Effects of grazing regime and vegetation changes on breeding birds in salt marshes of the Schleswig-Holstein Wadden Sea National Park and Halligen

Dissertation

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To Whom It May Concern:

As a native speaker I hereby confirm that the PhD of Cynthia Erb, entitled “Effects of grazing regime and vegetation changes on breeding birds in salt marshes of the Schleswig-Holstein Wadden Sea National Park and Halligen” is written in correct English grammar and in a well-composed manner.

Sincerely,

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Contents

1 General introduction

The Wadden Sea is a unique and highly dynamic landscape. This extreme habitat is dominated by the tides and the sea, and serves as a nursery for fish species of the North Sea, a significant site for migratory birds, and a globally important avian breeding habitat. The Wadden Sea is bordered by Denmark, Germany, and the Netherlands. The German part of the Wadden Sea is governed by the federal states of Schleswig-Holstein, Hamburg, and Lower Saxony. In 1985 the Schleswig-Holstein Wadden Sea became a national park, followed by the establishment of the Lower Saxony Wadden Sea and Hamburg Wadden Sea National Parks in 1986 and 1990, respectively. In 2009 the Dutch Wadden Sea, the Schleswig-Holstein Wadden Sea, and the Lower Saxony Wadden Sea became a UNESCO world natural heritage site. The Schleswig-Holstein Wadden Sea National Park aims at protecting natural processes and conserving the biodiversity of the Wadden Sea. The national park comprises sea, mudflats, estuaries, dunes, and more than 7800 ha of salt marshes (Esselink et al. 2009). When the national park was established in 1985, 80% of the salt marshes were intensively grazed by sheep (Kempf et al. 1987). In the early 1990s grazing was reduced or stopped. At present 62% of the salt marshes are ungrazed, 30% are intensively grazed, 7% are moderately grazed, and 1% is mown (Wanner et al. in prep.).

Unique to the Wadden Sea are the Halligen, 10 small islands (6–960 ha) without dykes and subjects to regular floods from autumn to spring. Five of the Halligen are inhabited (Langeneß, Oland, Gröde, Nordstrandischmoor and Hooge). The Schleswig-Holstein Wadden Sea National Park together with the Halligen forms the Biosphere Reserve Schleswig-Holstein Wadden Sea and Halligen. The Halligen fulfil an important function as habitat for plants and animals and serve as natural breakwaters. Conservation and protection of this unique habitat must be balanced with the fact that these islands serve as living and working space for the inhabitants. The grazing regime of the Hallig salt marshes is regulated by the Halligprogramm (MELFF 1986). Since 1987 the government of Schleswig-Holsteins has promoted moderate livestock grazing on the inhabited Halligen while giving consideration to both nature conservation and the needs of inhabitants (MNUL 1992). The grazing regime of the salt marshes in the national park differs strongly from the grazing regime of the salt marshes on the Halligen. While on the mainland salt marshes of the national park there is a tendency to reduce and cease grazing, the Hallig ranchers have the possibility to change their grazing regime from one year to the other within the regulations of the Halligprogramm. This leads to variable annual grazing regimes on Hallig salt marshes including extensive grazing, mowing and abandonment of areas.

Salt marshes form the transition between land and sea. They can be divided into three zones: Pioneer zone, low marsh, and high marsh (de Jong et al. 1998). Both flooding and salinity levels have considerable influence on the distribution of vegetation in salt marshes (Dierßen 1996). The pioneer zone extends from below to slightly above mean high tide and thus is flooded twice a day. *Salicornia europaea* and *Spartina anglica* are the dominating plant species. The low marsh extends from the mean high tide point to 40 cm above mean high tide. Flooding occurs less often than in the pioneer zone and the dominant plant species are *Puccinellia maritima* and *Halimione portulacoides*. The high marsh occurs in areas greater than 40 cm above the mean high tide line. This region of the salt marsh is infrequently flooded and is characterized by the presence of *Festuca rubra* ssp. *litoralis* and *Elymus athericus*.

More than 100,000 pairs of breeding birds are counted every year in the Schleswig-Holstein Wadden Sea National Park (Hälterlein et al. 2000). Birds select breeding habitats non-randomly by a series of choices that can be divided into three categories (Burger 1985): (1) General habitat selection such as forest, grassland, marsh, (2) territory selection, and (3) nest site selection. Many bird species have specific vegetation structure preferences for nesting sites (Durant et al. 2008). Terns, for example, require short vegetation (Glutz von Blotzheim 2001) whereas redshanks (as concealed breeders) need taller vegetation structure (Thyen & Exo 2005). Because livestock grazing affects vegetation, the influence of changes in grazing regime and vegetation on breeding birds has been a perennial issue for the national park during the last 25 years.

Previous studies dealing with the influence of changes in grazing regime and vegetation have focused either on the response of single bird species or on bird communities in very few areas. To date, no study has been conducted in the Schleswig-Holstein Wadden Sea National Park that examines the influence of changes in grazing regime and vegetation on breeding birds on a large scale and over a long period of time. To address this research need, the BASSIA project, consisting of three subprojects, was established to determine the effect of changing grazing regimes on a) salt marsh vegetation, b) breeding birds, and c) ecosystem functions. The BASSIA (Biodiversity, Management and Ecosystem functions of Salt marshes In the Schleswig-Holstein Wadden Sea National Park) project is a cooperation between the University of Hamburg and Schleswig-Holstein Wadden Sea National Park funded by the Bauer-Hollmann-Foundation. The present study utilizes existing breeding bird and vegetation mapping data. Data were made available by the Schleswig-Holstein's Government-Owned Company for Coastal Protection, National Parks and Ocean Protection (LKN-SH) and were collected within the Trilateral Monitoring and Assessment Program (TMAP). TMAP is part of the Trilateral Wadden Sea Cooperation of Denmark, Germany, and the Netherlands. TMAP collects and assesses data concerning the Wadden Sea (e.g., breeding birds, salt marsh vegetation, egg contaminants, fish and many others).

In the following two chapters I will address the interrelated aspects of breeding bird biology and changes in grazing regimes and vegetation within the Schleswig-Holstein Wadden Sea National Park. The first chapter deals with the interaction between grazing regime and vegetation changes on the breeding bird diversity. This study addresses species richness of breeding birds on a large scale (a total of 36 study sites in the national park and on the Halligen) and over a long period (1988–2006). The second chapter examines nest site selection of a single breeding bird species, the Eurasian Oystercatcher (*Haematopus ostralegus*), in 90 ha of a mainland salt marsh in the face of changing grazing regime and vegetation.

2 Chapter 1

Breeding bird species richness and grazing regime and vegetation diversity

2.1 Abstract

A perennial issue of the Schleswig-Holstein Wadden Sea National Park during the last 25 years has been livestock grazing and the influence this has on breeding bird diversity in salt marsh habitats. It is understood that grazing affects the diversity of salt marsh vegetation and that increased plant diversity provides a wider range of suitable breeding habitats for birds. It is also understood that the individual responses of bird species to grazing regime changes are varied. Nevertheless, no previous study has examined the influence of changes in grazing regime on breeding bird species richness on a large scale for a long time period. In this study existing data from breeding bird counts and vegetation mappings in Schleswig-Holstein Wadden Sea National Park were used. Twenty-seven mainland salt marshes and nine Hallig salt marshes were analysed for four time periods from 1988–2006. I investigated a) changes in breeding bird species richness and in grazing regime and vegetation diversity through time, b) differences in breeding bird species richness and in grazing regime and vegetation diversity between mainland and Halligen and c) influence of grazing regime and vegetation diversity on breeding bird species richness. I calculated the Shannon's diversity index for grazing regime and vegetation as a proxy for breeding bird habitat diversity. GIS was employed to spatially join bird and vegetation data. Multiple linear regressions and parametric and non-parametric tests were performed to analyse the effect of grazing regime and vegetation diversity, area and location on breeding bird species richness and to reveal potential differences through time and between mainland and Hallig salt marshes. Breeding bird species richness increased from 1988 to 2001 and thereafter decreased in 2006; however, these differences were not significant. Grazing regime and vegetation diversity increased significantly from 1988–2001, followed by a slight and non-significant decrease in 2006. Breeding bird species richness was higher on the Halligen compared to the mainland in all four periods although the difference was only significant in 2006. There was no difference in grazing regime and vegetation diversity between mainland and Halligen. Multiple linear regressions revealed that the relationship between breeding bird species richness and grazing regime and vegetation diversity was time-dependent. In 2001 breeding bird species richness increased with increasing grazing regime and vegetation diversity and decreased when the study site was situated on the mainland. In 2006 breeding bird species richness decreased when the study site was situated on the mainland; grazing regime and vegetation diversity did not have any effect on breeding bird species richness. The study emphasizes the distinctive nature of Hallig salt marshes compared to mainland salt marshes; possible reasons for this are discussed.

2.2 Introduction

Since its inception, the Schleswig-Holstein Wadden Sea National Park has undergone a considerable shift in grazing regimes. At the time of the establishment in 1985 80% of the salt marsh area was intensively grazed by sheep (Kempf et al. 1987). During the early 1990s, grazing was ceased or reduced in large parts of the national park. Nowadays only 30% of the national park area is still under intensive grazing pressure, 7% is moderately grazed, 62% is ungrazed and 1% is mown (Wanner et al. in prep.). These changes in grazing regime and their effects on both vegetative and avian diversity has become a significant issue (Stock et al. 1992; Eskildsen et al. 2000; Hälterlein 2002; Hälterlein et al. 2003; Schrader 2003).

Studies have revealed that the effects of grazing abandonment on vegetation are time-dependent: In the short-term, structural diversity of vegetation increases (Kiehl et al. 2000), whereas in the long-term, diversity decreases (Andresen et al. 1990; Bos et al. 2002). Once grazing pressures are removed, succession is no longer inhibited and late successional stages can develop. These late stages are often defined by large mono-dominant stands of e.g. *Elymus athericus* or *Phragmites australis* (under less saline conditions) which provide only little structural diversity (Bakker et al. 1997; Esselink et al. 2009).

Structural diversity of salt marshes is important for breeding bird diversity. Breeding bird species often have specific habitat requirements regarding mean vegetation height and structural diversity, respectively. Due to their short-legged morphology, terns (e.g. *Sterna hirundo*, *Sterna paradisaea*) require habitats defined by short vegetation (Glutz von Blotzheim 2001), lapwings (*Vanellus vanellus)* prefer short vegetation, too (Glutz von Blotzheim 2001). Redshanks (*Tringa totanus*) and other concealed breeding species require taller vegetation rich in structure (Thyen & Exo 2005; Durant et al. 2008). Gulls (e.g. *Larus fuscus)* also prefer taller vegetation for their nesting sites (Glutz von Blotzheim 2001). Eskildsen et al. (2000) demonstrated a link between increased structural diversity and both an increase in redshank population size and an increase in avian species richness after grazing abandonment. Other studies have shown that redshanks may also benefit from some grazing activities (Norris et al. 1997). Thus, it is unclear what the effects of grazing abandonment are on breeding bird communities.

It is important that changes in populations of marsh nesting birds be identified at local and regional levels. This distinction is significant because some species (e.g. *Larus ridibundus*) have experienced population declines on the mainland and increases on the islands (Koffijberg et al. 2006). In contrast terns have decreased on the Halligen and increased on the mainland (Südbeck et al. 1998). The five inhabited Halligen (Langeneß, Oland, Hooge, Nordstrandischmoor and Gröde) are not part of the national park but belong to the Biosphere Reserve Schleswig-Holstein Wadden Sea and Halligen. The national park aims to reduce grazing in order to increase biodiversity within the salt marshes and to protect natural processes. The Halligen, however, are subject to a different grazing regime which is regulated in the Halligprogramm (MELFF 1986). The objectives of the Halligprogramm include protection of nature and sustainable management. Current regulations allow for ranchers on the Halligen to change grazing regime, within certain regulations and short durations, e.g. from one year to the next. The different grazing regimes on the Halligen and on the mainland may have different effects on vegetation and birds. Additionally, there is a general assumption that predation on birds' nests on the Halligen is lower than the mainland due to a lack of mammalian predators. The anticipated benefit to breeding birds, however, is not documented.

To date studies dealing with the interactions between vegetation, grazing regime, and their effects on breeding birds in salt marshes have been limited to single species or species richness at a small number sites. No study has yet explored the effects of changes in grazing regime and vegetation on breeding bird species richness on a larger scale and for a longer period. This study uses existing data from the Trilateral Monitoring and Assessment Program (TMAP) to determine how breeding bird species richness is affected by changes in grazing regime and vegetation in the Schleswig-Holstein Wadden Sea National Park and the Halligen from 1988–2006. It is assumed that breeding bird species richness increases in habitats where grazing regime and vegetation diversity is high. Specifically, this study seeks to address three primary questions: a) How have grazing regime and vegetation diversity, and breeding bird species richness changed through time? b) How does breeding bird species richness and diversity of grazing regimes and vegetation differ between mainland and Hallig salt marshes? c)

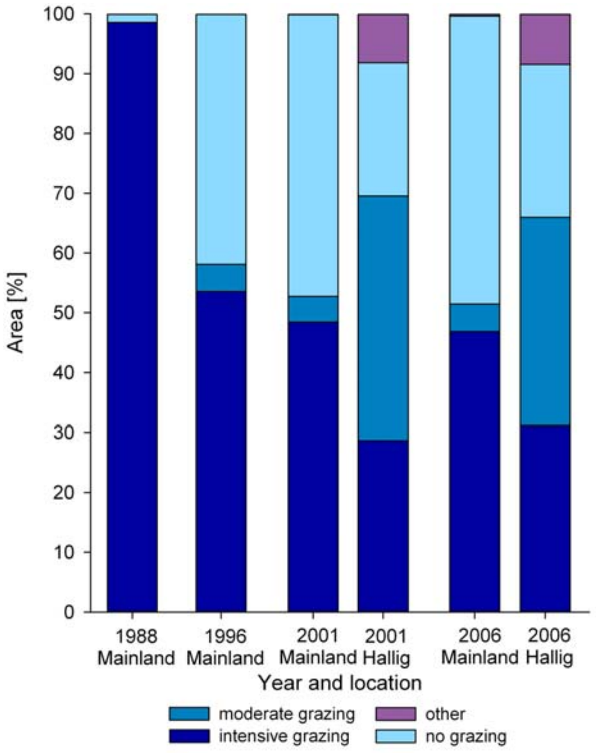
Do high levels of grazing regime and vegetation diversity result in a high amount of species richness among breeding birds?

2.3 Material & Methods

2.3.1 Study site and data

Breeding bird species (BBS) richness was analysed in 36 study sites situated along the western coast of Schleswig-Holstein, Germany (northernmost extent: 54°54′N, southernmost extent: 53°53′N, easternmost extent: 9°03′E and westernmost extent: 8°30′E). BBS was related to a compound and area based diversity measure which aggregates information on both grazing regime and vegetation type. For quantifying this diversity measure, information on grazing regime was added to each single vegetation polygon representing a vegetation type of a given study site. Based on the resulting compound information on grazing regime and vegetation type, the Shannon diversity index was calculated. In the following, I refer to this as "grazing regime and vegetation diversity" (GR&V diversity).

Twenty-seven sites are mainland salt marshes and nine of them are Hallig salt marshes. The size of study sites varies from 6 ha to 960 ha. Moreover, sedimentation and erosion processes cause land area changes per study site through time. All 36 study sites comprise salt marshes which had been undergoing a shift in grazing regime from 1988–2006 (figure 1); with the exception of three sites (VE11 Finkhaushalligkoog, VE13 Uelvesbüllerkoog & Jordfletherkoog and VN212 Lübkekoog Süd) that have been intensively grazed in all years. In 1985, when the national park was established, almost 100% of the sites were under intensive grazing; at the beginning of the 1990ies grazing was successively stopped or reduced to moderate grazing. Today less than half of the total area of all study sites is still under intensive grazing, and on the Halligen it amounts only to 30%. On the mainland almost 50% of the areas are ungrazed, a small proportion of 5% is moderately grazed and less than 0.5% are mown. On the Halligen about 25% of the areas are ungrazed, 35% are under moderate grazing and 8% are mown.



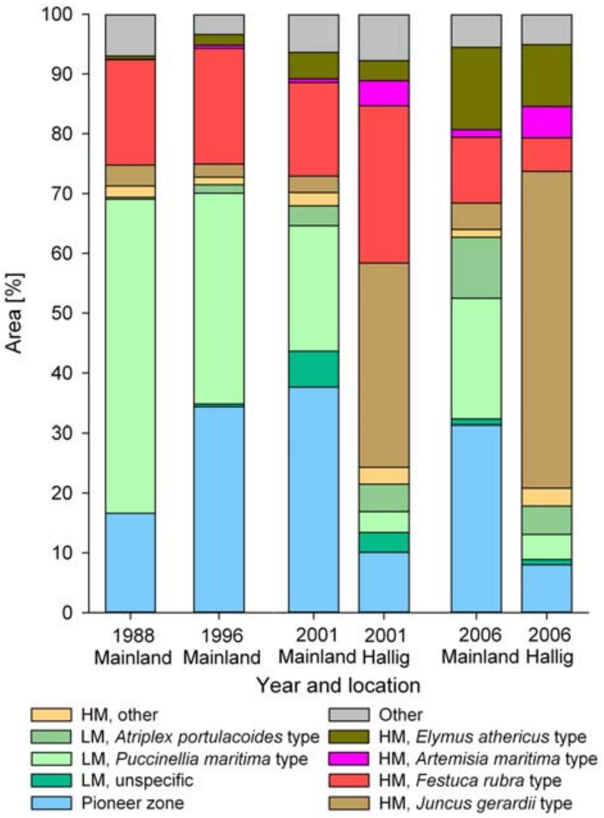


Figure 1: Changes in grazing regime for the 36 study areas. Note: Halligen data were only available for 2001 and 2006.

Figure 2: Changes in vegetation for the 36 study areas. Note: Halligen data were only available for 2001 and 2006; furthermore in 1988 mudflat-sided pioneer zone vegetation had not been mapped. LM=Low marh, HM=High marsh.

For analyses, I used bird, vegetation and grazing regime data collected by the Trilateral Monitoring and Assessment Program (TMAP) that were made available by the Schleswig-Holstein's Government-Owned Company for Coastal Protection, National Parks and Ocean Protection (LKN-SH). Breeding birds were counted annually in the study sites, and in 1988, 1996, 2001 and 2006 the area-wide salt marsh vegetation and the grazing regime of the salt marshes were mapped in study site according to the TMAP parameters. It should be noted that mudflat-sided pioneer zone vegetation had not been mapped in 1988. Halligen vegetation and grazing regime data were only available for 2001 and 2006 as no surveys were conducted in 1988 or 1996.

In addition to the shifts in grazing regime there were also shifts in vegetation (figure 2). On the mainland, vegetation of *Puccinellia maritima* type and *Festuca rubra* type decreased continuously from 1988–2001. Vegetation of pioneer zone increased until 2001 then decreased whereas vegetation of *Atriplex portulacoides* type and *Elymus athericus* type increased continuously from 1988–2006. The abrupt rise of pioneer zone vegetation from 1988 to 1996 is probably mostly due to the fact that this vegetation type had not been mapped in the mudflat-sided areas in 1988. On the Halligen vegetation of *Juncus gerardii* type and *Elymus athericus* type increased while vegetation of *Festuca rubra* type decreased strongly between 2001 and 2006.

2.3.2 Data analysis and statistics

A total of 44 breeding bird species were considered in analyses (see appendix). I treated Arctic tern (*Sterna paradisaea*) and Common tern (*Sterna hirundo*) as one species ("Red-footed terns") because phenotypic similarity can confound field identifications. I grouped breeding bird data around the four vegetation mapping years (1988, 1996, 2001, 2006), taking the mapping year itself and one year before and after into consideration (e.g., 1987–1989 = ″1988″). Then I counted all breeding bird species per 3-year-period and study site and used the value as BBS richness. In the following I will refer to each 3-year-period using the middle year which is synonym with the year of vegetation mapping (table 1). To account for the strong influence of colony-breeding birds compared to solitary-breeding birds, I took the maximum value of each species per 3-year-period and summed them per study site and 3-year-period, resulting in 144 sums (36 study sites in four 3-year-periods), set the maximum sum of them as 100 and converted all other sums accordingly. In this way I gained standardized values of sum of breeding pairs which are independent of species and size of study site.

Table 1: Years of breeding bird data taken into analysis. Each 3-year-period will be referred to using the middle year.

