and floristic characteristics, Ellenberg's indicators (1–6), and earthworm and epigeic macroinvertebrate fauna characteristics). As the explanatory variables (both the habitat and prey parameters) acted at the site level, data from different sub-plots and traps were averaged per site. The Statistica 7.0 software package was used for these calculations and significant correlations were found between

Table 1. Variables used in analyses, together with their abbreviations and values or range of values. For missing values see Appendices 1–3.

Variable	Abbre-viation	Value
Vegetation type	VGT	1 = coastal grassland; 2 = transient grassland; 3 = fresh floodplain grassland; 4 = wet floodplain grassland
Flooding type	OFT	1 = saline water; 2 = saline and fresh water; 3 = fresh water
Utilization type	UTT	1 = cows; 2 = mixed herd; 3 = mowing; 4 = combination of pasture and mowing
Numbers of plant species in 1 m^2 plot	NPS	Range 11–44 plant species per plot
Mean number of plant species / m^2	MNS	Range 1.8–20.0 plant species/m2
Grass height class	GHC	1 = low (less 30 cm); 2 = medium (30–70 cm); 3 = high (more 70 cm)
Appearance of foggage	FGA	1 = no; 2 = yes
Mean vascular plant coverage (%)	MPC	Range 75–100%
Mean vegetation Evenness	MVE	Range 0.52–0.71
Ellenberg's indicator 1 (temperature)	Etemp	Range 1.46–5.40
Ellenberg's indicator 2 (light)	Elight	Range 6.53–7.34
Ellenberg's indicator 3 (continentality)	Econt	Range 0.46–3.49
Ellenberg's indicator 4 (moisture)	Emoist	Range 4.02–8.64
Ellenberg's indicator 5 (salinity)	Esal	Range 0.00–4.68
Ellenberg's indicator 6 (nitrogen)	Enit	Range 2.75–4.96
Number of earthworms / m^2	Ne	Range 0–102
Number of earthworm species / m^2	Se	Range 0–7
Biomass (g) of earthworms / m^2	Be	Range 0.00–34.78
Number of endogeic earthworms / m^2	Endo	Range 0–88
Number of epigeic earthworms / m^2	Epi	Range 0–32
Number of epigeic invertebrates per trap	Nepi	Range 23.00–85.9
Number of species/taxon per transect	Sepi	Range 11–23
Soil moisture content (%)	Smc	Range17.75-65.88
Soil acidity (KCl)	pH	Range 5.26-7.46
Organic matter (%)	Org	Range 6.64-31.97
Soluble phosphorus concentration (mg / 100 g dry soil)	P	Range 1.14-10.7
Potassium concentration (mg / 100 g dry soil)	K	Range 3.8-50.7
Sodium concentration (mg / 100 g dry soil)	Na	Range 8.5-63.2
Hydrolytical activity of microbial community (OD / g dry soil)	Microb	Range 0.912-2.01

15 bird fauna, 24 habitat and 5 prey fauna variables.

A generalized linear model (GLM) was used to analyse the relationship between wader abundance, habitat characteristics and prey abundance. For this, the average number of each wader species per site in the period 2001 to 2003 (response variables) was related to the measured habitat characteristics and average prey numbers sampled at the same sites in 2005 (predictor variables). As abundance data were not normally distributed, they were analysed using log-linear models employing the Poisson distribution and using a log-link function (McCullough & Nelder 1989). The full model was generated, consisting of flooding + mean vascular plant Shannon evenness + number of invertebrates + number of epigeic earthworms + number of endogeic earthworms + hydrolytical activity of microbial community + Potassium concentration. All analyses were performed using Statistica 7 (StatSoft, Inc. 2004). For several waders in the original datasets (Oystercatcher *Haematopus*

Table 2. Relationships (GLMs) between the three-year average numbers of waders (total numbers, particular species) and habitat characteristics and total prey numbers (explanatory variables) per site. Abbreviations of the explanatory variables are given in Table 1. Statistically significant relationships are given in bold. θ = Wald test statistic.

