



Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species

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Abstract

Europe holds globally important populations of breeding waders. However, most of the species are in steep decline, including the Eurasian Curlew (*Numenius arquata*). Here, we studied the breeding-territory and nest-site preferences of a Curlew subpopulation that has, in contrast to the overall trend, been increasing, on the East Frisian Islands (Wadden Sea National Park of Lower Saxony, N Germany). The islands are mostly free from ground predators and intensive agriculture and thus offer the opportunity to examine habitat preferences in largely undisturbed habitats. Our study revealed that Curlews preferred breeding in habitat mosaics dominated by high marshes and dune grasslands, far from areas with human disturbance. For nest-building, heterogeneous microhabitats with intermediate vegetation cover and height and some bare ground were preferred. This reflects a trade-off between (i) sufficient shelter for nests and fledglings, (ii) early recognition of predators and (iii) readily available and accessible invertebrate prey. Such heterogeneous habitats, without mammalian predators, are largely missing in the intensively used agricultural landscapes of the European mainland. Consequently, Curlew populations on the mainland are mostly declining. In contrast, those on the East-Frisian Islands are stable and, therefore, of prime importance for the protection of the species. Thus, the study highlights the importance of isolated islands providing natural habitats like coastal dunes, which are free from ground predators and extensive human disturbance for the long-term survival of Curlew populations. Based on the results of this study we make suggestions to improve future conservation measures for degraded habitats to boost curlew populations.

Keywords Eurasian Curlew (*Numenius arquata*) · Grassland management · Habitat heterogeneity · Land-use change · Nest-site preference · Vegetation structure

Introduction

The global decline in biodiversity has reached alarming proportions. Global extinction rates are 1000 times higher than the natural background rate (Pimm et al. 2014). Despite great efforts in nature conservation, there are currently no signs of a trend reversal (Butchart et al. 2010). For terrestrial biomes, land-use change is assumed to be the major driver of the recent biodiversity loss (Sala et al. 2000; Foley et al. 2005; Cardoso et al. 2020). Although farmland is the most

important habitat for bird conservation in Europe (Donald et al. 2006; Sutcliffe et al. 2015), farmland exhibits the largest decrease in biodiversity across taxa such as plants, insects, and birds (Vickery et al. 2001; Donald et al. 2006; Flohre et al. 2011).

This decrease also applies to waders, which often occupy man-made landscapes and are among the most threatened birds globally (BirdLife International 2015). The European Union holds internationally important populations of breeding wader species (BirdLife International 2004; Keller et al. 2020). However, most of the species are in steep decline and are considered endangered or vulnerable on the European Red List of Birds (BirdLife International 2015). Decreasing availability of breeding habitats through agricultural intensification, afforestation, and land abandonment, as well as insufficient reproduction especially due to nest and chick predation, have been identified as the main reasons for declining wader populations (Wilson et al. 2004; Kaasiku

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et al. 2019; Plard et al. 2019). In the future, climate change is expected to become an additional serious threat, for example through changes in food availability and temporal mismatch (Pearce-Higgins et al. 2010; Renwick et al. 2012).

The Eurasian Curlew is Europe's largest wader and breeds in the boreal, temperate and steppe zones of Europe and Asia (Brooks et al. 1992; Bauer et al. 2012). The subspecies of the Eurasian Curlew *Numenius arquata arquata* (hereafter referred to as Curlew) breeds in west, north and central Europe to the west of the Urals (Thorup 2006). The Curlew has suffered major range losses and population decline throughout its breeding range (Keller et al. 2020). As more than 75% of the global population breeds in the northern half of Europe, Europe has a great responsibility for the long-term survival of this species (BirdLife International 2004). Two main reasons have been identified for the decline of the European Curlew population. On the one hand decreasing habitat availability and suitability due to afforestation and intensive agriculture, resulting in homogeneous swards (Berg 1994; Douglas et al. 2014; Franks et al. 2017). On the other hand, insufficient reproduction due to high egg and chick losses by predators and mechanized management practices (Grant et al. 1999; Zielonka et al. 2019).

Curlews depend on open landscapes with wide visibility unbroken by woodland in dry to wet terrain for nesting (Brooks et al. 1992). The original habitats of the species in Central Europe were bogs, heathlands and poorly drained wetlands, which have largely been destroyed and degraded by human activities like agriculture, drainage and land reclamation. Nowadays, a large proportion of the European and German Curlew population breeds in meadows, pastures and arable fields but still also in (rewetted) raised bogs and fens, heath and dunes (Brooks et al. 1992; Bauer et al. 2012).