Years	Period
1987 1988 1989	1988
1995 1996 1997	1996
2000 2001 2002	2001
2005 2006 2007	2006

After spatially joining breeding bird and vegetation and grazing regime mapping data using ESRI's ArcGIS 9.3, I calculated Shannon diversity index H′ for grazing regime and vegetation (GR&V diversity) per period for each study site with n_i = area of the *i*th grazing regime and vegetation type and N = the total area:

$$H' = -\sum \frac{n_i}{N} * log \frac{n_i}{N}$$

The effect of GR&V diversity, area and location (mainland or Halligen) on BBS richness was analysed by multiple linear regression. I performed multiple linear regression for the mainland data, using ″year″ as an additional variable to analyse a general effect of time. Statistical analyses were performed with SPSS 16.0 for Windows. If assumptions for parametric tests were met, I used standard parametric tests (ANOVA, t-test) to reveal potential differences in BBS richness and GR&V diversity through time and between mainland and Hallig salt marshes. If assumptions for parametric test were not met, non-parametric tests were used (Mann-Whitney-test and Kruskal-Wallis-test with multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction Holm 1979). Box-plots show the median and lower and upper quartiles (box) as well as 10th and 90th percentiles (whiskers); circles indicate outliers (values which are beyond the 10th or 90th percentiles).

2.4 Results

2.4.1 BBS richness and GR&V diversity: temporal shifts

Within the 36 study sites a total of 44 BBS were found from 1988–2006. In 1988, 30 BBS were found; in 1996, 32; in 2001; 35, and in 2006, 37. Thus, the total BBS richness increased continuously through time. Highest BBS richness was found in VN5 (mainland, Hamburger Hallig) with 21 species in 1996, 2001 and 2006, whereas the lowest one was found in VN222 (mainland, Neugalmsbüllkoog) in 1988 and in VD522 (mainland, Neufelderkoog Ost) in 2001 and 2006, all with only 5 BBS. The difference of BBS richness is 16 which are 36% of BBS found altogether. According to the total BBS richness, highest mean BBS richness was found in VN5 (mainland, Hamburger Hallig) with 18.50 ± 5.00 and lowest in VD522 (mainland, Neufelderkoog Ost) with 6.75 ± 2.36 (figure 3).The total mean of BBS richness calculated over all periods and sites is 11.76 ± 3.52 (table 2).

Table 2: BBS richness, GR&V diversity (Shannon index) and area [ha] of study sites. Mean and standard deviation are calculated over all periods per study site. Note: GR&V data of the Halligen were only available for 2001 and 2006. Abbreviations for study sites are adopted from TMAP. Temporal changes in area are due to sedimentation and erosion. MD=Mainland Dithmarschen, ME=Mainland Eiderstedt and MN=Mainland Nordfriesland.

Study sites		BBS richness						GR&V diversity		Area [ha]	
Abbr.	Name	1988	1996	2001	2006	Mean	SD	Mean	SD	Mean	SD
IH1	Hallig Langeneß	13	18	16	16	15.75	2.06	2.57	0.26	934.30	36.33
IH2	Hallig Oland	11	14	15	17	14.25	2.50	2.36	0.01	229.51	1.03
IH3	Hallig Gröde	11	12	13	15	12.75	1.71	2.19	0.08	186.09	2.75
IH4	Hallig Habel	8	10	9	16	10.75	3.59	1.76	0.28	5.59	0.02
IH5	Hallig Nordstrandischmoor	9	13	14	14	12.50	2.38	2.16	0.37	192.06	3.60
IH6	Hallig Hooge	14	14	17	19	16.00	2.45	2.28	0.25	491.60	8.98
IH7	Hallig Norderoog	12	12	13	14	12.75	0.96	1.63	0.38	9.95	0.66
IH8	Hallig Süderoog	12	14	15	13	13.50	1.29	2.53	0.13	57.60	0.53
IH9	Hallig Südfall	13	16	16	15	15.00	1.41	2.22	0.15	37.08	0.41
VD11	MD Hedwigenkoog	10	13	15	17	13.75	2.99	2.07	0.41	302.18	64.47
VD22	MD Helmsand	11	13	17	16	14.25	2.75	1.66	0.41	61.03	2.68
VD3	MD Friedrichskoog Nord	9	11	12	14	11.50	2.08	2.07	0.71	585.88	67.07
VD41	MD Dieksanderkoog Nord	8	15	12	11	11.50	2.89	2.10	0.66	428.49	59.16
VD42	MD Dieksanderkoog Süd	11	13	12	11	11.75	0.96	1.93	0.56	751.12	95.00
VD51	MD Kaiser-Wilhelm-Koog	6	11	14	11	10.5	3.32	2.17	0.50	266.27	14.40
VD521	MD Neufelderkoog West	8	12	9	9	9.50	1.73	2.09	0.26	290.59	19.29
VD522	MD Neufelderkoog Ost	7	10	5	5	6.75	2.36	1.66	0.33	124.24	13.87
VE11	ME Finkhaushalligkoog	9	9	10	10	9.50	0.58	1.55	0.58	69.54	35.93
VE12	ME Simonsbergerkoog	10	10	9	7	9.00	1.41	1.95	0.50	135.96	25.90
VE13	ME Uelvesbüllerkoog & Jordfletherkoog	8	9	6	7	7.50	1.29	1.28	0.18	165.39	32.69
VE2	ME Norderheverkoog	9	9	13	13	11.00	2.31	1.93	0.53	411.58	27.25
VE32	ME Westerhever	14	20	15	13	15.50	3.11	2.05	0.73	237.44	27.79
VE4	ME Tümlauer Bucht	13	15	13	12	13.25	1.26	2.19	0.35	435.21	38.93
VE61	ME Ehsterkoog	10	10	10	8	9.50	1.00	1.84	0.52	111.19	12.56
VE62	ME Grothusenkoog	8	7	10	7	8.00	1.41	1.74	0.46	43.78	21.33
VN1	MN Rickelsbüllerkoog	16	18	16	15	16.25	1.26	1.68	0.53	144.21	50.03
VN211	MN Lübkekoog Nord	7	10	8	11	9.00	1.83	1.49	0.68	249.96	68.80
VN212	MN Lübkekoog Süd	7	9	9	9	8.50	1.00	1.13	0.37	164.58	46.17
VN221	MN Marienkoog	7	12	13	8	10.00	2.94	1.66	0.81	254.42	27.68
VN222	MN Neugalmsbüllkoog	5	10	10	14	9.75	3.69	1.43	0.74	91.79	13.91
VN32	MN Osewoldterkoog	13	12	17	15	14.25	2.22	1.53	0.44	169.68	8.78
VN5	MN Hamburger Hallig	11	21	21	21	18.50	5.00	2.32	0.80	531.70	34.44
VN61	MN Sönke-Nissen-Koog Süd	20	10	10	11	12.75	4.86	1.46	0.89	164.79	11.03
VN8	MN Nordstrand Süd	8	14	12	12	11.50	2.52	1.69	0.64	452.30	43.17
VN91	MN Schobüller Bucht Nordstranddamm	8	8	11	6	8.25	2.06	1.25	0.44	96.03	8.30
VN921	MN Schobüller Bucht Schobüll	8	9	7	11	8.75	1.71	1.28	0.12	70.34	4.63

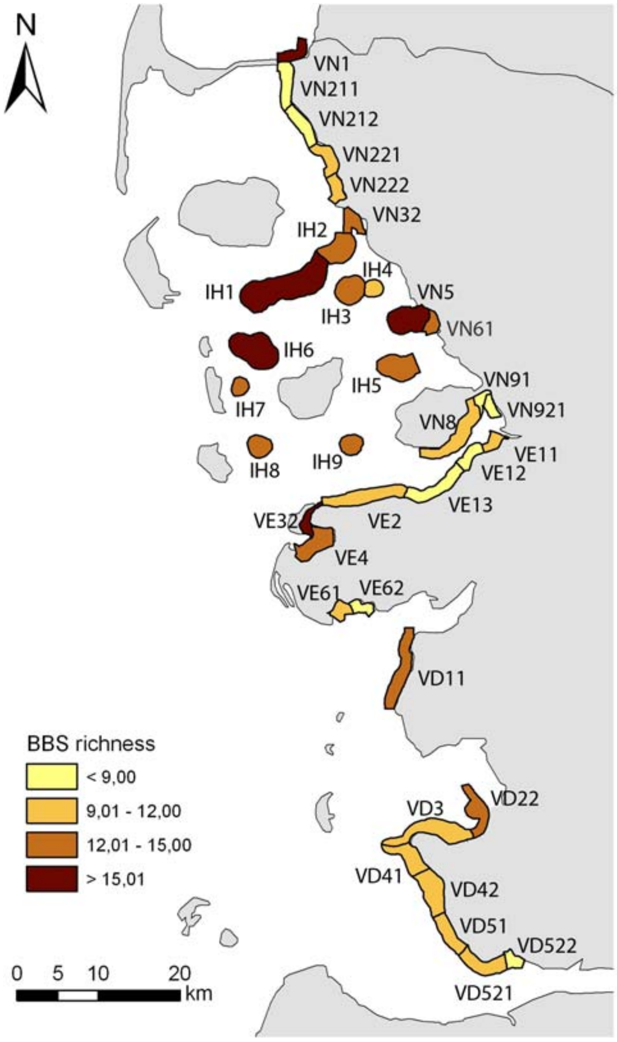


Figure 3: Mean BBS richness calculated over all periods per study site. The total mean calculated over all periods and sites is 11.76 ± 3.52.

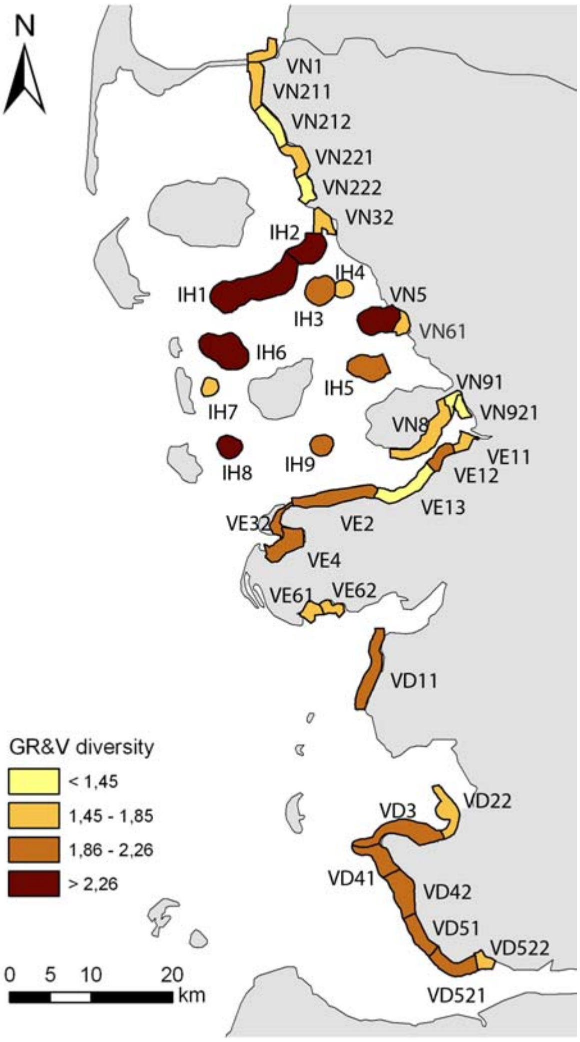


Figure 4: Mean GR&V diversity (Shannon index) calculated over all periods per study site. Note: GR&V data for the Halligen were available only for 2001 and 2006.

Looking at the four periods, mean BBS richness calculated for all study sites (figure 5) is with 9.67 ± 3.27 significantly lower in 1988 than 2001 (12.33 ± 3.51) and 2006 (12.31 ± 3.78) but not significantly lower than in 1996 (11.85 ± 3.49). All other means do not differ significantly from each other (One-way ANOVA: F=3.72, $p<0.05$; with Bonferroni-post-hoc-test; Halligen data for 1988 and 1996 not included). If Halligen data for 1988 and 1996 are included, than the pattern of change of BBS richness remains the same but BBS richness in 1988 is significantly different from all other periods and not only from 2001 and 2006; the other means do not differ from each other (One-way ANOVA: F=3.72, $p<0.05$; with Bonferroni-post-hoc-test). In either case there is a tendency towards increasing BBS richness from 1988–2001, followed by a slight decrease in 2006.

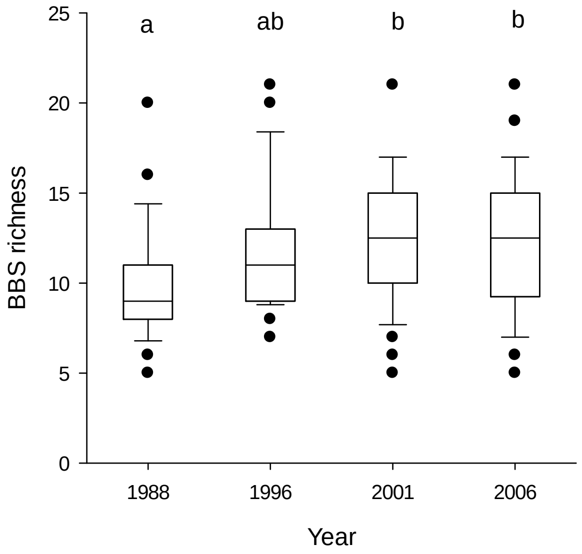


Figure 5: BBS richness differed significantly between time periods (One-way ANOVA: F= 3.72, p<0.05; with Bonferroni-post-hoc-test). Note: Halligen data were not included for 1988 and 1996. Different letters above box-plots indicate that means were significantly different.

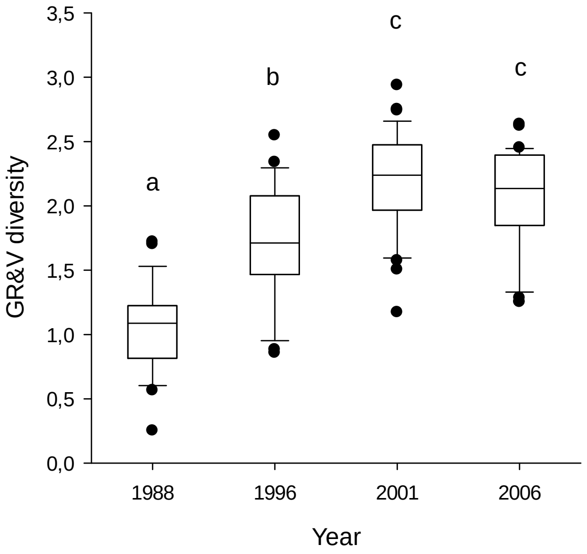


Figure 6: GR&V diversity (Shannon-index) differed significantly between periods (One-way ANOVA: F=49.716, p<0.01; with Bonferroni-post-hoc-test). Note: Halligen data were only available for 2001 and 2006. Different letters above box-plots indicate that means were significantly different.

Mean GR&V diversity (figure 6), calculated over all periods per study site, was highest in IH1 (Hallig Langeneß, mean=2.57 ± 0.26) and IH8 (Hallig Süderoog, mean=2.53 ± 0.13) and lowest in VN212 (mainland, Lübkekoog Süd, mean= 1.13 ± 0.37). Comparison of periods revealed a significant increase in GR&V diversity from 1988 (mean=1.06 ± 0.34) over 1996 (mean=1.73 ± 0.43) to 2001 (mean=2.19 ± 0.39), followed by a slight decrease in 2006 (mean=2.06 ± 0.41) which, however, is not significant (One-way ANOVA: F= 49.72, p<0.01; with Bonferroni-post-hoc-test). These temporal changes in GR&V diversity are, although more pronounced, similar to those in BBS richness.

2.4.2 BBS richness and GR&V diversity: differences between mainland and Halligen

In all periods BBS richness was higher on the Halligen than on the mainland (figure 7). However, these differences were only significant in 2006 (t-test: t=3.25, p<0.01, df=34) but not in 1988 (t-test: t=1.53, p>0.05, df=34), 1996 (t-test: t=1.45, p>0.05, df=34) and 2001 (t-test: t=1.93, p>0.05, df=34). In 1988 mean BBS richness was 11.44 ± 1.94 on the Halligen and 9.67 ± 3.27 on the mainland. In 1996 mean BBS richness on the Halligen (mean=13.67 ± 2.35) was also higher than on the mainland (mean=11.85 ± 3.49). The same can be found in 2001 (Halligen: mean=14.22 ± 2.39; mainland: mean=11.70 ± 3.64) and 2006 (Halligen: mean=15.44 ± 1.81; mainland: mean= 11.26 ± 3.70) where mean BBS richness on the Halligen exceeded the one on the mainland.

On the Halligen, BBS richness continuously increased from 1988–2006, whereas on the mainland BBS richness increased from 1988–1996 but exhibited declines after this time (figure 8). These changes in BBS richness were significant for the Halligen in 1988 compared to 2006 (One-way ANOVA: F=5.53, p<0.01; with Bonferroni-post-hoc-test) but not for the mainland (One-way ANOVA: F=2.18, p>0.05). There is, however, a trend towards an increasing difference between BBS richness on the Halligen and mainland.

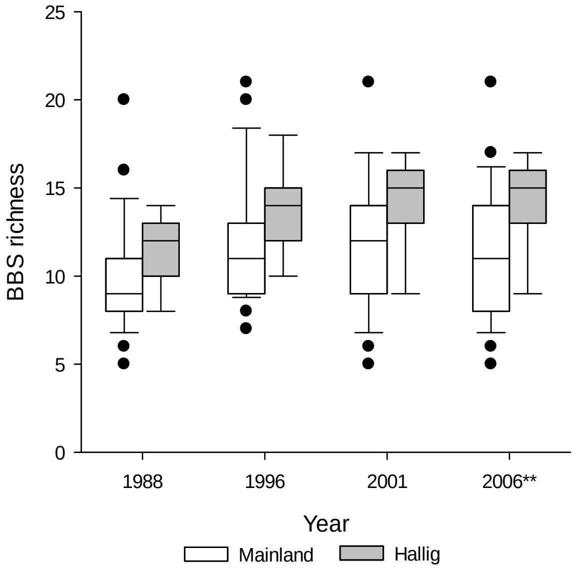


Figure 7: Comparison of BBS richness between mainland and Halligen for each single period. **= difference was highly significant with p<0.01.

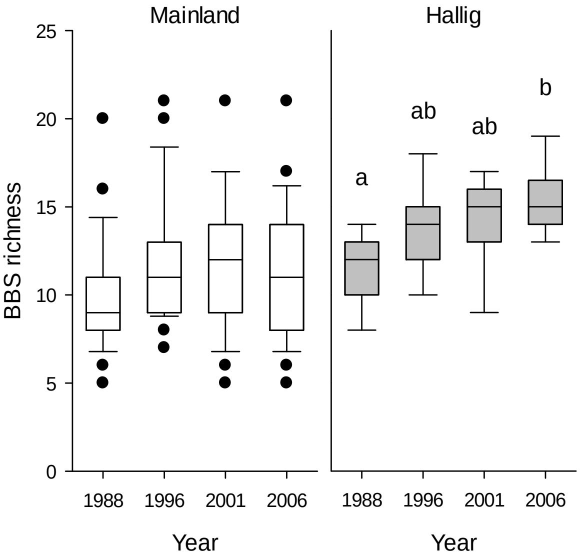


Figure 8: BBS richness differed significantly through time on the Halligen (One-way ANOVA: F=5.53, p<0.01; with Bonferroni-post-hoc-test) but not on the mainland (One-way ANOVA: F=2.18, p>0.05). Different letters above box-plots indicate that means were significantly different.

Looking at standardized sums of breeding pairs (figure 9), the median is significantly higher on the Halligen than on the mainland in all periods (Mann-Whitney-tests. Period 1988: U=45.00, p<0.01, n=36; period 1996: U=31.00, p<0.01, n=36; period 2001: U=23.00, p<0.01, n=36; period 2006: U=36.00, p<0.01, n=36). The smallest difference between Halligen (median=18) and mainland (median=4) was in 1988, and highest in 2001 (Halligen: median=46; mainland: median=7).

The standardized sums of breeding pairs increased marginally, though not significantly (Kruskal-Wallis-test: H=1.91, p>0.05, df=3) from 1988–2001 and then decreased again on the mainland (figure 10). The same pattern was observed on the Halligen with non-significance in the results (Kruskal-Wallis-test: H=5.64, p>0.05, df=3). The pattern of change is more obvious on the Halligen than on the mainland.