Wader species	Statistic	OFT	MVE	Nepi	Epi	Endo	Microb	K
Waders total	Estimate	1.0533	2.9225	–0.0157	0.0471	–0.0127	0.0584	0.0232
	SE	0.1799	3.8719	0.0071	0.0187	0.0045	0.3990	0.0096
	θ	34.2651	0.5697	4.8356	6.3254	8.0473	0.0214	5.8691
	P	**0.0000**	0.4504	**0.0279**	**0.0119**	**0.0046**	0.8836	**0.0154**
Lapwing	Estimate	1.5716	3.1523	–0.0221	0.1144	–0.0167	0.5899	0.0491
	SE	0.3683	8.1384	0.0155	0.0437	0.0103	0.8755	0.0213
	θ	18.2069	0.1500	2.0188	6.8566	2.5981	0.4540	5.2968
	P	**0.0000**	0.6985	0.1554	**0.0088**	0.1070	0.5004	**0.0214**
Dunlin	Estimate	16.0716	–10.4440	–0.2550	–0.0486	–0.0086	–4.9590	0.4039
	SE	0.9868	16.8890	0.0309	0.0608	0.0183	1.9219	0.0434
	θ	265.2700	0.3824	67.9120	0.6409	0.2227	6.6577	86.6157
	P	**0.0000**	0.5363	**0.0000**	0.4234	0.6367	**0.0099**	**0.0000**
Common Snipe	Estimate	–0.6594	26.9663	0.0703	0.0395	–0.0255	4.7804	–0.0927
	SE	0.5412	11.4324	0.0623	0.0343	0.0092	2.6463	0.0829
	θ	1.4842	5.5638	1.2747	1.3202	7.7208	3.2631	1.2502
	P	0.2231	**0.0183**	0.2589	0.2506	**0.0055**	0.0709	0.2635
Curlew	Estimate	0.3261	–8.7479	0.0078	–0.0009	–0.0089	–0.4976	–0.0330
	SE	0.6250	10.7515	0.0244	0.0403	0.0126	1.3803	0.0315
	θ	0.2723	0.6620	0.1016	0.0005	0.4985	0.1299	1.1000
	P	0.6018	0.4158	0.7500	0.9826	0.4802	0.7185	0.2943
Redshank	Estimate	1.7317	–1.8781	–0.0106	0.0479	–0.0047	0.2066	0.0252
	SE	0.6108	13.2284	0.0240	0.0604	0.0156	1.2190	0.0296
	θ	8.0374	0.0202	0.1951	0.6279	0.0906	0.0287	0.7276
	P	**0.0046**	0.8871	0.6587	0.4281	0.7634	0.8654	0.3937

ostralegus, Ringed Plover, Ruff, Great Snipe, and Common Sandpiper *Actitis hypoleucos*) the application of the GLM was not possible due to the low number of observations. As most of the explanatory variables appeared to be strongly related to flooding a Nonmetric Multidimensional Scaling (NMS) ordination of variables was performed, with all other explanatory variables reduced to this variable (McCune & Grace 2002). The NMS was performed using PC-Ord 5.0 for Windows (McCune & Mefford 2006).

3. Results

3.1. Relationship between wader abundance and breeding habitat characteristics and prey abundance

In total, eleven wader species were found breeding in the 11 study sites in the Matsalu Bay study area between 2001 and 2003 (Appendix 2, Fig. 1). The three-year mean (between 2001 and 2003) of all breeding waders varied between 5 and 124 pairs km^{-1} dependent on site. Total wader abundance was greatest on saline coastal grasslands, followed by fresh floodplain grasslands, transient grasslands and wet floodplain grasslands (Appendix 2). The number of bird species in each study site varied from three to nine, the highest number being on marine coastal grasslands and the lowest on floodplain grasslands. The three-year mean total abundance of all species over the whole study area in 2001–2003 was 37.4 pairs km^{-1}. The most abundant species was Lapwing followed by Common Snipe, Dunlin and Redshank *Tringa totanus*. Curlew and Redshank were found at all study sites and all grassland types, whereas Great Snipe and Common Sandpiper were at only one site and one grassland type (Appendix 2).

The number of plant species per 1 m^2 plot (small-scale species richness) and total coverage

Table 3. Spearman rank correlation coefficients (*R*) between the total number of wader species and their numbers and habitat characteristics and total prey species and numbers per site. Abbreviations of the variables are given in Table 1. Significance levels: ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. NPS = number of plant species; enit = Ellenberg's nitrogen; esal = Ellenberg's salinity; emoist = Ellenberg's moisture; se = number of earthworm species; ne = number of earthworms / m^2; epi = number of epigeic earthworms; endo = number of endogeic earthworms.

	Species total		Waders total		Lapwing		Dunlin		Black-tailed godwit		Curlew		Redshank	
Variable	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*	*R*	*P*
NPS	–0.09	ns	–0.05	ns	–0.26	ns	0.05	ns	0.19	ns	–0.79	*	–0.22	ns
Enit	–0.31	ns	–0.35	ns	–0.17	ns	–0.43	ns	–0.53	ns	0.85	**	–0.08	ns
Esal	0.5	ns	0.41	ns	0.5	ns	–0.80	**	0.6	ns	–0.21	ns	0.56	ns
Emoist	–0.50	ns	–0.56	ns	–0.43	ns	–0.77	**	–0.64	*	0.66	*	–0.36	ns
Se	–0.64	*	–0.64	*	–0.65	*	–0.64	*	–0.41	ns	–0.43	ns	–0.54	ns
Ne	–0.68	*	–0.80	**	–0.74	**	–0.66	*	–0.68	*	–0.31	ns	–0.65	*
Epi	0.64	*	0.74	**	0.71	*	0.73	*	0.78	**	0.36	ns	0.71	*
Endo	–0.44	ns	–0.45	ns	–0.51	ns	–0.49	ns	–0.56	ns	–0.78	**	–0.53	ns
Be	0.32	ns	–0.44	ns	–0.46	ns	0.31	ns	–0.23	ns	–0.56	ns	–0.41	ns

of vegetation were highest on transient species-rich paludified grassland, and lowest on wet flood-plain grassland with tall sedges (Table 1, Appendices 1 and 3, and Fig. 1). The Shannon evenness index of vegetation varied between 0.51 and 0.71, being highest on coastal grasslands and lowest on wet floodplains (Appendix 3).