While the German breeding population was estimated at 7,000 pairs in the early 1970s, it is now estimated at 3,600–4,800 pairs (Gerlach et al. 2019). This corresponds to a decrease of more than 40% (Hötker et al. 2007). Due to its steep decline during the last decades, the German breeding population is considered threatened with extinction (Ryslavý et al. 2021). However, on the German mainland the decrease has recently been halted in some populations through intensive conservation measures such as marking of nest locations to avoid destruction during agricultural work, electric fencing to prevent mammalian predation, rewetting, and habitat management (Kipp and Kipp 2003; Rüstringer Heimatbund e.V. and Landkreis Wesermarsch 2005; Boschert 2008). Despite further declines outside managed areas, this has led to a stabilization of the German population (Gedeon et al. 2014; Gerlach et al. 2019).

The strongholds of the German Curlew breeding population are the north-western lowlands and the East Frisian Islands (Gedeon et al. 2014). Colonization of the East Frisian Islands by breeding Curlews started as late as 1938

(Großkopf 1995). Since then, the population has increased rapidly. Between 2008 and 2017 there have been an average of 102 ± 3 (mean \pm SE) Curlew territories on the Islands, of which 16 ± 2 were situated on the island of Spiekeroog (Fig. 1a) (Schulze-Dieckhoff, pers. comm., Lower Saxonian Water Management, Coastal Defence and Nature Conservation Agency [NLWKN] 2018).

So far, the reasons for the different population trends are unknown. However, the lack of mammalian predators and the absence of intensive agriculture on the East-Frisian Islands are two possible causes. While several studies have investigated the habitat preferences of Curlews breeding in agricultural landscapes (e.g. Berg 1992; Valkama et al. 1998), very little is known about the habitat characteristics necessary for breeding in natural habitats on coastal islands. Several authors reported that the highest densities of Curlews on the Wadden Sea Islands occur in dune heath and wet dune slacks (= wet dune valleys) (e.g. Koffijberg et al. 2006). However, there are only very small areas of dune slacks on most East Frisian Islands and their extent has decreased in recent decades due to a lowering of the groundwater caused by drinking water production (Pott 2006, Geelen et al. 2017). At the same time, however, the number of breeding Curlews has increased (Hötker et al. 2007), which brings into question the importance of dune slacks for breeding Curlews on the East Frisian Islands.

To develop suitable conservation measures designed to counteract the decline of Curlews in Europe, more precise information on habitat preferences is needed urgently (Žmihorski et al. 2018). Therefore, we studied the habitat preferences of a stable Curlew population in natural habitats. The study area, the East Frisian Islands within the Wadden Sea National Park of Lower Saxony, are largely missing mammalian predators and agricultural disturbance. The aim of this study was to investigate habitat composition within territories and vegetation structure at nests in natural largely undisturbed refuge habitats. Based on the results of this study we make suggestions to improve future conservation measures for degraded habitats to boost curlew population.

Materials and methods

Study area

The study area comprised all the East Frisian Islands on which Curlew's breed (Borkum, Mellum, Juist, Norderney, Baltrum, Langeoog, Spiekeroog; Lower Saxony, Germany). The East Frisian Islands cover an area of about 150 km² and are sandy barrier islands, influenced by tides and characterised by extensive island tails (de Groot et al. 2017). The main habitats on the islands are beaches (18%), natural dune grasslands (13%) (Fig. 2a), mudflats (13%), saltmarshes

(35%) (Fig. 2b), built-up areas (4%), and dune heath (4%). Further habitats that cover smaller areas are copses (3%), white dunes (2%), shrubberies (2%), dune slacks (1%), reeds (1%), semi natural grassland and transition zones between marshes and natural dune grasslands called salty dune (1%) (Fig. 1b; Fig. 2c) (Petersen and Pott 2005; Petersen et al. 2014). All the East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony (corresponding to category II of the IUCN Protected Area Classification (Dudley 2013)), and the Wadden Sea World Heritage site (Kalisch 2012). The National Park is divided into three zones of different protection intensity: the core zone, intermediate zone, and recreational zone. During the breeding season, the core and intermediate zone are accessible for humans only on designated roads and paths. Only the recreational zone is fully accessible and open for human activities all year. Dogs are only allowed on a leash. Due to the promotion of ecotourism such as bird watching (Davenport and Davenport 2006) and intensive public relations work, visitor management and the use of National Park rangers and volunteers to control entry bans, disturbance in protected areas occurs rarely (cf. Kalisch 2012). Only small parts of the islands, primarily saltmarshes, are grazed by livestock.