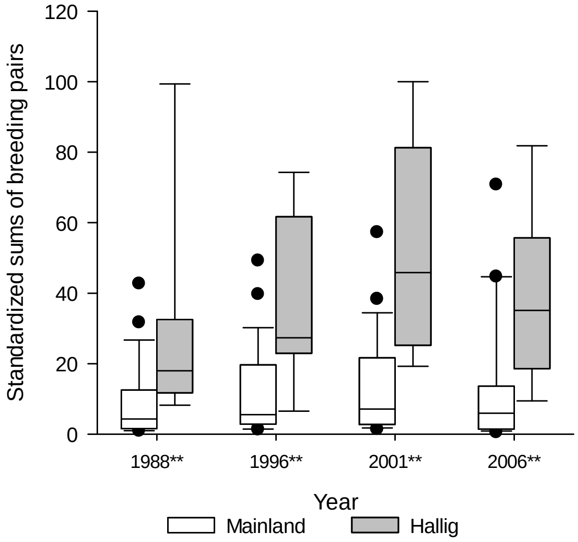


Figure 9: Comparison of standardized sums of breeding pairs between mainland and Halligen for each single period. **= difference was highly significant with p<0.01.

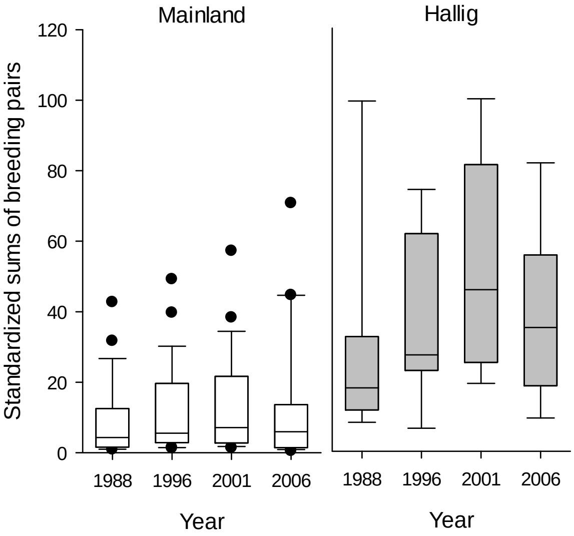


Figure 10: Standardized sums of breeding pairs did neither on the mainland (Kruskal-Wallis-test: H=1.91, p>0.05, df=3) nor on the Halligen (Kruskal-Wallis-test: H=1.91, p>0.05, df=3) differ significantly between periods.

GR&V diversity was not significantly different between Halligen and mainland in 2001 (t-test: t=0.59, p>0.05, df=34) and 2006 (t-test: t=0.54, p>0.05, df=34) (figure 11). In both years mean GR&V diversity was only slightly higher on the Halligen (2001: mean=2.26 ± 0.32 and 2006: mean=2.12 ± 0.39) than on the mainland (2001: mean=2.17 ± 0.41 and 2006: mean=2.04 ± 0.41).

Considering temporal shifts (figure 12) there was no significant difference (t-test: t=0.80, p>0.05, df=16) of GR&V diversity between 2001 (mean=2.26 ± 0.32) and 2006 (mean=2.12 ± 0.39) on the Halligen. In contrast, there were significant temporal differences on the mainland (One-way ANOVA: F=41.62, p<0.01; with Bonferroni-post-hoc-test): GR&V diversity was lowest in 1988 (mean=1.06 ± 0.34), increased over 1996 (mean=1.73 ± 0.43) to 2001 (mean=2.17 ± 0.41) and decreased again in 2006 (mean=2.04 ± 0.41). The difference between 2001 and 2006 was not significant, though. The pattern of change on the mainland is the same that could be found for mainland and Halligen taken together (figure 6) with lowest diversity in 1988 and highest in 2001 followed by a decrease in 2006.

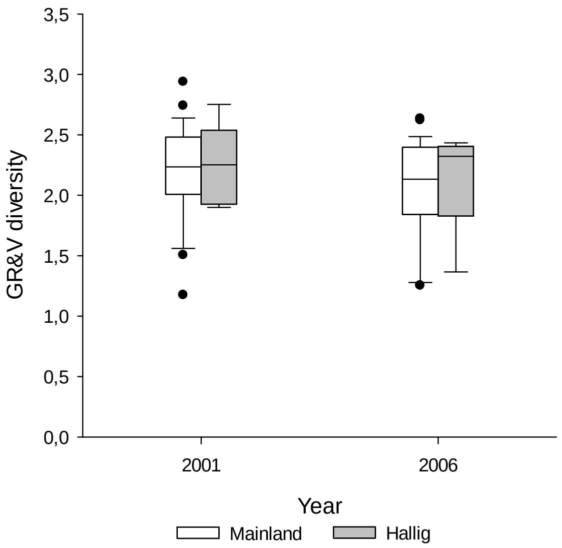


Figure 11: Comparison of GR&V diversity between mainland and Halligen for each single period (Halligen data for 1988 and 1996 not available). There were neither in 2001 (t-test: t=0.59, p>0.05, df=34) nor in 2006 (t-test: t=0.54, p>0.05, df=34) significant differences.

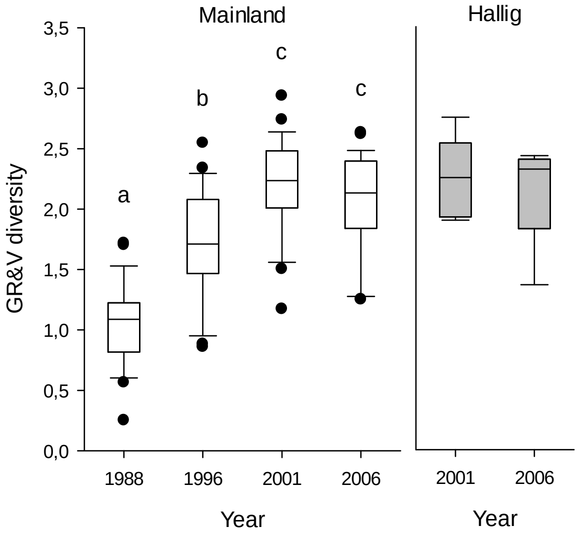


Figure 12: GR&V diversity differed significantly through time on the mainland (One-way ANOVA: F=41.62, p<0.01; with Bonferroni-post-hoc-test) but not on the Halligen (t-test: t=0.80, p>0.05, df=16). Different letters above box-plots indicate that means were significantly different.

2.4.3 BBS richness and GR&V diversity: coherencies in space and time

Multiple linear regressions demonstrated that the relationship between BBS richness and the considered variables was time-dependent (table 3): In 1988 high GR&V diversity did not lead to high BBS richness nor was the size of study site important; the model taken as a whole was in total not significant. In 1996, though, the model was significant but the single variables were not; GR&V diversity had a higher explanatory value than area. However, with Halligen data available in 2001 and 2006 models were both significant: In 2001 GR&V diversity and location were both significant with GR&V diversity having the greater explanatory value. BBS richness increased with increasing GR&V diversity and decreased in general when the study site was situated on the mainland. The corrected R^2 value was 0.36 giving the model a total explanation rate of 36% of the data. In 2006 the model was significant with an explanation rate of 29%. But here only the variable "location" was significant: If situated on the mainland, study sites had less BBS richness than on the Halligen. In none of the models size of study site contributed in a significant way to BBS richness. Analysing only the mainland data and taking into account "year" as variable resulted in a significant model: GR&V diversity contributed significantly to the explanation rate of 16%, whereas "year" did not (table 4).

Table 3: Results of multiple linear regressions for the relationship between BBS richness, GR&V diversity, area and location (mainland or Halligen) per period.

	1988				1996				2001				2006			
F	0.52				4.31				7.46				5.76			
p	0.60				0.03				0.00				0.00			
R	0.21				0.54				0.64				0.59			
R^2	0.04				0.26				0.41				0.35			
R^2 corrected	-0.04				0.20				0.36				0.29			
	B	Beta	t	p	B	Beta	t	p	B	Beta	t	p	B	Beta	t	p
Intercept	11.22		5.14.	0.00	5.74		2.17	0.04	4.76		1.25	0.22	15.56		4.06	0.00
GR&V diversity	-1.97	-0.20	-0.97	0.34	2.92	0.36	1.66	0.11	5.10	0.56	3.36	0.00	1.48	0.16	0.97	0.34
Area	0.00	0,.13	0.61	0.55	0.00	0.22	0.99	0.33	0.00	0.01	0.03	0.97	0.00	0.23	1.42	0.17
Location	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	-2.07	-0.26	-1.88	0.07	-4.18	-0.49	-3.37	0.00

Table 4: Results of multiple linear regression for the relationship between BBS richness, GR&V diversity, area and year on the mainland.

Mainland						
F	4.96		B	Beta	t	p
p	0.00	Intercept	5.61		3.08	0.00
R	0.44	GR&V diversity	2.33	0.38	2.46	0.02
R^2	0.20	Area	0.00	0.17	1.60	0.11
R^2 corrected	0.16	1988	0.89	0.11	0.71	0.48
		1996	1.37	0.17	1.46	0.15
		2001	0.16	0.02	0.18	0.86

2.5 Discussion

One important finding of this study is that high GR&V diversity does not generally lead to a high BBS richness. Actually, the relationship between both variables was time-dependent. In 1988 there was no relationship at all between GR&V diversity and BBS richness whereas in 1996 there was a significant relationship, yet none of the studied variables alone were significant contributors to this relationship. In 2001 BBS richness increased with increasing GR&V diversity, although explanation rate was rather low (36%). In contrast, in 2006 this relationship was no longer seen. Instead, location was the most important and only significant variable: BBS richness decreased when the study site was situated on the mainland. Considering only the mainland and looking at changes through time, no single year was decisive but there was a general increase of BBS richness with increasing GR&V diversity. However, explanation rate was low (16%) so that relationship is not conclusive.

Furthermore these results demonstrate that GR&V diversity increased significantly through time from 1988–2001 and decreased slightly and non-significantly in 2006. These results are consistent with Esselink et al. (2009) who reported for the salt marshes of Schleswig-Holstein that after a first increase in vegetation diversity late successional and climax stages of salt marsh vegetation occurred and led in several areas to mono-dominant stands of *Elymus athericus* and *Phragmites australis.* In the short term, structural diversity of salt marsh vegetation increases after reduction of livestock grazing (Kiehl et al. 2000) providing a wider range of breeding habitat. Eskildsen et al. (2000) documented an increase in number of breeding bird species on the Hamburger Hallig several years after reduction of grazing. Grassland breeding birds (e.g. redshank (*Tringa totanus*) and black-tailed godwit (*Limosa limosa*)) and duck species noticeably benefited, as they prefer taller vegetation at their breeding sites (Eskildsen et al. 2000). Although total BBS richness per period increased, mean BBS richness did not and my data do not support the hypothesis of relationship between GR&V diversity and BBS richness in general.

Another important consideration is the effect of location (i.e. Hallig or mainland). BBS richness is higher on the Halligen than on the mainland, although this difference was only significant in period 2006. The same applies to the standardized sums of breeding pairs which were significantly higher on the Halligen than on the mainland in all periods. Additionally, temporal changes of BBS richness and standardized sums of breeding pairs differ between mainland and Halligen as well. While BBS richness on the mainland by trend increased from 1988–2001 and thereafter decreased, BBS richness on the Halligen continuously (but not significantly) increased through time. If standardized sums of breeding pairs are considered, there is no change on the mainland through time but on the Halligen there is an increasing tendency until period 2001, followed by a decrease in period 2006.

Results of multiple regression analyses revealed location as the most important factor influencing BBS richness in 2006. This and the mentioned differences in BBS richness between mainland and Halligen emphasize the distinctive nature of the Halligen compared to the mainland. Halligen and mainland are subject to two different grazing regimes with stronger dynamics regarding changes in grazing regime on the Halligen. Given that GR&V diversity did not differ between the Halligen and mainland during 2001–2006, one must ask "What makes Halligen unique from a bird's point of view?".

One difference, which has often been mentioned, is the lack of mammalian predators on the Halligen (Grave & Lutz 2004). This absence is mainly due to two reasons: Mammalian predators cannot easily reach the Halligen, because most of them are completely enclosed by water and mud flats, respectively. Exceptions are the Halligen Oland, Langeneß and Nordstrandischmoor which are connected to the mainland by small railway embankments. In addition, mammalian predators would likely drown during flooding which naturally occur in autumn, winter and early spring on the Halligen. Mammalian predators, especially red fox (*Vulpes vulpes*), can severely reduce breeding success of salt marsh birds on the mainland (Langhans 2010). Particularly during the 1990s populations of red fox increased due to vaccination against rabies (Südbeck et al. 1998). However, my results show that the standardized sums of breeding pairs did not decrease through time. In contrast, based on my 27 mainland study sites there is a net increase of more than 7700 breeding pairs from 1988–2006. Thus, the influence of mammalian predators has not yet been demonstrated to cause a decrease of total breeding bird population. Thus, at least as the sole reason, the lack of mammalian predators becomes a dubious hypothesis for the higher attractiveness of the Halligen to breeding birds.

It is possible that the Halligen offer a greater food supply of benthic organisms like cockles and annelids in the mudflats during low-tide as well as of fish in the water during high-tide than is available on the mainland and that this may account for differences in bird diversity. On the mainland there is usually only a single borderline to the mudflats at the outer end of the salt marsh that makes distance to feeding grounds for most breeding pairs longer unless they find sufficient food in the drainage ditches. Additionally, the Halligen undergo stronger floodwater dynamics during flooding as they have less drainage ditches to make the water flow back from these areas. Thus, there are more non-linear, winding and more diverse tidal creeks and hollows present as a result of floodwater dynamics that may offer additional food supply. Nevertheless, food availability on the mainland is extremely good in some regions. This is the case in the salt marsh of the Neufelder Koog which is adjacent to the Elbe estuary and at the flood barrier of the Eider River. The colony of common tern

(*Sterna hirundo*) in the Neufelder Koog showed a net increase over the last decade (Schiffler 2011) and Arctic tern (*Sterna paradisaea*) at the Eider River also expanded during the last years (Schiffler et al. 2010). In both cases, the availability of fish is considered to be the cause for this (Schiffler et al. 2010). Thus, the issue of food availability has to be distinguished regionally and, just as predation, cannot exclusively explain avian attraction to the Halligen.

One limitation of the present study is the lack of information about vegetation and grazing regime on the Halligen before 1996. Thus, the coherency between BBS richness and GR&V diversity cannot be completely elucidated. Mappings of vegetation and birds had been conducted by various persons within and between years and this may result in differences of mapping accuracy and may therefore influence the results of analyses. In particular the mappings of Anatidae and other concealed breeding species might be biased. Another confounding factor is the vegetative classification of *Juncus gerardii* type. According to the TMAP parameters vegetation should be classified as *Juncus gerardii* type if 5% or more are covered with *Juncus gerardii* notwithstanding the cover of the remaining 95% of vegetation (Esselink et al. 2009). In the case of Hallig Langeneß according to mapping *Juncus gerardii* covered 64% of the Hallig in 2006 which does not conform to the actual, more diverse vegetation (personal observation).

Another issue is the inter-dependency of species and location. While Thyen & Exo (2003), Schrader (2003) and Grave & Lutz (2004) found higher breeding bird densities and even higher breeding success of waders on ungrazed areas compared to grazed ones, Oltmanns (2003) documented decreasing abundances on ungrazed sites. Oltmanns (2003) and Hälterlein (2002) emphasize species-specific avian diversity differences as a response to grazing regime changes. Furthermore grazing regime changes can lead to spatial shifts on a small scale, especially among colony breeding birds. This has for instance been the case on Hallig Hooge where both common and artic tern (*Sterna hirundo, S. paradisaea*, respectively) moved from their former breeding sites where grazing had been intensified to areas with lower grazing intensities (V. Hennig, personal communication 2012). These small-scale spatial shifts are only anecdotal, but show important responses of breeding birds to changes in grazing regime and emphasize the importance of scale when considering the influence of grazing regimes on breeding birds.

Based upon the results of this study, it is clear that GR&V diversity can neither explain changes of BBS richness through time nor differences in BBS richness between mainland and Halligen on a large scale. Though it is evident that grazing regimes affect breeding birds, these effects may be blurred by scale factors and not readily apparent. For example, there is only one value each for BBS richness and GR&V diversity for Hallig Langeneß (960 ha in size). The small-scale diversity and dynamics cannot be expressed appropriately in this way. In addition, my results emphasize the distinctive nature of of the Halligen with regard to BBS richness. This distinctive nature cannot be explained by GR&V diversity nor by predation nor food availability solely but may be a result of the combination of these and other factors. To adequately address these and other issues, future studies should focus on the effect of grazing regimes on a) small-scale spatial shifts of birds and b) on breeding bird communities rather than single species.

2.6 Appendix

Breeding bird species included into analysis. For each species the number of study sites in which it occurred is given per period. There were 36 study sites.

Englisch name	Latin name	1988	1996	2001	2006
Eurasian Spoonbill	*Platalea leucorodia*			1	1
Greylag Goose	*Anser anser*		4	4	6
Barnacle Goose	*Branta leucopsis*			2	2
Egyptian Goose	*Alopochen aegyptiacus*				1
Common Shelduck	*Tadorna tadorna*	23	35	32	30
Wigeon	*Anas penelope*	1		1	
Gadwall	*Anas strepera*	2	3	7	10
Teal	*Anas crecca*	2	2	2	
Mallard	*Anas platyrhynchos*	17	26	22	20
Pintail	*Anas acuta*		1	2	
Garganey	*Anas querquedula*	1			
Shoveler	*Anas clypeata*	3	4	6	12
Pochard	*Aythya ferina*	1			
Tufted Duck	*Aythya fuligula*	3	7	6	5
Common Eider	*Somateria mollissima*	6	8	5	9
Red-breasted Merganser	*Mergus serrator*	4	5	5	6
Marsh Harrier	*Circus aeruginosus*	2	3		4
Water Rail	*Rallus aquaticus*		1		1
Moorhen	*Gallinula chloropus*	1			4
Coot	*Fulica atra*			1	
Eurasian Oystercatcher	*Haematopus ostralegus*	36	36	36	36
Avocet	*Recurvirostra avosetta*	29	33	33	33
Little Ringed Plover	*Charadrius dubius*				1
Great Ringed Plover	*Charadrius hiaticula*	32	31	28	23
Kentish Plover	*Charadrius alexandrinus*	20	10	9	5
Northern Lapwing	*Vanellus vanellus*	32	31	33	32
Dunlin	*Calidris alpina schinzii*	2			
Ruff	*Philomachus pugnax*	4	3	1	2
Common Snipe	*Gallinago gallinago*		1	2	
Black-tailed Godwit	*Limosa limosa*	5	13	21	16
Eurasian Curlew	*Numenius arquata*				2
Common Redshank	*Tringa totanus*	36	36	36	36
Turnstone	*Arenaria interpres*	2	2	2	3
Mediterranean Gull	*Larus melanocephalus*			1	3
Black-headed Gull	*Larus ridibundus*	33	35	34	34
Common Gull	*Larus canus*	18	29	27	24
Lesser Black-backed Gull	*Larus fuscus*	2	8	10	15
Herring Gull	*Larus argentatus*	18	20	27	25
Great Black-backed Gull	*Larus marinus*		4	7	2
Gull-billed Tern	*Gelochelidon nilotica*		6	2	2
Sandwich Tern	*Sterna sandvicensis*	1	5	6	1
"Red-footed terns"	*Sterna hirundo & S. paradisaea*	28	31	29	31
Little Tern	*Sterna albifrons*	6	6	7	6
Short-eared Owl	*Asio flammeus*		4		1

3 Chapter 2

Nest site selection of oystercatchers: the importance of structural heterogeneity and ditches

3.1 Abstract

Suitable nest site is a crucial factor for breeding success in birds. Eurasian oystercatchers (*Haematopus ostralegus*) prefer to nest in open areas with only few vegetation cover and adjacency to shallow water bodies. Yet no study analysed the influence of salt marsh vegetation type and grazing regime on nest site selection. Influence of vegetation type, grazing regime, their interaction and of edge structures (ditches, vegetation type shifts, berm) on nest site selection of oystercatchers were studied in 1996, 2001 and 2006 in the salt marsh of Hedwigenkoog, Germany. It is assumed that the transition zone between two vegetation types comprises different and more diverse vertical structures than the two adjacent vegetation types. I used existing point data of breeding bird censuses and area-wide vegetation mappings, which were made available by the Schleswig-Holstein Wadden Sea National Park. I employed GIS to spatially join nest sites with vegetation mappings, calculate kernel nest density, generate random points to control for accidental effects, calculate shortest distance to edge structures and buffer vegetation polygons to control for temporal shifts in the extent of vegetation area. Non-parametric tests and correlations were used to analyse the effect of vegetation type, grazing regime and distance to edge structures on nest site selection of oystercatchers. Classification trees were used to determine which of the habitat factors (vegetation type, grazing regime and distance to edge structures) are most important to oystercatchers when compared to random points. Oystercatcher nest density was in none of the years affected by vegetation type. In 2001 nest density was highest in the ungrazed area and in 2006 oystercatchers showed a considerable preference for the "grazed again" areas. Interaction of vegetation type and grazing regime did in none of the years have an influence on the distribution of oystercatchers. Distance to vegetation edge shortened significantly through time whereas distance to ditches and berm showed no clear temporal tendency. Classification trees revealed distance parameters as more important to distinguish between oystercatcher nests and random points than vegetation type or grazing regime. I conclude that structural diversity and adjacency to ditches are most important for nest site selection of oystercatchers.