In the GLM, mean vegetation evenness (MVE) was not significantly related to the total abundance of waders although it was significantly related to Common Snipe abundance (Table 2). Plant species richness was not significantly correlated with the total abundance of all waders, although it was correlated with Curlew (Table 3). In the GLM,

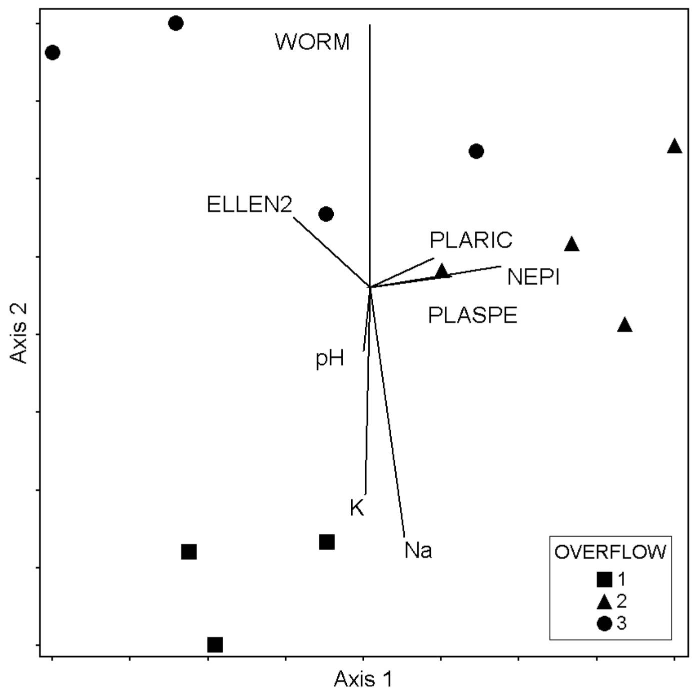

Fig. 2. NMS ordination plot related to flooding (Overflow). Flooding types: 1 – Brackish water; 2 – Mixture; 3 – Freshwater. Abbreviations: NEPI = Numbers of epigeic macroinvertebrates; WORM = Numbers of earthworms; ELLEN 2 = Ellenberg's 2 index; K = Potassium concentration; Na = Sodium concentration; PLARIC = Small-scale plant species richness; PLASPE = Number of plant species; pH = Acidity.

Table 4. Characterization of investigated invertebrate's communities in 2005 according to meadow type I–IV. I = Wet floodplain grassland, II = Fresh floodplain grassland, III = Transient grassland, IV = Coastal grassland. (Average ± SE). Location of study sites are indicated in Figure 1.

Characteristics	I	II	III	IV
Study sites	1, 2	3, 4, 5	6, 7, 8	9, 10, 11
Mean no. earthworm spp. per study area	1.66 ± 0.88	4.67 ± 1.2	4 ± 1	3 ± 1
Mean no. earthworms / m^2	13.33 ± 8.11	58.33 ± 22.15	55.33 ± 25.54	53 ± 31
Mean earthworm biomass g / m^2	5.15 ± 3.54	54.08 ± 8.04	42.66 ± 9.51	6.71 ± 2.1
Mean no. epigeic invertebrate groups per trap	17.67 ± 2.03	20.67 ± 1.86	15 ± 2	14 ± 1
Mean no. epigeic invertebrates per trap	32.27 ± 5.58	62.33 ± 11.85	32.6 ± 6.26	35.45 ± 9.05

flooding type (OFT) was found to be strongly related to the total of all wader species combined, and with the abundance of all individual bird species with the exception of Common Snipe and Curlew (Table 2). This relationship with abundance was positive for all wader species combined and for Lapwing, Dunlin and Redshank individually (Table 2). Both Curlew and Common Snipe were found to have a non-significant relationship with OFT (Table 2). This indicates that most typical coastal waders prefer breeding habitats with temporal flooding. Regarding soil parameters, potassium was found to be significantly, although not strongly related to the abundance of all waders combined, and to that of Lapwing and Dunlin individually (Table 2).

The results of the Spearman rank correlation analyses showed that Emoist was strongly negatively correlated with the abundance of Dunlin and Black-tailed Godwit, and positively correlated with the abundance of Curlew (Table 3). Salinity was negatively correlated with the abundance of Dunlin (Table 3). Nitrogen was positively correlated with the abundance of Curlew (Table 3).

The results of the NMS ordination analysis indicated that flooding determines 92.7% of the other explanatory variables, including soil and vegetation parameters and prey abundance (Fig. 2). Furthermore it suggests that total earthworm abundance is negatively related to Na and K in the soil and that earthworm abundance is greater where inundation is by fresh water, or mixed brackish and fresh water, as opposed to fully brackish (Fig. 2).

Small-scale plant species richness, plant species diversity, pH, light, and the number of epigeic invertebrates, were less influenced by flooding type than total worm abundance, soil K and soil Na.

A total of 44 epigeic macroinvertebrate species and higher taxa were collected from the pitfall traps in 2005. Diversity was greatest on transient grasslands (Σ 34 taxa for 3 sites), followed by wet floodplain grasslands (Σ 27 taxa for 2 sites), marine coastal grasslands (Σ 26 taxa for 3 sites) and fresh floodplain grasslands (Σ 22 taxa for 3 sites). The mean number of epigeic invertebrate groups per trap was greatest on fresh floodplain grasslands, followed by wet floodplain grasslands, transient grassland and coastal grassland respectively (Table 4). Mean total species diversity of epigeic macroinvertebrate fauna was greatest on marine coastal grasslands (99.3 ± 26.9 species and higher taxa; average ± SE); followed by wet floodplain grasslands (61.1 ± 10.0), fresh floodplain grasslands (50.8 ± 8.3) and transient grasslands (50.5 ± 6.0). The mean number of epigeic invertebrates per trap was significantly related to the abundance of Dunlin (Table 2), but there was no significant relationship with other species.

Site variability of earthworm species diversity was dependent on grassland type and varied between one and seven species per site. Mean earthworm species per site were: three (coastal grasslands), four (transient grasslands), five (fresh floodplain grasslands) and two (wet floodplain grasslands) (Table 4, Appendix 3). In total, eight earthworm species were detected across all sites in 2005. No earthworms were found at two coastal meadow sites close to the sea shore. The mean number and biomass of all earthworms per m^{-2} of soil surface per site was greatest on fresh floodplain grasslands, followed by transient, coastal and wet floodplain grasslands (Table 4). The number of epigeic earthworms per site was positively correlated with the number of wader species, wader abundance and the abundance of Lapwing, Dunlin, Black-tailed Godwit and Redshank (Table 3). The number of endogeic earthworms was negatively correlated with the abundance of Curlew (Table 3), although there was a significant negative relationship with total wader abundance (Table 2). The total number of earthworms per site was negatively correlated with the number of wader species, the total number of waders, and the abundance of Lapwing, Dunlin, Black-tailed Godwit and Redshank individually (Table 3). Earthworm biomass was not significantly related with the total abundance of waders or with any individual species (Table 3). The ecological explanation of these results is that deep soil-dwelling endogeic earthworms are inaccessible as prey for most waders despite their greater numbers within the study area in comparison to epigeic earthworms.

4. Discussion

This study demonstrated that flooding type, both by saline and/or fresh water is a strong determinate factor for the majority of the other explanatory variables. Ausden *et al*. (2001) and Zorn *et al*. (2004) showed that flooding duration strongly determines the occurrence, abundance and biomass of earthworms, an important food source for several waders. Although lack of data meant it was not possible to analyse the effect of flood duration directly within this study, our preliminary data support the importance of this factor in the Matsalu Bay area together with flooding type. It is possible to conclude that flooding determines the distribution of waders through its influence on other habitat characteristics such as edaphic parameters (Ward *et al*. 2010, vegetation composition (Ward 2012) and structure (Berg *et al*. 2012), which form the environmental conditions of breeding habitat.

Kuresoo *et al*. (2002) and Kuresoo and Mägi (2004) suggested that long-term trends in most wader populations correlate with habitat change in the Matsalu Bay coastal meadows. Ottwall and Smith (2006) showed that changes in grazing intensity on coastal grasslands in southern Sweden did not explain changes in overall breeding numbers but local changes in grazing management affected a local change in wader densities. The results of our study are in agreement and stress the importance of flooding as a determinant for habitat characteristics.

Thomas *et al*. (2006), Delany *et al*. (2009) and Verkuil *et al*. (2012) suggested that contemporary threats, most notably habitat loss and degradation at migratory stopover sites, are likely to be important for waders. However, Delany *et al*. (2009) and Zwarts *et al*. (2009) suggested that wader populations that use distinct wintering areas and migratory routes have synchronously decreased in the Baltic Sea region, indicating that there must also be factors in breeding sites that limit wader abundance.

4.1. Dunlin

The results of this study show a strong positive relationship between the abundance of Dunlin and OFT and a less significant negative correlation with Ellenberg's salinity and moisture indicators. The NMS ordination analysis also indicated that flooding strongly influences most of explanatory variables (Fig. 2). Thus, it is logical to assume that water level and the water regime affect the distribution of Dunlins through a complex combination of flooding dependent habitat characteristics. Kuresoo *et al*. (2002), Kuresoo and Mägi (2004) and Erit *et al*. (2008) noted the importance of flooding, soil moisture and, the occurrence of ephemeral mud patches around springs and ditches for breeding Dunlins on coastal grasslands in Matsalu. Thorup (2004) found similar relationships in Denmark and pointed out that the Dunlin has a very narrow breeding habitat niche. At Matsalu, according to our results, breeding Dunlins have a clear preference for saline and suprasaline paludified coastal grasslands with short-term flooding by saline water. This is most likely because this water regime promotes the formation of an ephemeral micro-topographical mosaic (Ward *et al*. 2013) which supports the appropriate environmental conditions for the preferred breeding habitat of this species.

The abundance of Dunlin was also positively related to the abundance of epigeic invertebrates and epigeic earthworms, but negatively to the abundance of endogeic earthworms and the total number of earthworm species combined. The breeding period diet of Dunlin consists of insects, spiders, Oligoheata including earthworms and small-size molluscs (Blotzheim *et al*. 1975, Cramp and Simmons 1983). The results of this study indicate that epigeic earthworms and other epigeic invertebrates are, and endogeic earthworms are not, the main food source for breeding Dunlins in the Matsalu grasslands.