3.2 Introduction

Nest site selection is a critical factor for breeding success in birds. In salt marshes the nest site should provide safety against flooding as well as against predation; moreover the availability of sufficient food sources is important for chick rearing. Ens et al. (1992) showed that high territory quality led to higher breeding success in Eurasian Oystercatcher (*Haematopus ostralegus*) mainly due to the adjacency to mudflats which were used as primary foraging habitat.

Eurasian Oystercatcher breeds in the western Palaearctic with a main occurrence on the coast of northern Atlantic and the North Sea. Oystercatchers use boulder, gravel rock and sand shores as well as salt marshes as breeding habitat and show a recent tendency of inland breeding on farmlands (Dircksen et al. 2001). They prefer open areas with only few vegetation cover as nest sites (Martinez et al. 1983; Goutner & Goutner 1987; Valle & Scarton 1996; Valle & Scarton 1999). Another important characteristic of oystercatcher nest sites is the presence of ephemeral stagnant pools near the nest (Valle & Scarton 1999). Oystercatchers feed their chicks, which is unusual for waders (Dircksen 1932; Lind 1965; Norton-Griffiths 1969) and adults are known to lead their chicks into feeding grounds that can be mudflats, ditches, or other shallow water bodies. Thus, oystercatchers prefer to nest close to shallow water bodies (Martinez et al. 1983; Goutner & Goutner 1987).

Previous studies of oystercatchers have focussed on either general habitat choice (Heinanen & von Numers 2009) or vegetation parameters such as height or cover at the nest site (Valle & Scarton 1996; Valle & Scarton 1999). No study has yet analysed the influence of salt marsh vegetation type on nest site selection. In the face of declining wader populations throughout Europe, the recognition and maintenance of high quality breeding habitats has become a critical issue. Populations of oystercatchers show a long-term decline in the Wadden Sea, particularly in Schleswig-Holstein and the Netherlands (JMBB 2010). In the Netherlands this trend is mainly due to the extensive shellfish fishery (Verhulst et al. 2004), but in the case of the Schleswig-Holstein Wadden Sea other factors, like changes in breeding habitat, have to be considered. Studies conducted on a small spatial scale level are important because habitat management efforts usually focus on small or intermediate levels and seldom on a landscape level. If new management schemes are successful in maintaining or restoring high quality habitats at small or intermediate levels, they can subsequently be applied at the landscape level.

In this study I use existing data from the Trilateral Monitoring and Assessment Program (TMAP) to analyse the effect of vegetation type, grazing regime and presence of ditches on nest site selection of oystercatcher from 1996–2006 in the salt marshes of Hedwigenkoog, Germany. (Maier et al. 2010) showed that some of the TMAP vegetation types have significantly different vertical structures and that grazing regime also has a considerable effect on vegetation structure. I consider vegetation type and grazing regime as a proxy for vertical structure and examined the influence of vegetation edges (i.e. the line between two vegetation types) on nest site selection. Given that the spatial shift from one vegetation type to another is not a sharp line as in the vegetation mappings, but rather a continuous transition, I assume that this transition zone comprises different and more diverse vertical structures than the two adjacent vegetation types. This study also seeks to address the role of ditches as foraging grounds in nest site selection of oystercatcher. This study considers areas with high densities of oystercatcher nests as "preferred" and focusses on the following questions: a) Does vegetation type, grazing regime, or the interaction of these factors influence nest density? b) Do oystercatchers demonstrate specific edge structures preferences in nest site selection?

3.3 Material & Methods

3.3.1 Study site and data

The study site is located in the salt marshes of Hedwigenkoog (54°12′N, 8°49′E) south of the estuary of the Eider River, Schleswig-Holstein, Germany. The study site comprises a salt marsh bordered by a dyke to the east and mudflats to the west; northern and southern ends are bordered by large drainage channels. The site is characterized by various ditches and tide-ways, collectively referred to as "ditches" in this study. Due to sedimentation processes the area increased from 73–93 ha from 1996–2006. At the beginning of the 1990s the entire area was intensively grazed by sheep. In 1996 only a 40–200 m broad band (in sum 14 ha) adjacent to the dyke was still grazed, resulting in an area of 58 ha ungrazed. In 1999 the grazed area was extended again to 27 ha, which did not change until 2009 (figure 13). The three gazing regimes "grazed" (i.e. intensively grazed), "ungrazed" and "grazed again" were considered in this study.

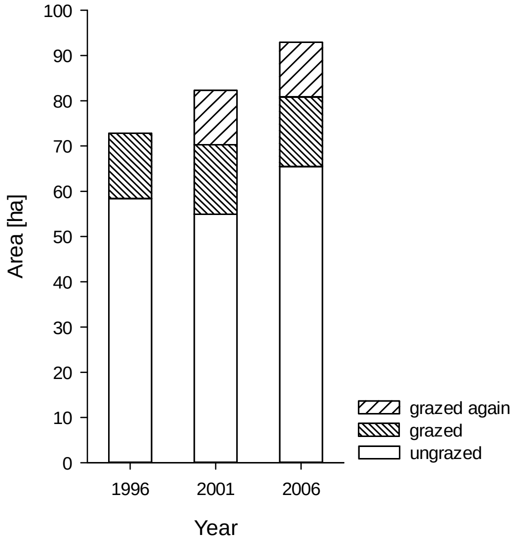


Figure 13: Area [ha] per grazing regime and year in the salt marshes of Hedwigenkoog. Because of sedimentation the study area enlarged from 73 ha in 1996 to 93 ha in 2006. Thereof affected were only the ungrazed areas.

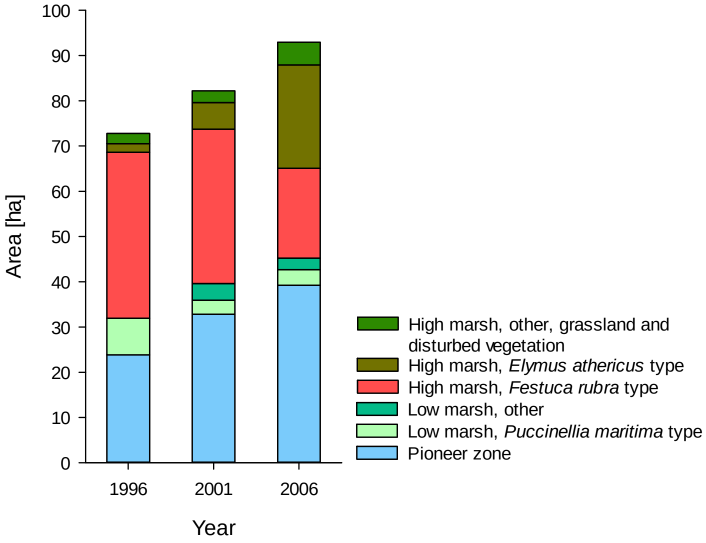


Figure 14: Area [ha] per vegetation type and year in the salt marshes of Hedwigenkoog; less dominant types were lumped. Sedimentation processes caused an enlargement of approximately 10 ha from one mapping year to the next.

Bird and vegetation data collected by TMAP were made available by the Schleswig-Holstein's Government-Owned Company for Coastal Protection, National Parks and Ocean Protection (LKN-SH). The study site is one of the "census areas" of the national park in which all breeding bird species are counted annually. In addition, the hatching success of oystercatchers is monitored every year in the study site by systematic searches for oystercatcher nests. Search efforts are repeated every 5 days so that all nests are found. From 1993–2009 nests were individually marked and mapped. In 1996, 2001 and 2006 salt marsh vegetation was mapped according to the TMAP parameters. All vegetation types present at the study site are listed in table 5 (see also figure 14).

Table 5: Survey of vegetation types and coverage area [ha] from TMAP survey.

TMAP code	TMAP vegetation type	Abbreviation	1996	2001	2006
S 1	Pioneer zone, unspecific	PZ		3.55	
S 1.1	Pioneer zone, *Spartina anglica* type	SA	16.91	18.78	27.06
S 1.2	Pioneer zone, *Salicornia* type	SE	6.94	10.50	12.16
S 2	Low marsh, unspecific	LM		2.77	2.53
S 2.1	Low marsh, *Puccinellia maritima* type	PM	8.08	3.12	3.47
S 2.4	Low marsh, *Atriplex portulacoides* type	AI		0.90	
S 3	High marsh, unspecific	HM		0.78	
S 3.2	High marsh, *Juncus gerardii* type	JG	2.24	0.02	0.45
S 3.3	High marsh, *Festuca rubra* type	FR	36.68	34.13	19.84
S 3.5	High marsh, *Artemisia maritima* type	AM			4.25
S 3.7	High marsh, *Elymus athericus* type	EA	1.92	5.86	22.88
S 3.9	High marsh, *Atriplex prostrata* type	AP		0.06	0.16
S 3.11	High marsh, *Plantago coronopus* type	PC		0.06	
S 3.13	High marsh, *Elymus repens* type	ER			0.04
S 6.1	Fresh grassland, *Lolium perenne* type	LP		1.64	
N	Vegetation disturbed	VD			0.11
Total area			72.78	82.17	92.94

There had been considerable changes in vegetation patterns between 1996–2006 (figure 14 and figure 15). Most conspicuous is the increase in area dominated by *Elymus athericus* and the concurrent decrease in area dominated by *Festuca rubra*. While the shifts between these two vegetation types were less pronounced between 1996–2001, vegetation of *Festuca rubra* type decreased from 34 ha in 2001 (42% of total area) to 20 ha in 2006 (21% of total area), whereas *Elymus athericus* type vegetation almost quadruplicated from 6–23 ha between 2001–2006. Moreover the pioneer zone increased by about 10 ha during the same 5-year-period as a result of sedimentation. Number of vegetation types was highest in 2001 although some types occurred in very small proportions.

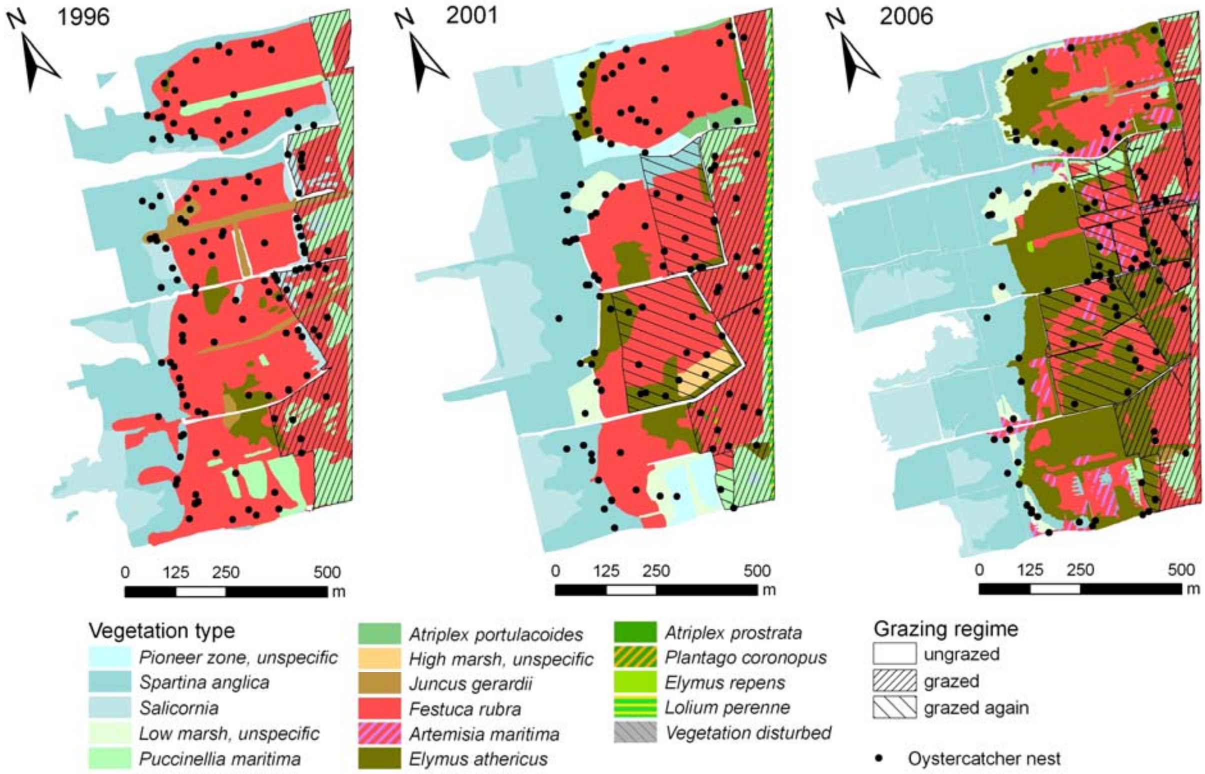


Figure 15: Vegetation types, grazing regimes and location of oystercatcher nests in the study area Hedwigenkoog in the three study years 1996, 2001 and 2006.

All ditches which were potentially suitable for foraging were digitized. The smallest ones, which occurred regularly every 10 m, were excluded. The transition from low/high salt marsh to pioneer zone was marked by a 0.5 m high berm in all years. Ditches and berm were considered as important edge structures in this study (figure 16).

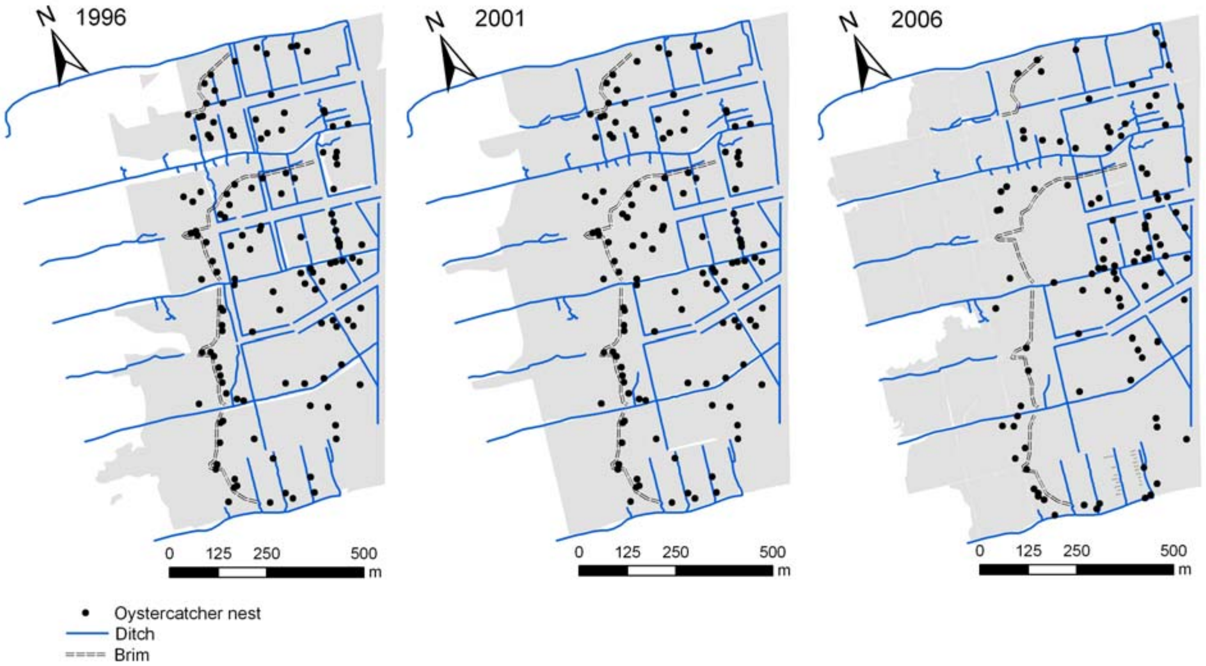


Figure 16: Ditches suitable for foraging, berm and location of oystercatcher nests in the study area Hedwigenkoog in the three study years 1996, 2001 and 2006.

3.3.2 Data analysis and statistics

For the purpose of analyses, data from three vegetation mapping surveys (1996, 2001 and 2006) and the corresponding breeding bird data for the same years were considered. Additionally, the development of the oystercatcher population at the study site is shown for the period from 1993–2009. I only used first clutches for analysis and excluded the dyke and any evidence of oystercatchers breeding on the dyke from the study. I spatially joined the vegetation and oystercatcher mappings using ESRI's ArcGIS 9.3. Kernel density was calculated for all oystercatcher nests per year and the accordant density value was allocated to each single nest using Spatial Analyst in ESRI's ArcGIS 9.3. The kernel density estimates the probability density. Based on each data point it searches within the search radius (i.e. 70 m in this analysis) for further data points and on this basis estimates the probability of the occurrence of data points. Between the points a surface of probability density is interpolated. The resulting kernel density value is high in areas with many data points and low in areas with few data points. The advantage of the kernel density is that no further spatial data are required as the estimation is solely done on the basis of the input data points.

The influence of a) vegetation type, b) grazing regime and c) interaction of these factors on 1) the percentage of oystercatcher nests and 2) kernel nest density was analyzed by non-parametric tests (Two-samples-Kolmogorov-Smirnov-test, Mann-Whitney-test, Kruskal-Wallis-test followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction Holm 1979 and 1-sample-Chi^2-test).

I determined the shortest distance from each nest to four categories of edge structures: 1. vegetation edge (i.e. the line between two different vegetation types), 2. ditch, 3. ditch or vegetation edge and 4. ditch or berm; these calculations were done in ESRI's ArcView GIS 3.2a with the "Nearest feature" extension (Jenness Enterprises). I tested for correlations between nest density and distance from nests to these edge structures. Moreover, I verified differences in distances during the three study years

(Kruskal-Wallis-tests followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction).

I used spatial buffers to control for changing distances to vegetation edge caused by shifts in the extent of vegetation areas over the years. I buffered each single vegetation polygon inwardly with multiple ring buffers of 5 m. When the polygon was filled with buffers or when no new buffer could be built, buffer building was automatically stopped. The number of nests per buffer distance was counted and the percentage of buffers used by oystercatchers and of available buffers per distance was calculated. The distributions of buffers were compared to each other (Two-samples-Kolmogorow-Smirnov-test).

Random points were generated to control for accidental effects in the adjacency of oystercatcher nests to edge structures. The number of random points was in accordance with the number of nest sites per year. I excluded all pioneer zone vegetation types (i.e. pioneer zone unspecific, *Spartina anglica* and *Salicornia*) from the salt marsh area available to allocate these random points. Since these types are found in large areas of bare or only sparsely vegetated moist soil (inundated twice a daily the tides), oystercatchers can only nest on small hummocks. This makes the pioneer zone not as suitable as other salt marsh types for nesting and may confound results. Differences between oystercatcher nests and random points were analysed with regard to distances to edge structures (Mann-Whitney-test).

Classification trees were used to analyse which of the habitat factors (vegetation type, grazing regime and distance parameters) are most important to distinguish between oystercatcher nests and random points. Classification trees were built using the rpart package in R. Trees were grown with Gini splitting citeria, 10-fold cross validation and pruned back to the nodes where cross validation error was least. Statistical analyses were performed with SPSS 16.0 for Windows and R, respectively. Box-plots show the median and lower and upper quartiles (box) as well as 10th and 90th percentiles (whiskers); circles indicate outliers (values which are beyond the 10th or 90th percentiles).