In the 1960s about 50% of Dunlins in Estonia bred in Matsalu, a proportion that has not changed significantly since (Onno 1963, Erit *et al*. 2008). At present, Dunlins predominantly breed on coastal meadows in Western-Estonia and the Western Archipelago as well as in West-Estonian mires. According to monitoring data, Dunlin populations have steadily decreased in Estonia since the 1970s, with the most recent population estimates between 180–230 pairs (Kuresoo 2010, Elts *et al*. 2013).

Baltic Dunlin populations have decreased in every country within its range (Malchevski & Bukinski 1983, Perttula 1990, Jönsson 1991, Thorup 2004, Delany *et al*. 2009). The main reasons for these declines are believed to be a decrease in grazing management of salt marshes and semi-natural coastal meadows on the Baltic coast (Berg *et al*. 2012), causing a degradation and loss of breeding habitats and an increase in predators (Betzholtz *et al*. 2010). The results of this study suggest that factors such as habitat type and quality, and the influence of this on prey availability, strongly influence Dunlin abundance and could be a factor influencing the future viability of Baltic Dunlin populations.

4.2. Black-tailed Godwit

Results from this study have identified a positive relationship between epigeic earthworm abundance and Black-tailed Godwit abundance. According to Blotzheim *et al*. (1977) and Snow and Perrins (1998), earthworms are an important food source for Black-tailed Godwits. Godwit chicks have also been found to feed mostly on arthropods and their larvae (Schekkerman & Beintema 2007, Kleijn *et al*. 2010). In Estonia the diet of Black-tailed Godwit has not been investigated although it seems likely that earthworms and insects feature within the diet of breeding Black-tailed Godwits in Matsalu. The negative correlation found in this study indicates that endogeic earthworms are not likely to be a major prey source for Black-tailed Godwits in Matsalu, as the majority of endogeic earthworms occur deep in the soil profile and are not accessible (Ivask *et al*. 2006, 2007). An additional reason may be that the dominant soil types in the study area, Calcari-skeletted gleysoil and Stagni-hyposalic fluvisol (Ivask *et al*. 2007), are poorly penetrable to the relatively long but soft bills of Black-tailed Godwits. In several studies in the Netherlands, endogeic worms were suggested to be an important prey for Black-tailed Godwits (Blotzheim *et al*. 1977, Groen *et al.* 2012) due to the more penetrable coastal and inland soils that occur there.

According to Van der Vliet *et al*. (2010) and Groen *et al*. (2012), Black-tailed Godwits in the Netherlands preferred herb rich polders with high groundwater levels and the presence of foot drains. The results showed that there were no significant correlations between Black-tailed Godwit abundance and plant species richness and evenness, and only a weak negative correlation with site moisture (Table 3). However, as mentioned previously, flooding has a strong influence on most habitat variables; hence flooding is likely to indirectly affect Black-tailed Godwit abundance through other habitat variables.

Long-term population dynamics of the Black-tailed Godwit are similar to that of the Dunlin at Matsalu (Kuresoo & Mägi 2004, Kuresoo 2010). The Black-tailed Godwit population crash in the Matsalu coastal grasslands in the mid-1980s coincided with a major shift of breeding waders to other nearby habitats such as inland mires (Kumari 1972, Leivits *et al*. 2009). The main reasons for this are likely to have been the reduction and/or degradation of coastal breeding habitats due to abandonment of management practices in many semi-natural coastal grasslands in Estonia (Kuresoo & Mägi 2004, Berg *et al*. 2012). Unfortunately the re-settling of Black-tailed Godwits in inland mires has not reversed the overall decline in Estonia (Elts *et al*. 2013). This is most likely to be related to a simultaneous encroachment in mires by shrubs and trees in recent decades, and the subsequent degradation of wader breeding habitat quality (Leivits *et al*. 2009).

4.3. Other waders

This study has shown a significant and positive relationship between the abundance of Common Snipe and the Shannon index of evenness. This suggests that Common Snipe prefer species-rich vegetation without single species dominance. At Matsalu the abundance of Common Snipe was highest on species-rich paludified grassland and wet floodplain grassland with tall sedge or floodplain fens (see Appendices 1 and 2, and Fig. 1). The negative relationship between the abundance of Common Snipe and the number of endogeic earthworms (Table 2) reflects the negative relationship between earthworms and site wetness (Ivask *et al*. 2007). This also suggests that deep soil-dwelling earthworms are likely to be inaccessible to Common Snipe on grasslands at Matsalu. According to Blotzheim *et al*. (1977) and Cramp and Simmons (1983), earthworms (and other macroinvertebrates) are an important food source for Common Snipe, however at Matsalu earthworms are probably not a major prey source, at least during the breeding season.

Lapwing abundance was strongly and positively related with flooding, indicating a preference for wet habitats. Milsom *et al*. (2002) showed the importance of temporally flooded wet rills for breeding Lapwing and Redshank on coastal grazing marshes in England. They concluded that wet soils in rills may be more penetrable to the bills of probing waders than those that have dried out, as soil strength is often correlated with water content (Armstrong 2000). Durant *et al*. (2008) found that the two main predictors of nest site choice by Lapwing and Redshank in wet grasslands on the Atlantic coast of France were sward structure and surface water. The results of our study confirm the importance of site wetness although not vegetation structure.

We found a strong positive relationship between the number of Lapwings and the number of epigeic earthworms (Table 2). According to Blotzheim *et al*. (1975), up to 10% of Lapwing diet during the breeding period may consist of earthworms, predominantly *Lumbricus* and *Aporrectodea.* At Matsalu, the sites with the highest abundance of Lapwing were saline and suprasaline grasslands. At these sites the most common endogeic earthworm was *Aporrectodea caliginosa* with a considerably greater number found compared to the second and third most common earthworms *Lumbricus rubellus* and *Aporrectodea rosea*. *Aporrectodea caliginosa* is the most tolerant earthworm species with respect to soil pH, organic matter content and moisture (Ivask *et al*. 2007). This suggests that both *Aporrectodea caliginosa,* and to a lesser extent *Lumbricus rubellus,* may be important prey for breeding Lapwings in Matsalu grasslands.

Curlew was not found to be significantly related to epigeic earthworm abundance (Table 2). Furthermore, Curlew was found to be negatively correlated with endogeic earthworm abundance and small scale plant species richness, and positively correlated with nitrogen (Table 3). According to Blotzheim *et al*. (1977) and Cramp and Simmons (1983), Curlew feed on a variety of soil invertebrates including worms, although at inland breeding sites they feed mostly on insects. The results presented in this study suggest that Curlew prefer to nest on wet and fresh floodplains in the Kasari River delta (see Appendix 2 and Fig. 1) but often feed outside the breeding territory on cultural grasslands where plant cover consists of plant species with higher demand for soil nitrogen and where the number of endogeic earthworms is greater. This suggests that the prey sampled in our study may not represent the complete diet for this species.

Similar to most other waders, Redshank exhibited a significant positive relationship with flooding and the abundance of epigeic earthworms, and a negative relationship with the abundance of endogeic earthworms (Table 2). However, there were no significant relationships with any vegetation characteristics (Table 2). Milsom *et al*. (2002) found that Redshank density on coastal grazing marshes in England was significantly and positively correlated with the number of rill branches per marsh and the extent of flooding. Smart *et al*. (2006) found that breeding locations and breeding densities within fields were positively related to the length of pool edge and all wet features. Furthermore, they suggested that nest site location was principally influenced by vegetation characteristics and soil penetrability. According to Durant *et al*. (2008) the two main predictors of nest site for Redshanks were mean sward height, tussock frequency and water surface. Lapwings preferred low sward height but Redshanks exploited a larger range of sward height. This in part explains why no significant relationships between the number of Redshank and vegetation characteristics was found in this study. Redshank was also found to be positively correlated with epigeic earthworm abundance and negatively correlated with endogeic earthworms (Table 3). These correlations indicate that epigeic earthworms are probably an important food source for breeding Redshank in Matsalu grasslands. The negative correlation with endogeic earthworm abundance can be explained by low numbers in wet floodplain grasslands and limited soil penetrability in coastal grasslands, as noted for Black-tailed Godwit.

Population data were also collected for Oystercatcher, Ringed Plover, Ruff, Great Snipe and Common Sandpiper. However, their numbers and distribution across different grasslands were too low for statistical analysis. According to Mägi and Pehlak (2008), Ruff populations started to decline in Matsalu and throughout Estonia in the late 1970s and this trend has continued up to the present. The Estonian population of Ruff has been estimated at 10–30 pairs in 2012 (Elts *et al*. 2013). According to national monitoring data (Kuresoo 2010, Elts *et al*. 2013), the Estonian population of Oystercatcher has been relatively stable during recent decades but has decreased on coastal grasslands in West-Estonia. Great Snipe and Ringed Plover have decreased steadily the 1970s, and Common Sandpiper has exhibited no significant change in population size.

4.4. Synthesis

In summary, this study has shown that local abundance and distribution of most wader species is highly dependent on flooding type, i.e., temporally flooded by brackish or fresh water, and to a lesser extent on vegetation structure. The greatest bird abundance was found on saline coastal grasslands followed by fresh floodplain, transient and wet floodplain. Wader species diversity was greatest on marine coastal and lowest on floodplain grasslands. Common Snipe and Curlew were most abundant on floodplain grasslands, Black-tailed Godwits and Dunlins on coastal grasslands, and Redshank and Lapwing abundant on both floodplain and coastal grasslands. Several wader species (Dunlin, Black-tailed Godwit, Lapwing and Redshank) were strongly related to the abundance of epigeic earthworms but not with endogeic earthworms. Curlew was not found to be strongly related to epigeic earthworms or other epigeic invertebrates, most likely due to its opportunistic feeding habits.

The results of this study suggest that epigeic earthworms are an important food source for most coastal waders in Matsalu as they are relatively abundant and readily accessible. Endogeic earthworms are also abundant at most sites but are not easily accessible to birds as they occur deep in the soil profile and soils at these sites have limited penetrability. Due to the strong relationship between habitat type/quality as well as prey abundance and the flood regime shown in this study, the impacts of future sea level rise and changes in precipitation related to climate change could influence future populations of these wader species. The findings of this study should be taken into account in future conservation planning within this important bird area.