3.4 Results

3.4.1 Population dynamics and kernel nest density

From 1993–2009 the oystercatcher population in the salt marsh of Hedwigenkoog was highest in 1993 with 166 breeding pairs. This maximum was followed by a virtually constant decline with the lowest value in 1999 with only 81 breeding pairs — less than half of the population of 1993. From 2001–2006 the population fluctuated between 100–120 breeding pairs per year and can be considered as more-or-less stable. For the three study years (1996, 2001, 2006) the numbers of breeding pairs were 130, 117, and 102, respectively (figure 17).

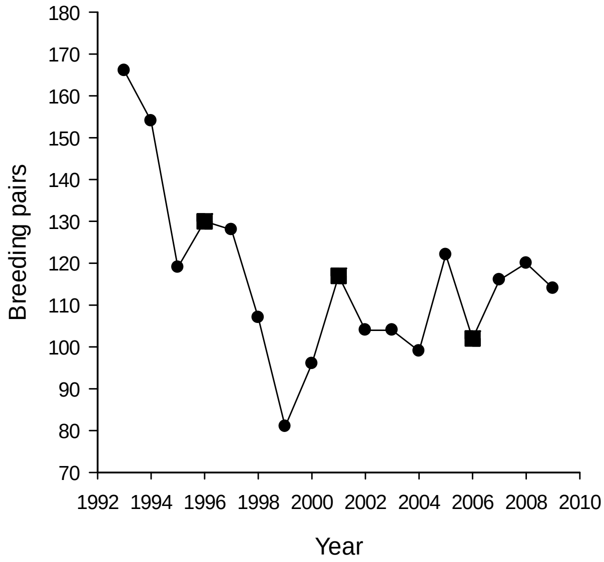


Figure 17: Number of breeding pairs of oystercatchers in the study area Hedwigenkoog from 1993–2009; squares indicate the three years taken into analysis.

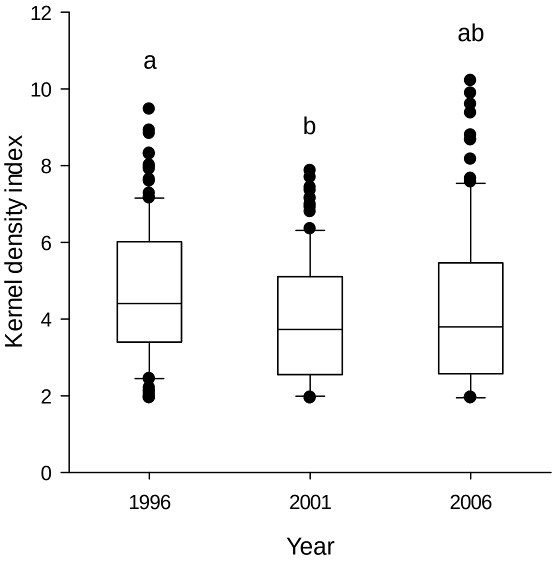


Figure 18: Kernel density of oystercatcher nests in the study area Hedwigenkoog for the years 1996, 2001 and 2006. Different letters above box-plots indicate that medians were significantly different (Kruskal-Wallis-test followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction).

The kernel nest density during the study period was highest in 1996 (median=4.40) corresponding to the highest population in that year. In 2001 (median=3.73) and 2006 (median=3.80) the medians do not differ significantly from each other (Kruskal-Wallis-test: H=12.31, p<0.01, df=2; followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction). Nest density was significantly lower in 2001 than 1996. Moreover, the range of density in 2001 was smaller than in the other two years indicating that oystercatcher nests were more equally dispersed in the salt marsh (figure 18). In 1996 and 2001 high nest densities were found close to the berm. In contrast, these density centres shifted to areas near to the dyke in the middle of the study area and larger parts showed extreme low or even no nesting in 2006 (figure 19). The latter is probably due to the fact that the number of breeding pairs in 2006 was at the lowest point of the study period.

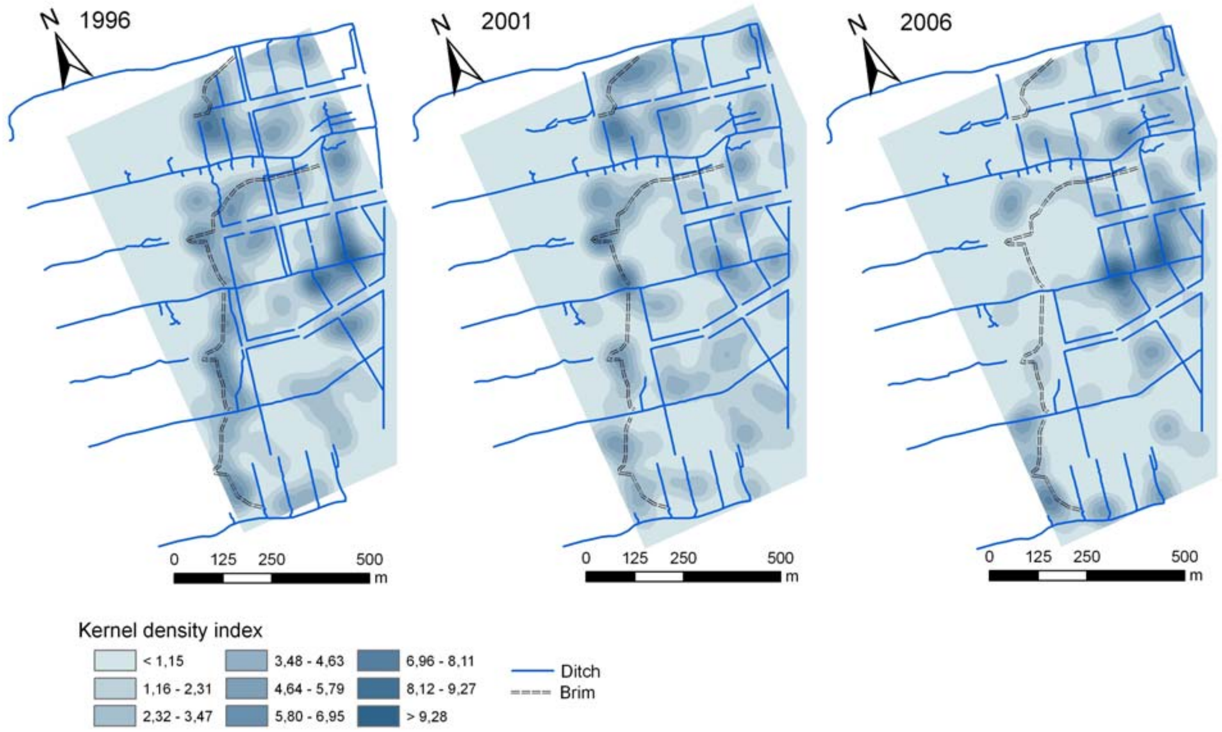


Figure 19: Spatial distribution of kernel densities for breeding oystercatchers in the study area Hedwigenkoog in 1996, 2001 and 2006.

3.4.2 Influence of vegetation type on nest distribution and density

There is no evidence that a single vegetation type significantly influenced the occurrence of oystercatcher nests during this study. The percentage of nests did not significantly differ from the percentage of area per vegetation type (Two-samples-Kolmogorov-Smirnov-test for 1996: Z=0.29, p>0.05, n=12; for 2001: Z=0.98, p>0.05, n=26 and for 2006: Z=0.85, p>0.05, n=22). In 1996 and 2001 the *Festuca rubra* type was the most dominant vegetation type and most oystercatcher nests were found in these areas. In 2006 most of the area was covered by *Festuca rubra* type, *Elymus athericus* type or *Spartina anglica* type and percentage of oystercatcher nests was highest in areas dominated by *Elymus athericus* type followed by the *Festuca rubra* type (figure 20). However, in 1996 median nest density (calculated as kernel density per nest) was highest in the *Juncus gerardii* type, followed closely by the *Salicornia* type (figure 21). In 2001 *Spartina anglica* type and *Puccinellia maritima* type had the highest nest densities. The differences in the density medians per vegetation type were significant for these two years (Kruskal-Wallis-test for 1996: H=16.82, p<0.01, df=5 and for 2001: H=27.60, p<0.01, df=12). In 2006 nest density did not differ between vegetation types (Kruskal-Wallis-test: H=17.01, p>0.05, df=10).

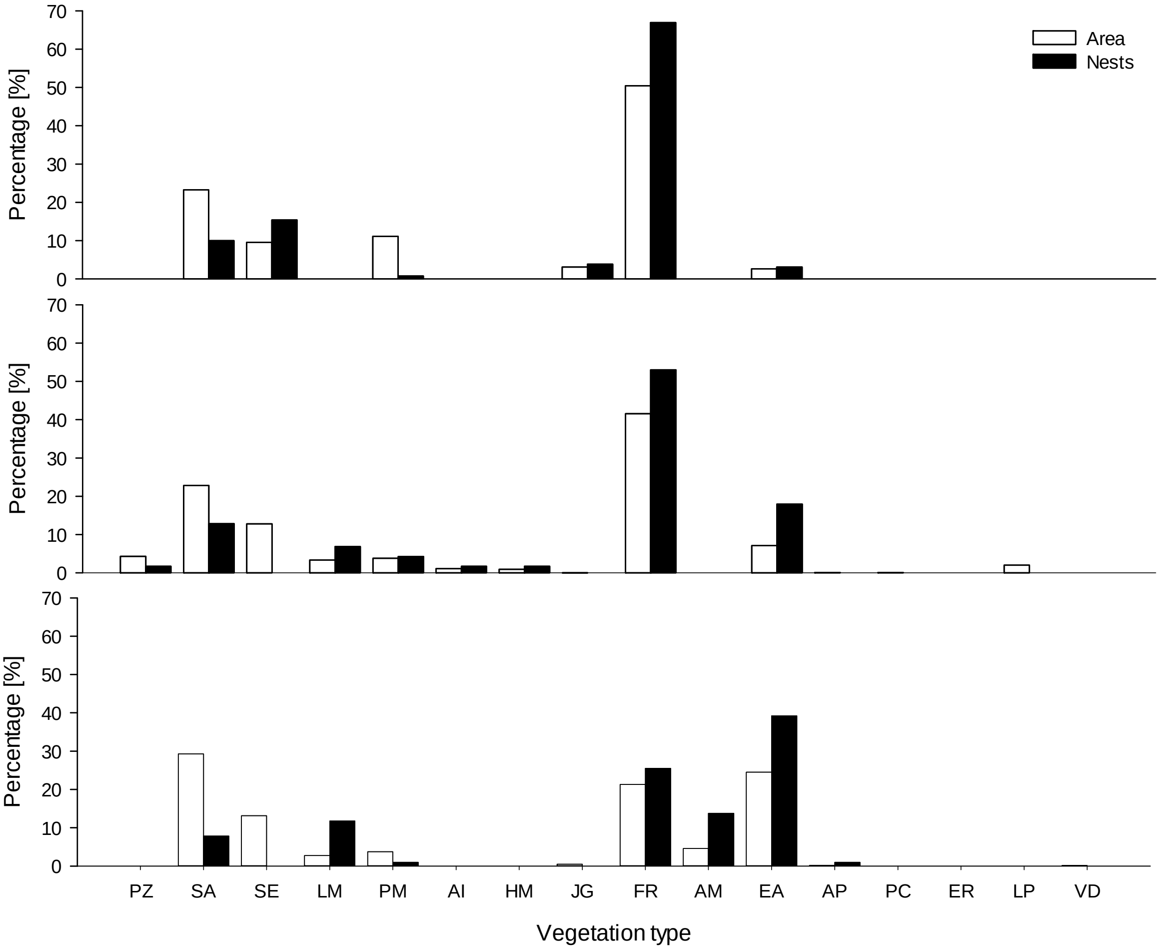


Figure 20: Percentage of oystercatcher nests and percentage of area per vegetation type in the study area Hedwigenkoog in 1996, 2001 and 2006. The distributions did not differ significantly from each other in any year (Two-samples-Kolmogorov-Smirnov-test for 1996: Z=0.29, p>0.05, n=12; for 2001: Z=0.98, p>0.05, n=26 and for 2006: Z=0.85, p>0.05, n=22).

PZ=Pioneer zone, unspecific, SA=*Spartina anglica* type, SE=*Salicornia* type, LM=Low marsh, unspecific, PM=*Puccinellia maritima* type, AI=*Atriplex portulacoides* type, HM=High marsh, unspecific, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, AM=*Artemisia maritima* type, EA=*Elymus athericus* type, AP=*Atriplex prostrata* type, PC=*Plantago coronopus* type, ER=*Elymus repens* type, LP=*Lolium perenne* type, VD=Vegetation disturbed.

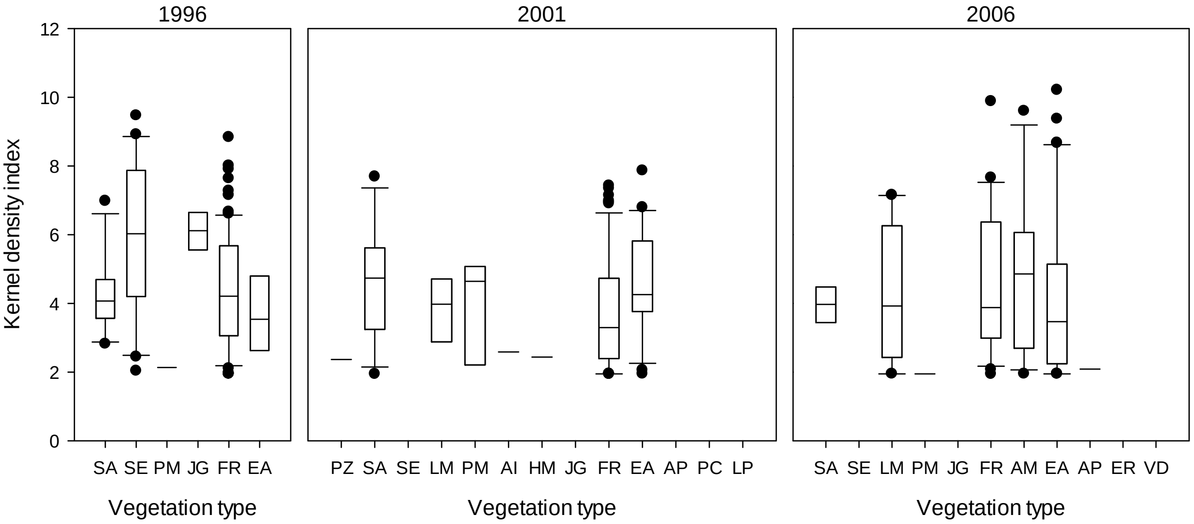


Figure 21: Kernel density of oystercatcher nests per vegetation type and year in the study area Hedwigenkoog.

In 1996 and 2001 the densities differed significantly (Kruskal-Wallis-test for 1996: H=16.82, p<0.01, df=5 and for 2001: H=27.60, p<0.01, df=12). On the contrary there was no difference in nest density between vegetation types in 2006 (Kruskal-Wallis-test: H=17.01, p>0.05, df=10).

PZ=Pioneer zone, unspecific, SA=*Spartina anglica* type, SE=*Salicornia* type, LM=Low marsh, unspecific, PM=*Puccinellia maritima* type, AI=*Atriplex portulacoides* type, HM=High marsh, unspecific, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, AM=*Artemisia maritima* type, EA=*Elymus athericus* type, AP=*Atriplex prostrata* type, PC=*Plantago coronopus* type, ER=*Elymus repens* type, LP=*Lolium perenne* type, VD=Vegetation disturbed.

3.4.3 Influence of grazing regime on nest distribution and density

The occurrence of oystercatcher nests did not differ between grazing regimes in 1996 and 2001 (1-sample-Chi^2-test for 1996: χ^2=0.12, p>0.05, df=1 and for 2001: χ^2=1.35, p>0.05, df=2). In 2006 more oystercatchers nested in the area which was grazed again (1-sample-Chi^2-test: χ^2=9.49, p<0.01, df=2). Figure 22 shows the percentage of oystercatcher nests according to the percentage of area per grazing regime. In 1996 and 2001 the percentage of oystercatcher nests corresponds to the percentage of area per grazing regime (grazed vs. ungrazed), with the greatest number of nests in ungrazed areas. However, in 2006 higher percentages of oystercatcher nests were found in the "grazed again" area than was expected given the available area. Since the enlargement of the pioneer zone led to ungrazed areas not suitable for nesting sites, the shifts in percentage should be considered with caution. There was, however, a clear change in the distribution of oystercatchers from 2001–2006. Oystercatchers relocated from ungrazed areas to grazed or "grazed again" areas.

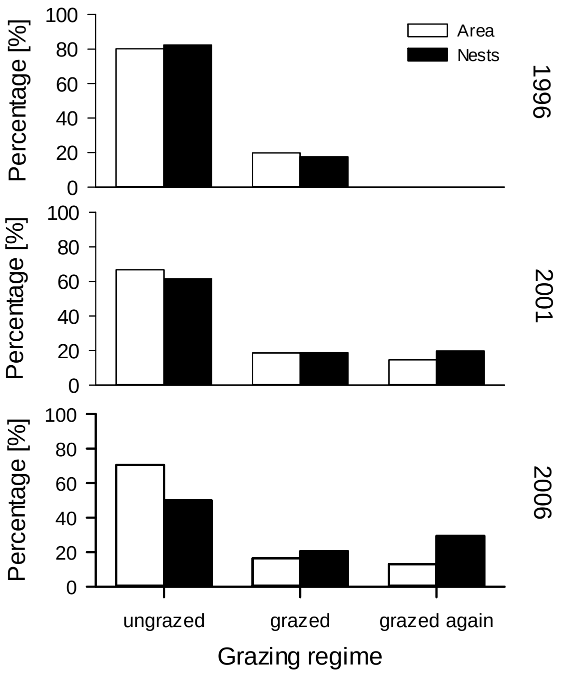


Figure 22: Percentage of oystercatcher nests and percentage of area per grazing regime in the study area Hedwigenkog in the study years 1996, 2001 and 2006. Note: Study area enlarged over the years and this gain belongs to the ungrazed area.

The grazing regime did not directly correlate to nest density in 1996 (Mann-Whitney-test: U=1037.00, p>0.05, n=130). Whereas in 2001 and 2006, however, grazing regime had a significant influence on nest density (Kruskal-Wallis-test for 2001: H=10.52, p<0.01, df=2 and for 2006: H=6.90, p<0.05, df=2; both followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction); however, the effect differed between years. In 2001 median nest density was highest in the ungrazed area and differed significantly from those in the grazed and "grazed again" areas. In 2006 median nest density was highest in the area which was grazed again and differed significantly from the ungrazed area but not from the grazed area (figure 23).

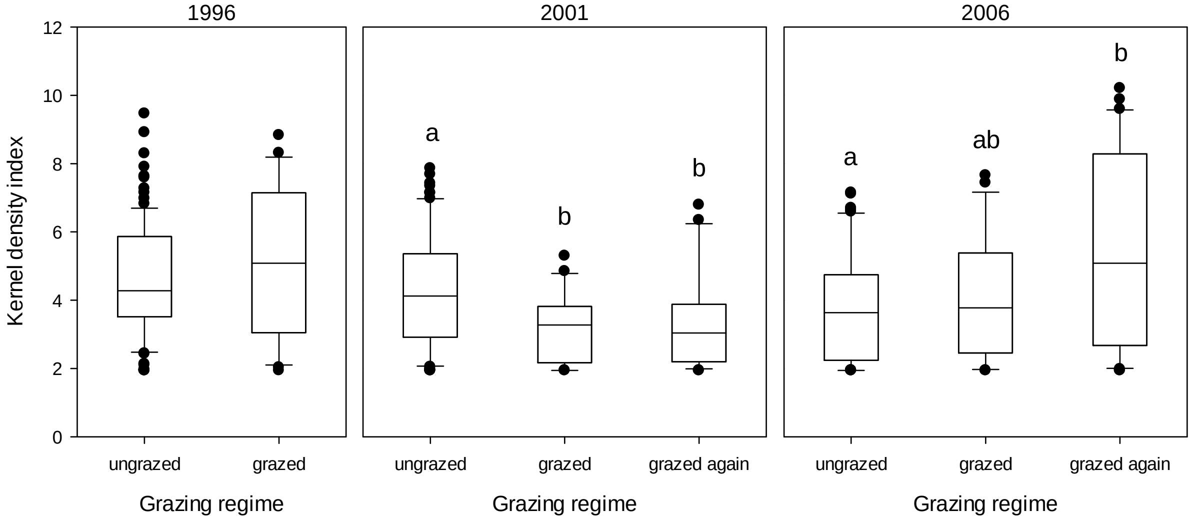


Figure 23: Nest density of oystercatchers per grazing regime and year in the study site. In 1996 only two grazing regimes existed. Different letters above box-plots indicate that medians were significantly different (Kruskal-Wallis-test followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction).