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Kahlaajien runsaus suhteessa pesimähabitaatin piirteisiin Eestin Matsalunlahdella

Kahlaajapopulaatiot ovat vähentyneet maailmanlaajuisesti, herättäen kysymyksen mitkä ympäristötekijät vaikuttavat niiden populaation kasvuun. Monet tutkimukset ovat keskittyneet habitaattien muutosten vaikutuksiin kahlaajilla, johtuen ilmastonmuutoksesta, maatalouden tehostumisesta tai viljelysmaan hylkäämisestä. Toisaalta, harvat tutkimukset ovat tarkastelleet kahlaajakantojen suhdetta saalislajien saatavuuteen. Tässä tutkimuksessa selvitetään pesivien kahlaajien esiintymistä suhteessa habitaatin piirteisiin ja ruuan saatavuuteen erityyppisillä ranta ja tulvaniityillä, läntisen Eestin Matsalunlahdella vuosina 2001–2005.

Tulokset osoittivat, että useimpien kahlaajien runsaus oli voimakkaasti suhteessa habitaatin tulvimisen laatuun, mutta ei niinkään kasvien lajien runsauteen tai lajiston tasaisuuteen, eikä keskimääräiseen kasvillisuuden peittävyyteen. Maan päällä elävien lierojen paikallinen runsaus korreloi positiivisesti kahlaajien lajidiversiteetin ja runsauden kanssa. Lajikohtaisia korrelaatioita oli myös töyhtöhyypän, mustapyrtsökuirin ja punajalkaviklon runsauksien kanssa. Maassa elävien lierojen runsaus ei ollut merkitsevästi yhteydessä kahlaajien yhdistettyyn runsauteen, joskin joillakin lajeilla löytyi heikko negatiivinen suhde.

Kirjoittajat päättelivät, että maanpäälliset lierot ovat tärkeä ravinnonlähde useimmille kahlaajalajeille Matsalun niityillä, kun taas maassa elävät lierot tuskin ovat tärkeä ravinnonlähde. Kaikkeaan kahlaajien runsaus oli voimakkaimmin suhteessa tulvimiseen (habitaatin piirteenä), sekä maanpäällisten lierojen runsauteen (ruuanlähteenä). Siten, nämä ovat tärkeitä rannikkojen kahlaajien paikalliseen esiintymiseen vaikuttavia ympäristötekijöitä.

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Appendix 1. Characterization of investigated vegetation categories (modified by Ivask *et al.* 2006). Locations of study sites are indicated in Figure 1.

Vegetation types/ Characteristics	I. Wet floodplain grassland	II. Fresh floodplain grassland	III. Transient grassland	IV. Coastal grassland
Study sites	1, 2	3, 4, 5	6, 7, 8	9, 10, 11
Community types	Wet floodplain grasslands with tall sedge or floodplain fens: *Caricetum distichae*, *Caricetum acutae*	Moderately moist floodplain meadows, sometimes described as dry impove-rished floodplain grass-lands	Species rich paludified grassland: *Scorzonero-Caricetum pallescentis*, in grazed *Deschampsio-Ranunculetum acris*	From saline to supra-saline paludified grass-land: *Junco-Glaucetum, Deschampsio-Caricetum nigrae*
Herb layer	High and lush, sometimes lodged; dominated by *Carex disticha, Carex acuta, Deschampsia caespitosa*	Lush and dens, rather species-rich, high diversity of vegetation associations; dominaded by *Lychnis flos-cuculi, Sesleria coerulea, Geum rivale, Filipendula ulmaria*	Medium and species rich (comparable with boreo-nemoral grasslands), in grazed sites, lower, poorer and tufted; domina-ted by *Scorzonera humilis, Ranunculus acris, Deschampsia caespitosa*	Variable, from low and sparse to high and lush; dominated by Juncus *gerardii, Glaux maritima, Triglochin maritimum;* character species *Carex nigra, Potentilla anserina, Festuca* sp.
Mean vascular plant coverage in 1 m² ± SE (%)	79.3 ± 2.5	94.5 ± 2.2	92.1 ± 2.5	88.5 ± 2.8
Mean number of plant species in 1 m² ± SE	6.6 ± 0.5	13.4 ± 0.9	16.4 ± 0.9	10.6 ± 0.8
Utilization type	Mowing since 10th July	Mowing since 10th July	Grazing by cattle	Grazing by cattle
Demand for salinity (mean ± SE)	0.04 ± 0.02 Affected by fresh water	0.08 ± 0.03 Fresh water	0.13 ± 0.03 Saline and fresh water	2.44 ± 0.78 Saline water
Flood duration in spring 2013 (days ± SE)	41.5 ± 0.5	59.0 ± 0.0	39.3 ± 2.3	0.0

Appendix 2. Counts of waders, 3-year average number of pairs km^{-1} and total number of species km^{-1}, on the coastal grasslands in Matsalu study area, 2001–2003, by study site and vegetation type (VGT). See Figure 1 for location of study sites and Table 1 for habitat characteristics of sites. The total length of census transects has been 16.5 km in each year.