3.4.4 Influence of both vegetation type and grazing regime on nest distribution and density

The interaction between vegetation type and grazing regime had no detectable effect on the distribution of oystercatcher nests. The percentage of oystercatcher nests per combined vegetation type and grazing regime did not differ from the percentage of area per vegetation type and grazing regime type in any year (Two-samples-Kolmogorov-Smirnov-test for 1996: Z=0.64, p>0.05, n=22; for 2001: Z=0.17, p>0.05, n=40 and for 2006: Z=1.23, p>0.05, n=42). In 1996 most oystercatchers were breeding in ungrazed vegetation of *Festuca rubra* type, representing the dominant vegetation type and grazing regime. In 2001 most oystercatchers were also breeding in *Festuca rubra* type although *Festuca rubra* type was no more the dominant vegetation type. There were several vegetation types with high coverage and oystercatcher percentages corresponded to that.

In 2006 ungrazed vegetation of *Spartina anglica* type was most dominant, due primarily to the enlargement of the area in this part of the study site (see above and figure 24). As a result, the percentage of oystercatchers is rather low here as this vegetation is less suitable for breeding sites. Percentage of oystercatchers corresponded to the percentage of each area except for the already mentioned *Spartina anglica* type. Furthermore, oystercatchers occurred far more often in "grazed again" *Elymus athericus* type than was expected given the available area.

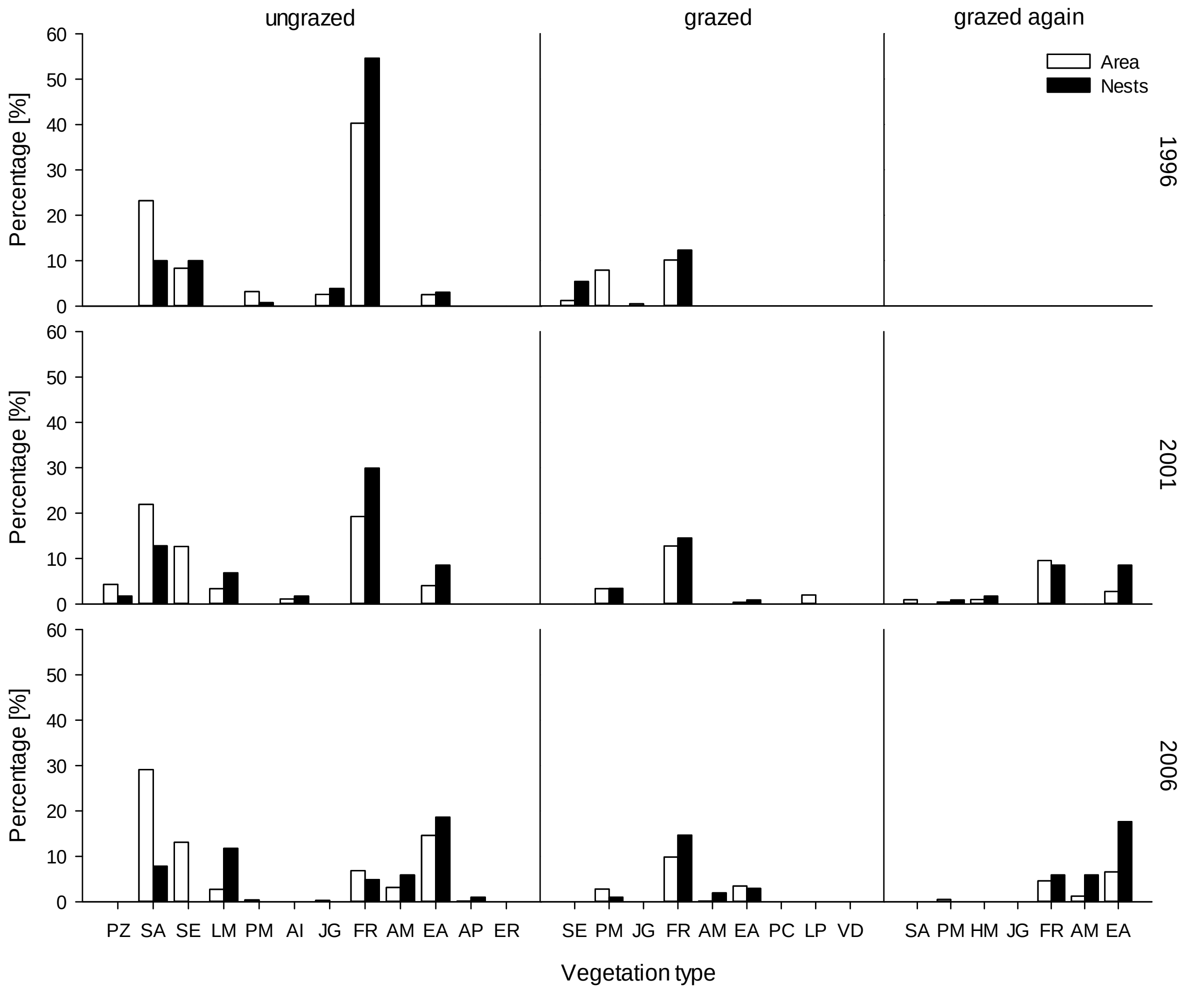


Figure 24: Percentage of oystercatcher nests and percentage of area per combined vegetation type and grazing regime in the study area Hedwigenkoog in 1996, 2001 and 2006. The distributions did not differ in any year (Two-samples-Kolmogorov-Smirnov-test for 1996: Z=0.64, p>0.05, n=22; for 2001: Z=0.17, p>0.05, n=40 and for 2006: Z=1.23, p>0.05, n=42).

PZ=Pioneer zone, unspecific, SA=*Spartina anglica* type, SE=*Salicornia* type, LM=Low marsh, unspecific, PM=*Puccinellia maritima* type, AI=*Atriplex portulacoides* type, HM=High marsh, unspecific, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, AM=*Artemisia maritima* type, EA=*Elymus athericus* type, AP=*Atriplex prostrata* type, PC=*Plantago coronopus* type, ER=*Elymus repens* type, LP=*Lolium perenne* type, VD=Vegetation disturbed.

The interaction between vegetation type and grazing regime had an influence on nest density in all three years (Kruskal-Wallis-test for 1996: H=25.59, p<0.01, df=10; for 2001: H=48.71, p<0.01, df=19 and for 2006: H=34.51, p<0.05, df=19). In 1996 median nest density was highest in grazed vegetation of *Salicornia* type, whereas in 2001 it was highest in ungrazed vegetation of *Elymus athericus* type. In both cases percentage of nests was clearly higher than expected by percentage of area indicating a more clumped distribution of nests. In 2006 the greatest median density occurred in *Festuca rubra* type vegetation being grazed again (figure 25).

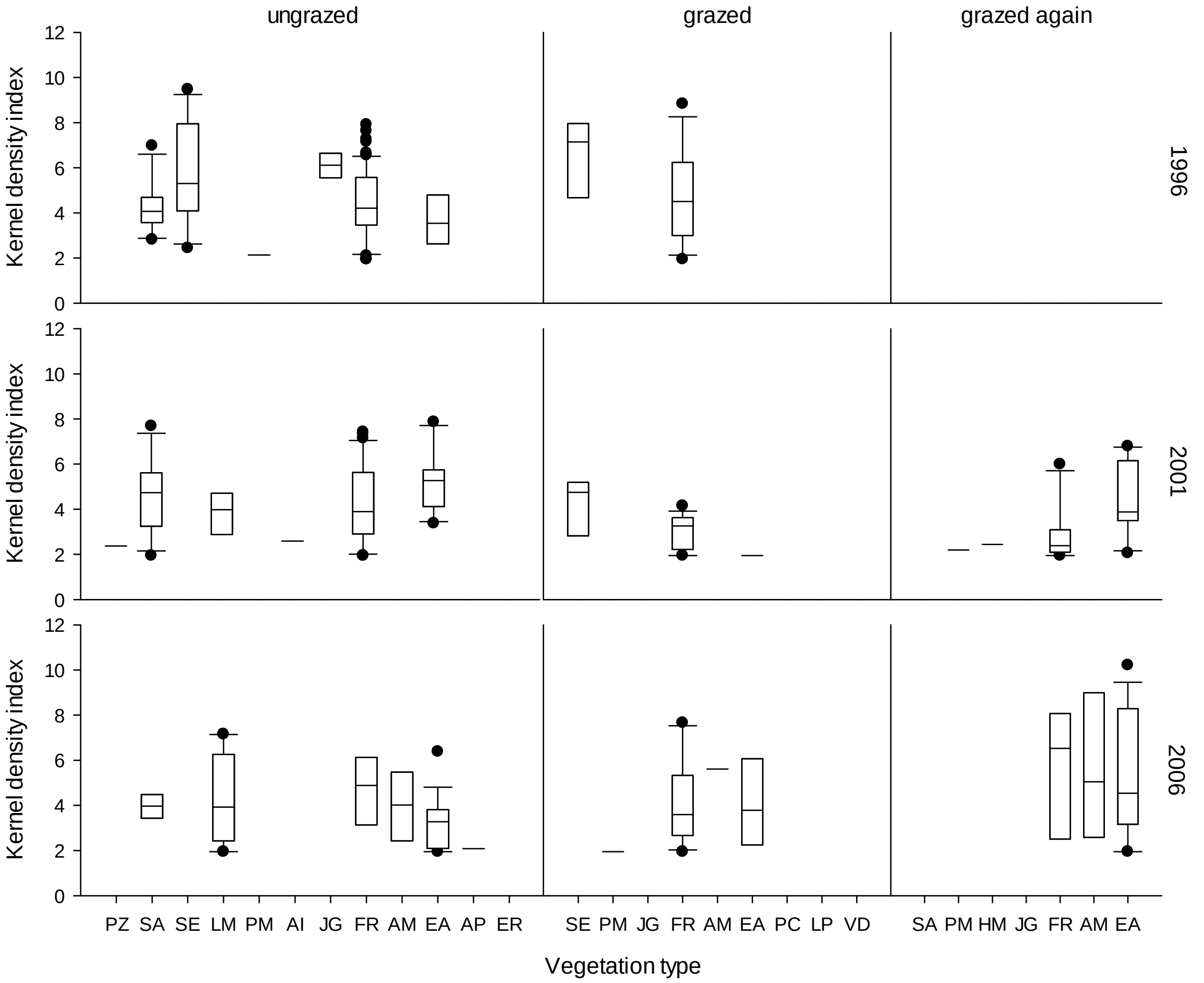


Figure 25: Nest density per combined vegetation type and grazing regime in the study area Hedwigenkoog in 1996, 2001 and 2006. Nest density differed significantly between combined vegetation type and grazing regime in each year (Kruskal-Wallis-test for 1996: H=25.59, p<0.01, df=10; for 2001: H=48.71, p<0.01, df=19 and for 2006: Kruskal-Wallis-test: H=34.51, p<0.05, df=19).

PZ=Pioneer zone, unspecific, SA=*Spartina anglica* type, SE=*Salicornia* type, LM=Low marsh, unspecific, PM=*Puccinellia maritima* type, AI=*Atriplex portulacoides* type, HM=High marsh, unspecific, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, AM=*Artemisia maritima* type, EA=*Elymus athericus* type, AP=*Atriplex prostrata* type, PC=*Plantago coronopus* type, ER=*Elymus repens* type, LP=*Lolium perenne* type, VD=Vegetation disturbed.

3.4.5 Nest density and distance to edge structures

In 1996 nest densities were significantly higher close to vegetation edges and ditches or berm (see table 6 for statistical data). Distance to ditches and distance to ditches or vegetation edge showed no significant correlation with nest density. However, correlations between oystercatcher nests and distance parameters show a triangular pattern and distribution is positive skew (figure 26). Oystercatchers nest in variable densities per distance and the smaller the distance the larger is the range of nest densities that can be found per distance. High nest densities do not occur in large distances from any edge structure. For all edge structures there is an upper bound beyond which oystercatchers do not nest at all. Looking at the year 2001, high breeding densities were significantly correlated with short distances to vegetation edge, ditches or vegetation edge and to ditch or berm but not with distance to ditches alone. All significant correlations were greater than those observed in 1996. The upper bound found in 1996 for all edge structures is far less obvious in 2001. In contrast to the previous years, none of the distance parameters was correlated with nest density in 2006.

However, the upper bound for distance to ditches and to ditch or berm was existent again. Considering the distance to vegetation edge and to ditch or vegetation edge, high nest densities only occurred very close to these structures and generally oystercatchers nested much closer to these structures than in the former years (see below).

Table 6: Spearman correlations between nest density and distance parameters.

Year	Shortest distance to	Spearman's R	N	P
1996	ditch	-0.02	130	0.84
1996	vegetation edge	-0.18	130	0.04*
1996	ditch or vegetation edge	-0.12	130	0.19
1996	ditch or berm	-0.22	130	0.01*
2001	ditch	0.15	117	0.12
2001	vegetation edge	-0.39	117	0.00**
2001	ditch or vegetation edge	-0.29	117	0.00**
2001	ditch or berm	-0.24	117	0.01**
2006	ditch	-0.05	102	0.61
2006	vegetation edge	-0.10	102	0.34
2006	ditch or vegetation edge	-0.05	102	0.61
2006	ditch or berm	0.06	102	0.58

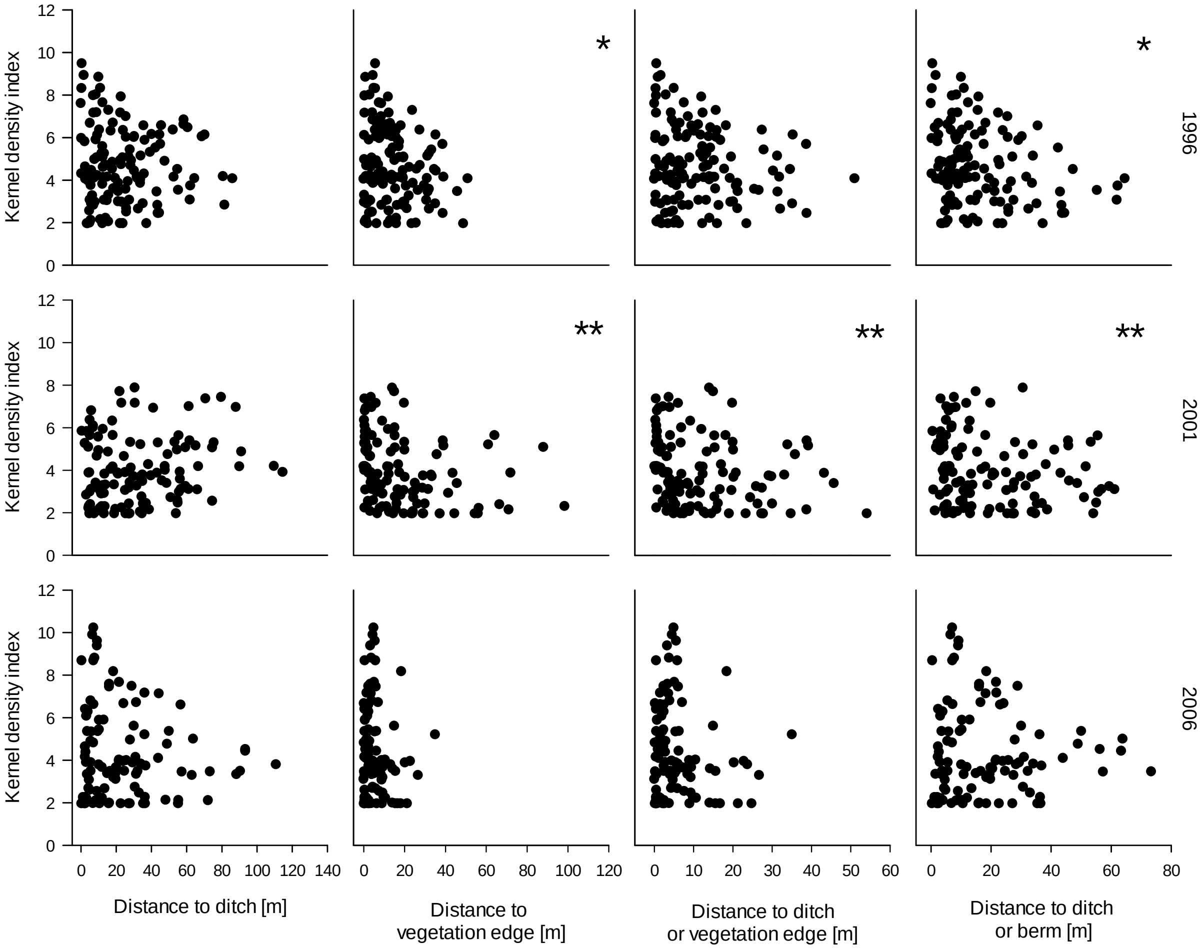


Figure 26: Correlations between nest density and shortest distance from each nest to ditches, vegetation edge, ditches or vegetation edge and ditches or berm in the study are Hedwigenkoog in 1996, 2001 and 2006. *= correlation is significant with p<0.05 and **= correlation is highly significant with p<0.01.

There is a significant difference among the three years in the median distances to vegetation edge (Kruskal-Wallis-test: H=45.37, p<0.01, df=2; followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction), with greatest median values observed in 1996 and lowest in 2006 (figure 27). The distance from nests to vegetation edge shortened on average from 12 m in 1996 to 4 m in 2006, thus, oystercatchers bred significantly closer to vegetation edge in 2006 than in the two former years. The same pattern is observed in the distance to ditches or vegetation edge (Kruskal-Wallis-test: H=26.36, p<0.01, df=2; followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction): The median was highest in 1996, lowest in 2006 and the distance from nests to ditches or vegetation edges shortened on average from 8 m in 1996 to 4 m in 2006.

The median distance to ditches was highest in the year 2001 (27 m) and significantly lower in 1996 and 2006 at 18 m in both years (Kruskal-Wallis-test: H=10.47, p<0.01, df=2; followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction). There was no difference in the distance to ditches or berm between the study years (Kruskal-Wallis-test: H=2.90, p>0.05, df=2).

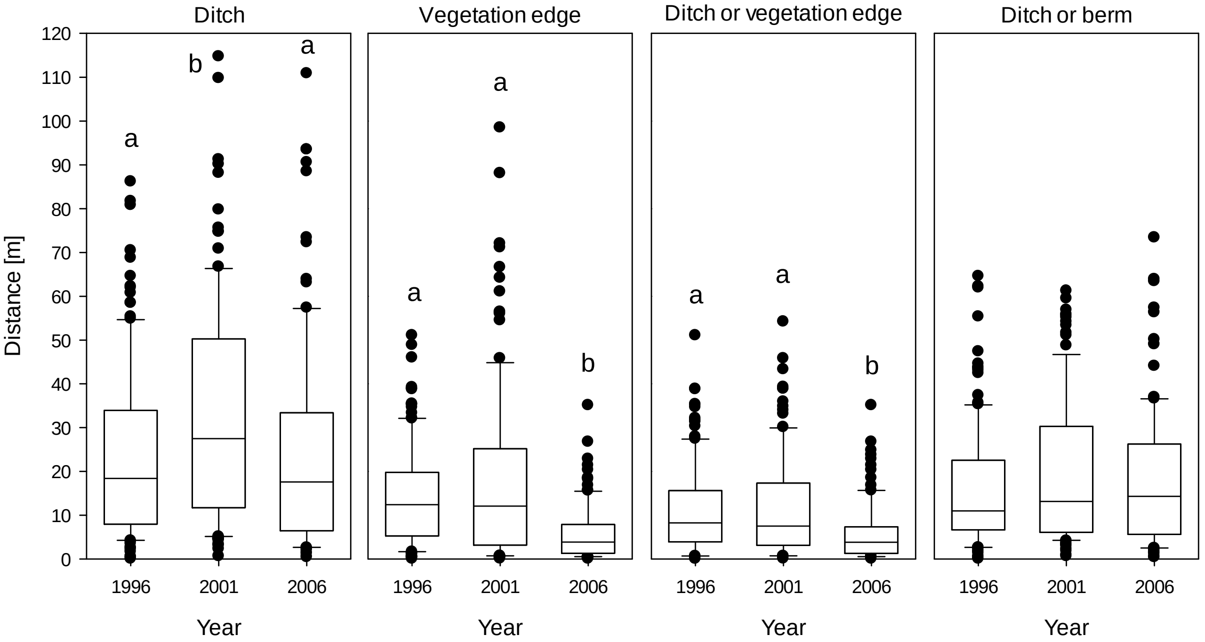


Figure 27: Shortest distance from oystercatcher nests to ditches, vegetation edges, ditches or vegetation and ditches or berm in the study area Hedwigenkoog in 1996, 2001 and 2006. Different letters above box-plots indicate that medians were significantly different (Kruskal-Wallis-test followed by multiple comparisons Mann-Whitney-test with Bonferroni-Holm correction).

The distributions of available buffers and of buffers used by oystercatchers did not differ in 1996 (Two-samples-Kolmogorov-Smirnov-test: Z=1.06, p>0.05, n=32) or 2001 (Two-samples-Kolmogorov-Smirnov-test: Z=1.13, p>0.05, n=50). Both percentage of buffers available and percentage of buffers used by oystercatchers decreased continuously from the edge inwardly (figure 28) although in 2001 more oystercatchers nested in the 0–5 m buffer than was expected. However, in 2006 there was a significant difference in the two distributions (Two-samples-Kolmogorov-Smirnov-test: Z=1.72, p<0.01, n=34) indicating that most oystercatchers (60% of the breeding pairs) selected a nesting site in the 0–5 m buffer from vegetation edge in 2006. The remaining 40% were dispersed in a decreasing manner from the 5–10 m buffer to the 35–40 m buffer. Buffers at 45–85 m were not used by oystercatchers in 2006.

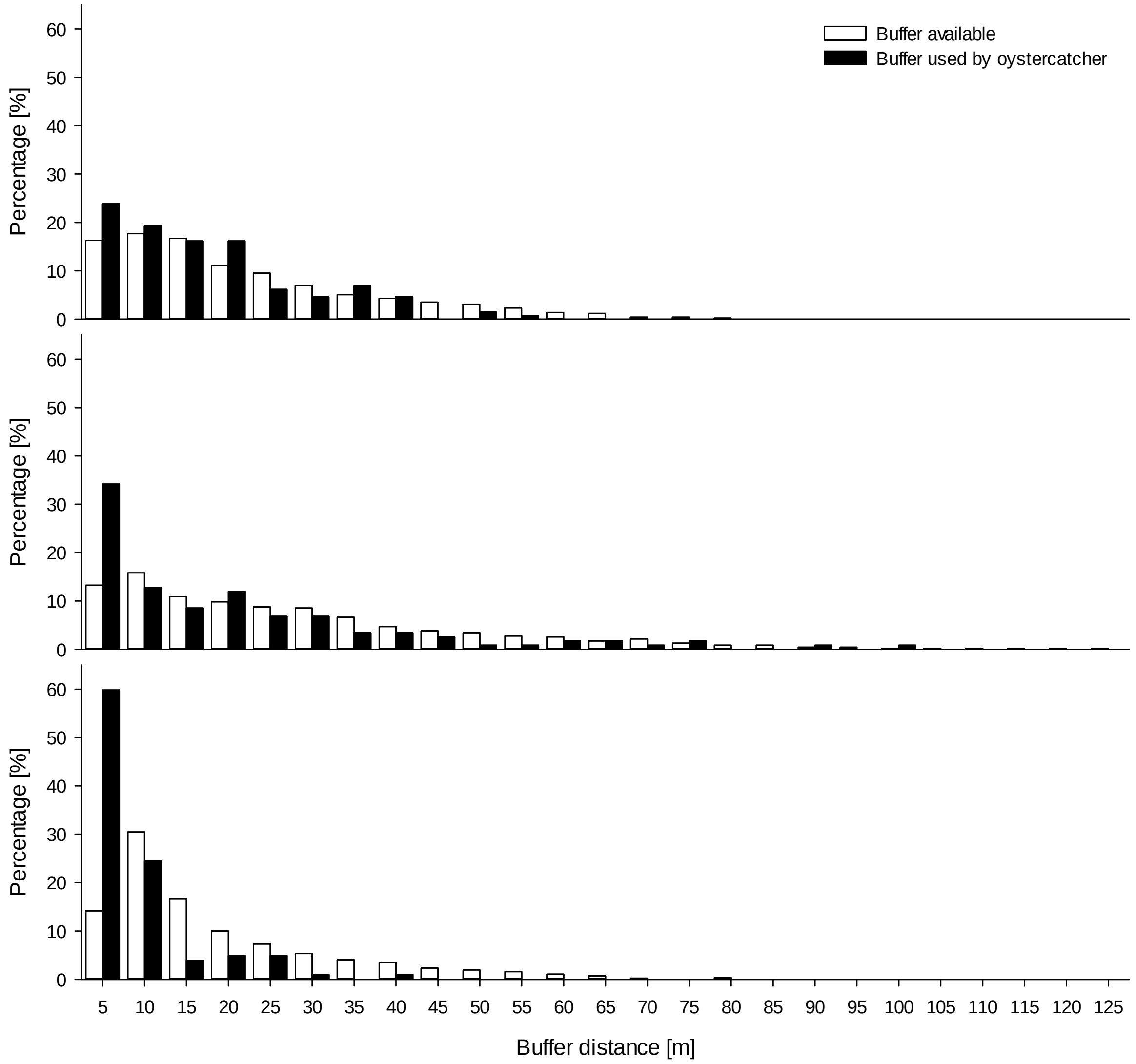


Figure 28: Distributions of buffers available and buffers used by oystercatchers in the study area Hedwigenkoog in 1996, 2001 and 2006. The distributions did not significantly differ in 1996 and 2001 (Two-samples-Kolmogorov-Smirnov-test for 1996: Z=1.06, p>0.05, n=32 and for 2001: Z=1.13, p>0.05, n=50), but in 2006 (Two-samples-Kolmogorov-Smirnov-test: Z=1.72, p<0.01, n=34).

There were no differences between oystercatcher nests and random points (figure 29 and table 7) in 1996 for distance to ditch (Mann-Whitney-test: U=4580.00, p>0.05, n=194) and distance to vegetation edge (Mann-Whitney-test: U=3993.00, p>0.05, n=194). However, oystercatcher nests were on average 2 m farther from ditches or vegetation edges than random points (Mann-Whitney-test: U=3876.00, p<0.05, n=194) and were an average of 8 m closer to ditch or berm (Mann-Whitney-test: U=3697.00, p<0.05, n=194). There was no significant difference between oystercatcher nests and random points in any distance parameters in 2001. Conversely, in 2006 all parameters were significantly different between oystercatcher nests and random points. Oystercatcher nests were closer to edge structures than random points. On average, oystercatcher nests were 11 m closer to ditches (Mann-Whitney-test: U=3401.00, p<0.01, n=188), 3 m closer to vegetation edge (Mann-Whitney-test: U=3550.00, p<0.05, n=188) and to ditch or vegetation edge (Mann-Whitney-test: U=3595.00, p<0.05, n=188) and 12 m closer to ditch or berm (Mann-Whitney-test: U=3183.00, p<0.01, n=188) compared to random points.

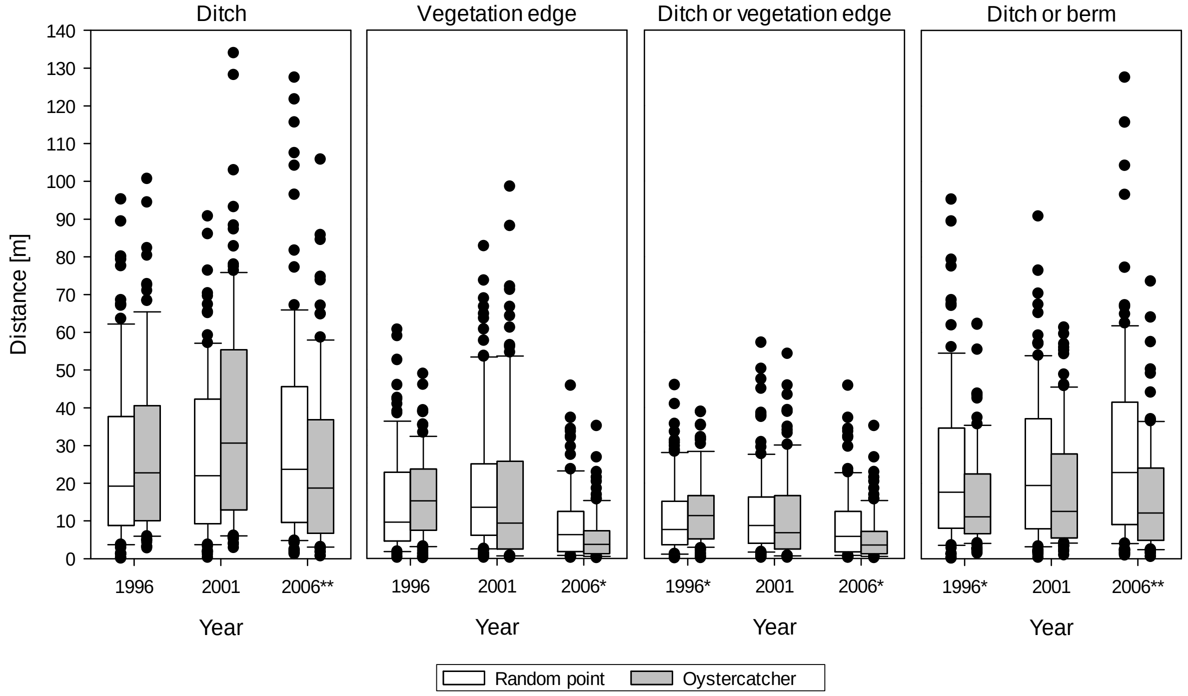


Figure 29: Comparison of shortest distance from oystercatcher nests and random points to ditches, vegetation edge, ditches or vegetation edge and ditches or berm in the study area Hedwigenkoog in 1996, 2001 and 2006. *= difference is significant with p<0.05 and **= difference is highly significant with p<0.01.

Table 7: Comparison of oystercatcher nests and random points with regard to shortest distance to edge structures in 1996, 2001 and 2006.

Year	Shortest distance to	Mann-Whitney-U	N	P
1996	ditch	4580	194	0,75
1996	vegetation edge	3993	194	0,07
1996	ditch or vegetation edge	3876	194	0,03*
1996	ditch or berm	3697	194	0,01*
2001	ditch	4675	200	0,43
2001	vegetation edge	4389	200	0,14
2001	ditch or vegetation edge	4469	200	0,19
2001	ditch or berm	4272	200	0,08
2006	ditch	3401	188	0,01**
2006	vegetation edge	3550	188	0,02*
2006	ditch or vegetation edge	3595	188	0,03*
2006	ditch or berm	3183	188	0,00**

Classification tree analysis (figure 30–32) showed that in 1996 the most important criterion to distinguish between oystercatcher nests and random points is the *Puccinellia maritima* vegetation type. This type was occupied primarily by random points. All other splits were done by distance parameters. In particular, the distance to vegetation edge was used several times as splitting criterion, though in different directions. Distance parameters were the only criteria used in 2001 to grow the tree. The distance to vegetation edge was the most distinctive: With a high degree of probability all records closer than 1 m from vegetation edge were oystercatchers. In subsequent splits the distance to ditches and to ditches or berm occurred most often, similar to 1996, but in different directions. In 2006 distance to ditch or berm was used as first split criterion. All data records having a distance of less than 38 m to ditch or berm were classified as oystercatcher nests. In subsequent splits vegetation type was used to distinguish between oystercatchers and random points.

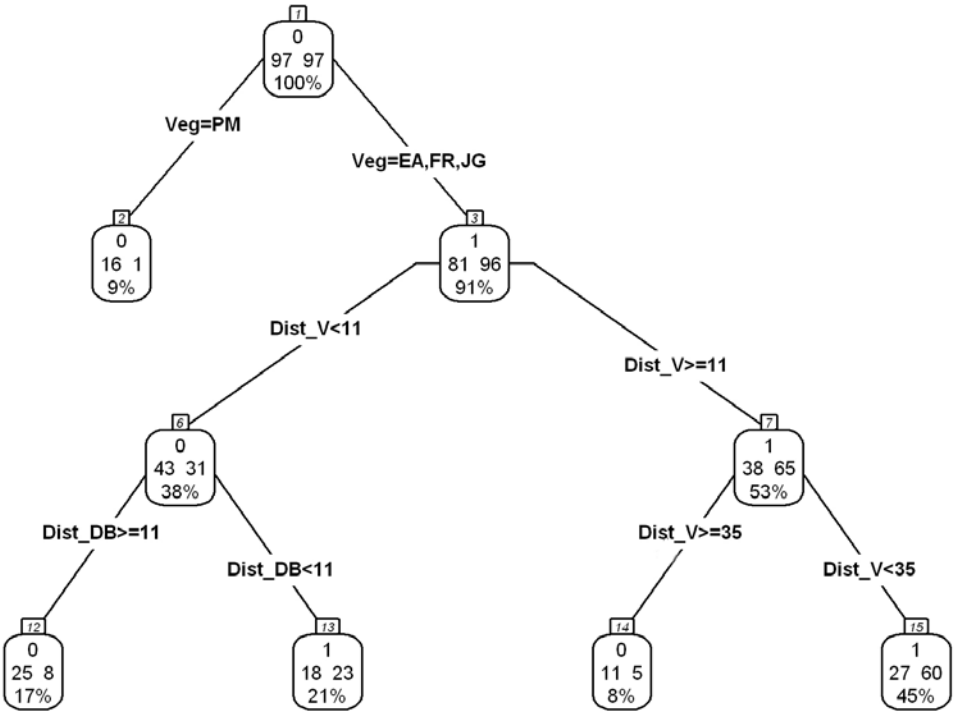


Figure 30: Classification tree of preferred nest site characteristics of oystercatchers in the study area Hedwigenkoog in 1996. All data records start at the top node and go left at decision nodes if they are classified as random points and right if they are classified as oystercatcher nests (indicated as "0" for random points and "1" for oystercatchers). Decision criterion is shown for each child node. Small numbers above nodes are the node number. In each node the number of records per class (left: random points, right: oystercatchers) before splitting is given. Percentages give the portion of records per node.

Veg=Vegetation type, PM=*Puccinellia maritima* type, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, EA=*Elymus athericus* type. Dist_V=Distance to vegetation edge, Dist_DB=Distance to ditch or berm.

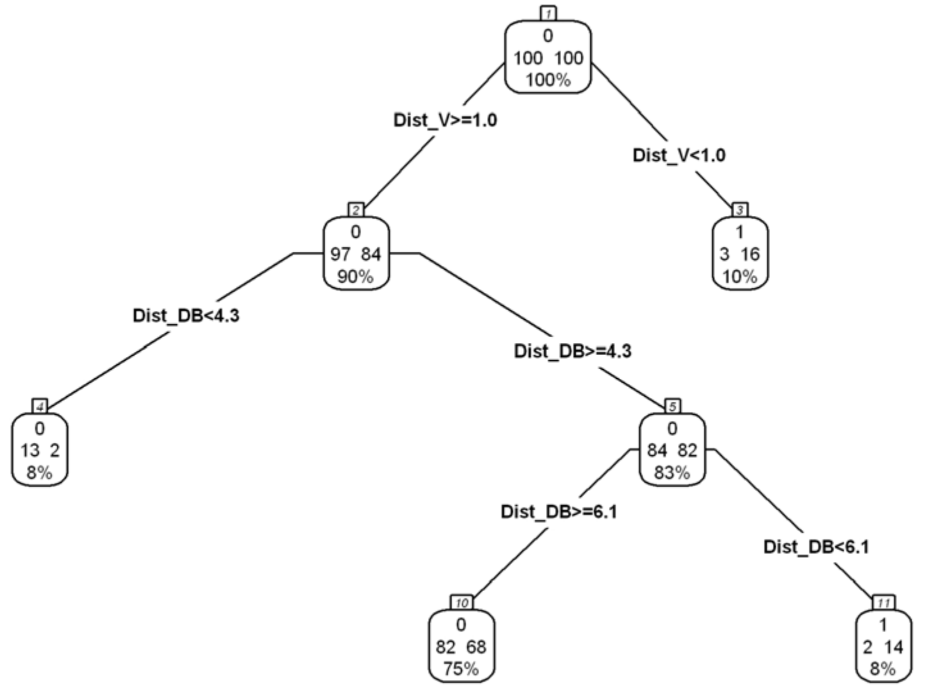


Figure 31: Classification tree of preferred nest site characteristics of oystercatchers in the study area Hedwigenkoog in 2001. All data records start at the top node and go left at decision nodes if they are classified as random points and right if they are classified as oystercatcher nests (indicated as "0" for random points and "1" for oystercatchers). Decision criterion is shown for each child node. Small numbers above nodes are the node number. In each node the number of records per class (left: random points, right: oystercatchers) before splitting is given. Percentages give the portion of records per node.

Dist_V=Distance to vegetation edge, Dist_DB=Distance to ditch or berm.

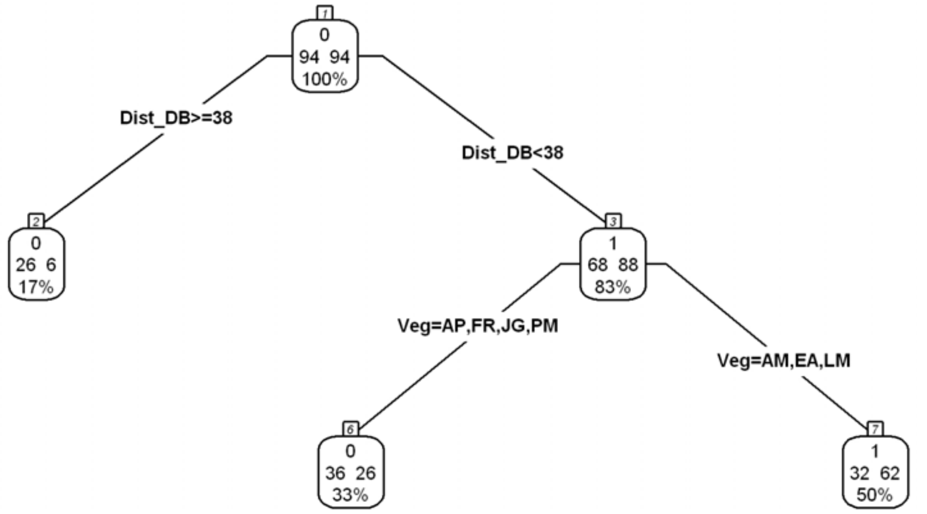


Figure 32: Classification tree of preferred nest site characteristics of oystercatchers in the study area Hedwigenkoog in 2006. All data records start at the top node and go left at decision nodes if they are classified as random points and right if they are classified as oystercatcher nests (indicated as "0" for random points and "1" for oystercatchers). Decision criterion is shown for each child node. Small numbers above nodes are the node number. In each node the number of records per class (left: random points, right: oystercatchers) before splitting is given. Percentages give the portion of records per node.

Veg=Vegetation type, LM=Low marsh, unspecific, PM=*Puccinellia maritima* type, JG=*Juncus gerardii* type, FR=*Festuca rubra* type, AM=*Artemisia maritima* type, EA=*Elymus athericus* type, AP=*Atriplex prostrata* type. Dist_DB=Distance to ditch or berm.

3.5 Discussion

3.5.1 Does vegetation type, grazing regime or their interaction influence nest density of oystercatchers?

Results of this study suggest that vegetation type does not have an influence on the distribution of oystercatcher nesting sites. In all years oystercatchers used vegetation types in the same manner as expected by availability of area. In 1996 nest density was highest in *Juncus gerardii* type but only very few individuals were breeding in these small areas at all. *Salicornia* type showed also high nest density, though the majority of these nests were placed along ditches, probably the actual reason for nest site selection (see below). In 2001 nest densities were highest in the small area of *Puccinellia maritima* type, where, as in the *Juncus gerardii* type in 1996, only a few oystercatchers nested. Additionally, two-thirds of oystercatchers nested very close to the berm in the *Spartina anglica* type. In 2006 there was no significant difference in nest densities between the different vegetation types. According to Valle & Scarton (1999) and Martinez et al. (1983) oystercatchers prefer open areas with short vegetation as nesting sites. A preference by oystercatchers for less dense and short vegetation types like *Festuca rubra* and an avoidance of higher and denser types (e.g. *Elymus athericus*) could not be supported by this study. No conclusive preference for vegetation types could be detected and thus it seems that vegetation type alone is not important in oystercatcher's nest site selection. Sheep grazing has a significant effect on vegetation patterns (structure and composition) and thus, it is necessary to include this factor in analyses.