Species	Site 1 VGT 4	Site 2 VGT 4	Site 3 VGT 3	Site 4 VGT 3	Site 5 VGT 3	Site 6 VGT 2	Site 7 VGT 2	Site 8 VGT 2	Site 9 VGT 1	Site 10 VGT 1	Site 11 VGT 1	Sum Count 2001–2003	Mean
Oystercatcher	0	0	0	0	0	0	0	0	0	0.7	1.4	2	0.1
Ringed Plover	0	0	0	0	0	0	0	0	0	12.7	8.6	25	1.5
Lapwing	8.2	10.0	3.3	0	0	7.4	8.9	2.5	22.2	34.0	32.9	179	10.5
Baltic Dunlin	0	0	0	0	0	0	0.7	0	32.2	42.7	25.7	113	6.6
Ruff	0.6	0	0	0	0	0	0	0	0	1.3	2.9	5	0.3
Common Snipe	2.9	8.1	6.0	1.7	2.1	10.0	18.5	10.0	4.4	0	4.3	131	7.7
Great Snipe	0	0.5	0	0	0	0	0	0	0	0	0	1	0.1
Black-tailed Godwit	0	0	1.3	0	0	2.2	2.6	0	3.3	10.7	11.4	41	2.4
Curlew	3.5	6.2	6.0	1.7	3.6	1.3	2.2	0.6	2.2	1.3	2.9	50	2.9
Redshank	2.4	3.8	0.7	1.7	0.7	2.6	2.2	0.6	17.8	20.7	15.7	86	5.1
Common Sandpiper	0	0	0	0	0	0	0	1.1	0	0	0	2	0.1
All species	17.6	30.0	18.0	5.0	7.1	23.5	38.5	16.9	83.3	124.0	105.7	635	37.4
Number of species	5	5	5	3	3	5	6	5	6	8	9	11	5.3
Transect length, km	1.7	2.1	0.6	0.9	1.5	2.3	2.7	1.6	0.9	1.5	0.7	16.5	–

Appendix 3. Habitat characteristics (mean values) of study sites and their abbreviations in the Matsalu Bay study area, 2005. See Figure 1 for the locations of study sites and Table 1 for values of VGT, OFT, UTT, GHC and FGA.

Variable	Site 1	Site 2	Site 3	Site 3	Site 3	Site 3	Site 3	Site 3	Site 9	Site 10	Site 11
Vegetation type, VGT	4	4	3	3	3	2	2	2	1	1	1
Flooding type, OFT	3	2	3	3	3	2	2	2	1	1	1
Utilisation type, UTT	3	3	3	3	3	4	1	3	2	1	2
No. of plant species in the study site, NPS	13	11	12	25	29	44	35	38	17	–	27
Mean no. of plant species / m^2, MNS	8.0	4.6	7.2	13.0	13.8	14.3	15.6	20.0	10.4	–	1.8
Grass height class, GHC	3	3	2	2	3	2	1	2	1	1	2
Appearance of fog gage, FGA	1	1	2	1	2	2	1	1	1	1	2
Mean vascular plant coverage, MPC	85	75	78	93	96	86	92	100	83	–	94
Mean vegetation evenness, MVE	0.59	0.52	0.61	0.71	0.67	0.65	0.67	0.70	0.65	–	0.71
Ellenberg's indicator 1 (temperature), Etemp	3.01	5.39	2.87	2.28	4.25	2.87	1.67	3.55	5.4	–	1.46
Ellenberg's indicator 2 (light), Elight	6.42	7.11	7.34	7.32	7.24	6.82	6.53	6.66	7.15	–	6.56
Ellenberg's indicator 3 (continentality), Econt	0.46	0.78	0.71	2.78	1.69	2.17	2.38	3.49	0.48	–	1.13
Ellenberg's indicator 4 (moisture), Emoist	7.34	8.5	8.64	6.97	7.48	6.2	4.02	6.07	4.22	–	5.57
Ellenberg's indicator 5 (salinity), Esal	0.12	0.02	0.00	0.06	0.09	0.08	0.26	0.06	4.68	–	0.20
Ellenberg's indicator 6 (nitrogen), Enit	4.96	4.51	4.23	3.60	4.43	2.82	2.75	2.83	3.01	–	3.38
Mean no. of earthworms / m^2, Ne	84	22	14	102	50	43	30	102	0	12	28
Mean no. of earthworm species / m^2, Se	4	2	3	6	3	7	3	4	0	2	3
Mean biomass (g) of earthworms / m^2, Be	5.46	1.25	0.87	32.64	9.15	10.75	8.55	34.78	0	3.38	12.07
Mean no. of endogeic earthworms / m^2, Endo	52	0	2	80	38	23	6	88	0	12	14
Mean no. of epigeic earthworms / m^2, Epi	32	22	12	22	12	20	24	14	0	0	14
Mean no. of epigeic invertebr. per trap, Nepi	44.5	26.4	23.3	30	44.5	85.9	52.8	48.3	31.5	23	42.3
Total no. of taxon per transect, Sepi	13	15	11	17	17	23	22	17	18	14	21