In 1996 and 2001 grazing regime did not have an effect on the distribution of oystercatchers but nest density were significantly higher in the ungrazed area in 2001 than in grazed or "grazed again" areas. This is consistent with Grave & Lutz (2004) who found a preference by oystercatchers for ungrazed areas. In the ungrazed area greatest density of nests were located along the berm. The berm is probably a good nest site because it is adjacent to the pioneer zone providing an abundance of open, wet ground for foraging (Becker 1987; Ens et al. 1992). The berm is 0.5 m higher than the pioneer zone and thus reduces the risk of flooding. In 2006 oystercatchers showed a strong preference for the "grazed again" area where density hotspots were close to a large drainage ditch which possessed a density hotspot in the previous two study years. These results indicate that grazing regime had a strong influence on both the nest distribution and density.

When considering the interaction between vegetation type and grazing regime it is clear that these factors had no influence on the distribution of oystercatcher nests in any year. However, in 2006 many more oystercatchers than expected (given the available area) nested in the "grazed again" *Elymus athericus* type, but most individuals nested in the persistent density hotspot area close to a large drainage channel. Highest nest density in 1996 occurred in grazed *Salicornia* type where all oystercatchers nested close to ditches, most in the persistent hotspot area. In 2001 highest nest density was found in ungrazed *Elymus athericus* type close to the berm. In both 1996 and 2006, highest nest density was found in "grazed again" *Festuca rubra* type and the area where nests were placed overlapped with the persistent hotspot area. The question arises whether there is a real preference for the "grazed again" area or if the increase in number of nests here is due to other factors making the area around this ditch especially suitable for nesting. Further studies of this area will be necessary to address this question.

Livestock can severely reduce breeding success of waders. Although Heppleston (1972) found that the loss of clutches is because of trampling, other studies propose different explanations. Hart et al. (2002)

suggested that livestock disrupt incubation and this leads to an increased predation risk. Another possibility is that nest concealment is reduced in shorter vegetation. MacDonald & Bolton (2008) suggested that in most cases shorter vegetation has no effect on predation rates. Although waders try to minimize nest predation from avian predators by choosing an adequate nest site (MacDonald & Bolton 2008), this appears to be ineffective as most predators use non-visual methods for foraging or incidentally find nests and then predate them. (Langhans 2010) found that the portion of predated clutches of oystercatchers increased significantly in my study area from 1993-2009 whereas the losses by sheep were in all years very low.

3.5.2 Do oystercatchers demonstrate specific edge structures preferences in nest site selection?

Nest densities in 1996 and 2001 were significantly negatively correlated with distance to edge structures, but the correlations were rather weak and did not follow a linear function at all. Instead nearly all correlations, regardless of the level of significance, showed a triangular form indicating that oystercatchers prefer edge structures as nest sites. Highest nest densities always occurred close to edge structure. This is especially true for the distance to vegetation edge in 2006. In this context it is enlightening to look at the changes in distance parameters over time. The most obvious change can be found in the significantly shortened distance to vegetation edge from 1996–2006. Buffer analyses indicate this is not due to shrinkage in vegetation patch area. This result is underscored by the random point analyses that revealed a significant shorter distance from oystercatcher nests to vegetation edge compared to random points in 2006. Additionally, classification tree analyses showed that distance parameters are more important to distinguish between oystercatcher nests and random point than vegetation type or grazing regime.

Structural diversity of vegetation increases with decreasing grazing intensity in the short term (Kiehl et al. 2000). However, in the long term ungrazed areas become often dominated by tall-growing plants like *Elymus athericus* (Bos et al. 2002). It can thus be assumed that succession, particularly in the ungrazed areas, led to more homogeneous and tall vegetation with less diverse range of vertical structures making these areas less attractive for oystercatchers. The observed accumulation of oystercatchers (density hotspot) in the "grazed again" area can in part be explained by the increase of structural diversity through shifting grazing regimes. Hockey (1982) found that African Black Oystercatchers (*Haematopus moquini*) prefer to nest adjacent to plants and Milsom et al. (2000) showed that for some wader species the heterogeneity of vegetation height is more important than mean vegetation height. Milsom et al. (2000) also found that heterogeneity of vegetation did not favour oystercatchers but instead made areas less likely to be occupied. My results, however, show that heterogeneity of vegetation is a crucial factor for nest site selection of oystercatchers.

The presence of large ditches is important for two reasons. First, vegetation species richness is higher in areas with ditches (Morzaria-Luna et al. 2004), probably they provide diverse and changing vertical structures than does vegetation alone. Second, ditches themselves are crucial for breeding waders as they are used as foraging grounds (Milsom et al. 2000; Milsom et al. 2002). Thus, the shortening in distance to vegetation edge or ditch is most likely due to a decreased distance-to-vegetation-edge and not to ditches because foraging is generally needed and distance to ditches did not shorten through time. It is yet not clear why the distance to ditches is significantly larger in 2001 compared to the two other years.

Although not a result of changes of distance to ditch or berm, berm lost its attraction as nest site. This can be seen in the location of density hotspots and distribution of nests. It may be that spread of

Elymus athericus in the ungrazed area influenced this result. Succession leads to large stands of *Elymus athericus* producing high, dense and homogenous structures when grazing pressure is removed (Bos et al. 2002). Compared to random points, oystercatchers were significantly closer to all edge structures in 2006 indicating the importance of structural heterogeneity of vegetation in nest site selection of oystercatchers.

3.5.3 Limitations and conclusions

As with any study, the limitations of this one must be considered. The vegetative mapping was based on no smaller than 25 x 25 m plots. This size is very large when considering nest sites. As a result, distance calculations might be imprecise. Nevertheless, it is assumed that any imprecision is averaged out by the number of observations. Additionally, interactions with other bird species, as suggested by Heinänen et al. (2008) and Valle & Scarton (1999), may be significant in nest site density and location. Finally, a good quality nest site does not automatically lead to breeding success. Though, I did not analyse breeding success it would seem that without a suitable habitat, breeding is not possible at all.

Finally, this study demonstrates that heterogeneity of vegetation structures and the presence of ditches are important factors for nest site selection in oystercatchers on mainland salt marshes. Highest nest densities were found close to ditches and in the areas which had been grazed again. The shift in grazing regime may have promoted structural heterogeneity of vegetation. In contrast, intensive sheep grazing is known to produce short uniform swards with only low breeding densities (Norris et al. 1998). I suggest promoting shifting sheep grazing regimes to promote structural diversity.

4 General abstract

The effects of grazing and abandonment in salt marshes on breeding bird diversity have been a perennial issue in Germany's Schleswig-Holstein Wadden Sea National Park during the last 25 years. When the national park was established in 1985, 80% of the salt marshes were intensively grazed by sheep. By the early 1990s, grazing in the park had been significantly reduced, and in some areas ceased. After an initial increase in plant diversity resulting from these changes in grazing regime, large mono-dominant stands of late successional plants occurred in some areas and plant diversity decreased once again. Because salt marshes are an important breeding habitat for birds, these changes in grazing regime and plant diversity affected avian diversity within the park. The responses of breeding birds to habitat changes were various and yet no study has specifically addressed these responses on a large scale and over a long time period. In this study I use existing vegetation mappings and bird count data to address the effects of changes in grazing regime and vegetation on breeding birds in four periods from 1988–2006 at two different spatial scales.

In the first part of this study, 27 mainland and 9 Hallig salt marshes were examined to address three issues: (1) Changes in breeding bird species richness, grazing regime and vegetation diversity through time; (2) Differences in breeding bird species richness and grazing regime and vegetation diversity between mainland and Halligen; (3) The influence of grazing regime and vegetation diversity on breeding bird species richness. The Halligen, small islands without dykes, are not part of the national park but belong to the Biosphere Schleswig-Holstein Wadden Sea and Halligen and thus are subject to a different and more dynamic grazing regime of salt marshes. Shannon's diversity index was calculated for grazing regime and vegetation diversity, and GIS was used to spatially join vegetation and bird data. Breeding bird species richness increased from 1988–2001 but subsequently declined by 2006. These differences, however, were not significant. Similarly, grazing regime and vegetation diversity increased significantly from 1988–2001, followed by a slight, and non-significant, decrease in 2006. Breeding bird species richness was higher on the Halligen compared to the mainland in all of the four periods although the difference was only significant in 2006. Breeding bird species richness did not differ through time on the mainland but increased continuously, and significantly, on the Halligen. Standardized sums of breeding pairs in all periods were significantly higher on the Halligen than on the mainland and trended towards increasing from 1988–2001, with a subsequent decrease in 2006 on the former. No differences in grazing regime and vegetation diversity between mainland and Halligen were detected. Additionally, no general increase of breeding bird species richness with increasing grazing regime and vegetation diversity was revealed. These results highlight the distinctive nature of Hallig versus mainland salt marshes. This distinctive nature and the changes in breeding bird species richness cannot be explained by grazing regime and vegetation diversity on spatiotemporal scale of this study.

The second part of this study addresses the nest site selection of oystercatchers (*Haematopus ostralegus*) in the mainland salt marsh of Hedwigenkoog, Germany. I examine the relationship between nest site selection and vegetation types, grazing regimes (grazed, ungrazed, grazed again), and distances to edge structures (ditches, shift of vegetation type, brim) from 1996–2006. GIS is used to spatially join nest site locations with vegetation mappings, calculate kernel nest density, generate random points to control for accidental effects, and calculate shortest distance to edge structures. Results of this study indicate that oystercatcher nest site selecting is not affected by vegetation type, however, grazing regime seems to play a significant role in this aspect of their reproductive biology. Paradoxically, in 2001 nest density was highest in the ungrazed area, and in 2006 strong preference for "grazed again" areas was observed. Interaction between vegetation types and grazing regimes did not affect the distribution of oystercatchers. Analyses of distance-to-edge parameters in relation to nest density showed that high nest densities never occurred far from edges. Furthermore the distance to vegetation edge shortened significantly through time whereas no trends were detected with respect to the distances from nest to ditches, to ditch or vegetation edge, or to ditch or brim. In 1996 oystercatcher nests were significantly farther from ditch or vegetation edge than random points but significantly closer to ditch or brim. Distances from nests to ditch and distances from nests to vegetation edge did not differ significantly. In 2001 no significant differences in the distance to edge parameters were found. In 2006, however, oystercatcher nests were significantly closer to all edge parameters compared to random points. Distance parameters were more important to distinguish between oystercatchers and random points than vegetation type or grazing regime. This study concludes that structural heterogeneity of vegetation and proximity to ditches are the most important factors in Oystercatcher nest site selection.

While on the large spatiotemporal scale in chapter one no effect of vegetation and grazing regime on breeding bird species richness could be detected, chapter two revealed the influence as well as the importance of small-scale heterogeneity on the nest site selection of oystercatchers. This emphasizes the importance of spatial scale and resolution of data when analysing the relationships between breeding birds and vegetation and grazing regime. Considering the large spatial scale of 36 study sites and the laminar bird data there is no general increase of breeding bird species richness with increasing grazing regime and vegetation diversity. The results of chapter two and of other studies, however, showed that several bird species are affected by vegetation and grazing regime. Other bird species may be more affected by factors like for instance food supply. This may also explain the distinctive nature of the Halligen compared to the mainland considering increasing breeding bird species richness and standardized sums of pairs. Although not visible in the data, the salt marshes of the Halligen are subject to small-scale dynamics in grazing regime compared to the mainland with only few changes and thus probably provide effectively a more diverse breeding habitat.

5 Allgemeine Zusammenfassung

Der Einfluss von Beweidung und Beweidungsaufgabe auf die Diversität von Brutvögeln in Salzmarschen des Nationalparks Schleswig-Holsteinisches Wattenmeer war innerhalb der letzten 25 Jahre ein beständiger Diskussionspunkt. Zum Zeitpunkt der Gründung des Nationalparks im Jahre 1985 waren 80% der Salzweisen intensiv durch Schafe beweidet. Mit Beginn der 1990er Jahre wurde die Beweidung in großen Teilen des Nationalparks schrittweise reduziert oder eingestellt. Nach einem anfänglichen Anstieg der pflanzlichen Vielfalt aufgrund dieser Beweidungsänderungen entstanden in einigen Gebieten jedoch auch großflächige, mono-dominante Bestände von Pflanzen der späten Sukzessionsstadien, wodurch die pflanzliche Vielfalt wieder sank. Da Salzmarschen ein wichtiges Bruthabitat für viele Vogelarten sind, beeinflussten die Beweidungsänderungen und die damit einhergehenden Änderungen in der Vegetation auch die Brutvögel im Nationalpark. Die Reaktionen der Brutvögel auf die Habitatveränderungen sind jedoch vielgestaltig und bisher hat keine Studie diese in einem größeren räumlichen und zeitlichen Maßstab untersucht. In der vorliegenden Arbeit habe ich bestehende Daten zu Vegetation und Brutvögeln verwendet, um den Einfluss von Beweidungs- und Vegetationsänderungen auf Brutvögel der Salzmarschen im Nationalpark in vier Jahren zwischen 1988 und 2006 auf zwei räumlichen Skalenebenen zu analysieren.

Im ersten Teil der Studie wurden 27 Festland- und neun Halligsalzmarschen hinsichtlich folgender drei Punkte untersucht: (1) zeitliche Veränderungen in der Brutvogelartenvielfalt und der Beweidungs- und Vegetationsvielfalt; (2) Unterschiede in der Brutvogelartenvielfalt und der Beweidungs- und Vegetationsvielfalt zwischen den Halligen und dem Festland; (3) Einfluss von Beweidungs- und Vegetationsvielfalt auf die Brutvogelartenvielfalt. Die 5 bewohnten Halligen (kleine Inseln ohne Deich) gehören nicht zum Nationalpark, sondern zum Biosphärenreservat Schleswig-Holsteinisches Wattenmeer und Halligen und unterliegen deshalb einem anderen, dynamischeren Beweidungsmanagement der Salzmarschen. Der Shannon-Diversitätsindex wurde für die Beweidungs- und Vegetationsvielfalt berechnet und mittels GIS-Software wurden die Vegetations- und Brutvogeldaten räumlich miteinander verknüpft. Die Brutvogelartenvielfalt stieg zwischen 1988 und 2001 an, sank bis 2006 jedoch wieder. Diese Veränderungen waren allerdings nicht signifikant. Ebenso stieg die Beweidungs- und Vegetationsvielfalt zwischen 1988 und 2001 an, gefolgt von einem nicht-signifikanten Rückgang im Jahr 2006. Die Brutvogelartenvielfalt war in allen vier untersuchten Jahren auf den Halligen höher als am Festland; der Unterschied war jedoch nur im Jahr 2006 signifikant. Die Brutvogelartenvielfalt zeigte am Festland keine zeitliche Veränderung, stieg jedoch auf den Halligen über die Jahre stetig und signifikant an. Die standardisierten Paarsummen waren in allen vier Jahren auf den Halligen größer als am Festland und wiesen auf den Halligen eine zunehmende Tendenz zwischen 1988 und 2001 auf, gefolgt von einem Abfall im Jahr 2006. Es gab keine Unterschiede in der Beweidungs- und Vegetationsvielfalt zwischen den Halligen und dem Festland. Außerdem konnte kein genereller Anstieg der Brutvogelvielfalt mit zunehmender Beweidungs- und Vegetationsvielfalt gefunden werden. Diese Ergebnisse betonen die Andersartigkeit der Salzwiesen auf den Halligen gegenüber denen am Festland. Diese Andersartigkeit und die Veränderungen in der Brutvogelartenvielfalt können auf diesem zeitlich-räumlichen Maßstab nicht durch die Beweidungs- und Vegetationsvielfalt erklärt werden.

Der zweite Teil der Studie beschäftigt sich mit der Nistplatzwahl des Austernfischers (*Haematopus ostralegus*) in einer Salzmarsch des Hedwigenkoog-Vorlandes. Ich habe die Beziehung zwischen Nistplatzwahl, Vegetationstyp, Beweidungsmanagement (beweidet, unbeweidet, wieder beweidet) und der Entfernung zu Grenzstrukturen (Priele, Übergang zwischen zwei Vegetationstypen, Abbruchkaten) zwischen 1996 und 2006 analysiert. Mittels GIS-Software wurden die Nistplätze mit den Vegetationskartierungen räumlich verknüpft. Weiterhin wurden die Kerndichte der Nester berechnet, Zufallspunkte erstellt um auf zufällige Effekte zu prüfen und die kürzesten Distanzen von jedem Nest zu den Grenzstrukturen berechnet. Die Ergebnisse zeigen, dass Austernfischer in ihrer Nistplatz nicht vom Vegetationstyp beeinflusst werden, allerdings scheint das Beweidungsmanagement eine wichtige Rolle zu spielen. Im Jahr 2001 traten die höchsten Nestdichten in den unbeweideten Bereichen auf, wohingegen im Jahr 2006 eine starke Präferenz für die wieder beweideten Bereiche festgestellt wurde. Die Kombination von Vegetationstyp und Beweidungsmanagement hatte keinen Einfluss auf die Verteilung der Austernfischer. Die Analyse der Entfernungen zwischen Nestern und Grenzstrukturen ergab, dass hohe Nestdichten nie weit entfernt von Grenzstrukturen auftreten. Außerdem verkürzte sich die Entfernung zwischen Nestern und Vegetationsgrenze (Übergang zwischen zwei Vegetationstypen) signifikant über die Jahre. Im Gegensatz dazu wurden keine eindeutigen zeitlichen Tendenzen für die Entfernung zwischen Nestern und den übrigen Grenzstrukturen gefunden. Im Jahr 1996 waren Austernfischernester signifikant weiter von Prielen oder Vegetationsgrenze entfernt als die Zufallspunkte aber signifikant näher an Prielen oder Abbruchkante. Die Entfernung zwischen Nestern und Prielen und die Entfernung zwischen Nestern und Vegetationsgrenze unterschieden sich nicht signifikant. Im Jahr 2001 gab es keine Unterschiede zwischen Austernfischernestern und Zufallspunkten bezüglich der Entfernung zu Grenzstrukturen. Im Gegensatz dazu waren im Jahr 2006 Austernfischernester signifikant näher an allen Grenzstrukturen als die Zufallspunkte. Es zeigte sich, dass die Entfernung zu Grenzstrukturen wichtiger war um zwischen Austernfischernestern und Zufallspunkten zu unterscheiden als Vegetationstyp oder Beweidungsmanagement. Diese Studie kommt zu dem Ergebnis, dass strukturelle Heterogenität der Vegetation und Nähe zu Prielen die wichtigsten Faktoren in der Nistplatzwahl des Austernfischers darstellen.

Während im großen räumlichen und zeitlichen Maßstabes des ersten Kapitels keine Effekte der Beweidungs- und Vegetationsvielfalt auf die Brutvogelartenvielfalt gefunden wurde, zeigte Kapitel zwei sowohl den Einfluss als auch die Wichtigkeit kleinräumiger Heterogenität auf die Nistplatzwahl des Austernfischers auf. Dies betont die Wichtigkeit von räumlichem Maßstab und Auflösung der Daten bei der Analyse der Beziehung zwischen Brutvögeln und Vegetation bzw. Beweidungsmanagement. Bezogen auf den großen räumlichen Maßstab von 36 Untersuchungsgebieten und die flächigen Brutvogeldaten gibt es keinen generellen Anstieg der Brutvogelartenvielfalt mit steigender Beweidungs- und Vegetationsvielfalt. Die Ergebnisse von Kapitel zwei und anderen Studien zeigen jedoch, dass einige Vogelarten sehr wohl durch Beweidungsmanagement und Vegetation beeinflusst werden. Andere Vogelarten können wiederum mehr durch andere Faktoren wie zum Beispiel Nahrungsverfügbarkeit beeinflusst sein. Dies könnte auch die Andersartigkeit der Salzwiesen auf den Halligen im Vergleich zu jenen am Festland in Bezug auf steigende Brutvogelartenvielfalt und standardisierte Paarsummen erklären. Obwohl in den Daten nicht erkennbar, sind die Salzwiesen auf den Halligen einer stärkeren kleinräumigen Dynamik hinsichtlich des Beweidungsmanagements unterworfen als die Festlandsalzwiesen, wo nur wenige Veränderungen stattfinden; dies könnte auf den Halligen zu einer effektiv höheren Vielfalt an Bruthabitaten führen.

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