The East Frisian Islands are principally free of mammalian predators except for domestic cats (*Felis catus*) (Walter and Kleinekuhle 2008). However, in recent years foxes (*Vulpes vulpes*) were present on the island of Norderney (Andretzke et al. 2017). Other mammals that occur on almost all East Frisian Islands and are known to cause clutch loss are common rat (*Rattus norvegicus*) and hedgehog (*Erinaceus europaeus*). Since 2010 a scheme to control

population size of these introduced mammals has been carried out on the islands of Borkum, Norderney and Langeoog (Andretzke and Oltmanns 2016; Andretzke et al. 2017). By contrast, breeding density of potential avian predators (e.g., Herring gull (*Larus argentatus*), Lesser black-backed gull (*Larus fuscus*), Marsh harrier (*Circus aeruginosus*) are high on most islands (Gedeon et al. 2014).

A detailed analysis of nest-site preferences was conducted on the island of Spiekeroog, which hosts a large part of the Curlew breeding population on the East-Frisian Islands. In addition, the proportion of Curlews, breeding in natural undisturbed habitats within the core zone of the National Park is particularly high there, which enables the investigation of Curlews in low-disturbance, natural habitats without predatory mammals. Spiekeroog is about 2 km wide and 10 km long, producing a total area of 18 km² (Petersen and Pott 2005).

Sampling methodology

Breeding-territory preferences

To evaluate the habitat preferences of Curlews on the East Frisian Islands, we compared habitat-type composition within Curlew territories with those on the islands in general. Habitat data were available through the Trilateral Monitoring and Assessment Program (TMAP) (Petersen et al. 2014; person. comm. Wadden Sea National Park of Lower Saxony 2017). Data on Curlew territories in 2017 were based on territory mapping during six visits (Südbeck et al. 2005; cf. Bibby et al. 2000) and provided by

Fig. 1 a) Location of the studied East Frisian Islands (from left to right): Borkum, Mellum, Juist, Norderney, Baltrum, Langeoog, Spiekeroog and average number of territories on different islands between 2007 and 2017 (person. comm., NLWKN 2018). b) Distribution of habitat types as well as of theoretical territories and controls using the example of Spiekeroog

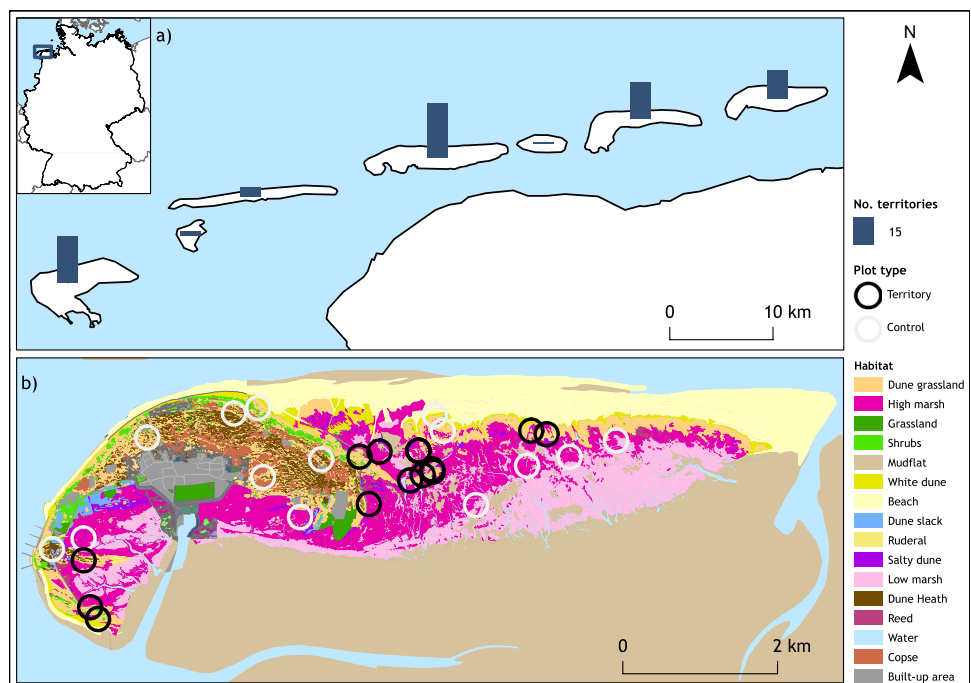
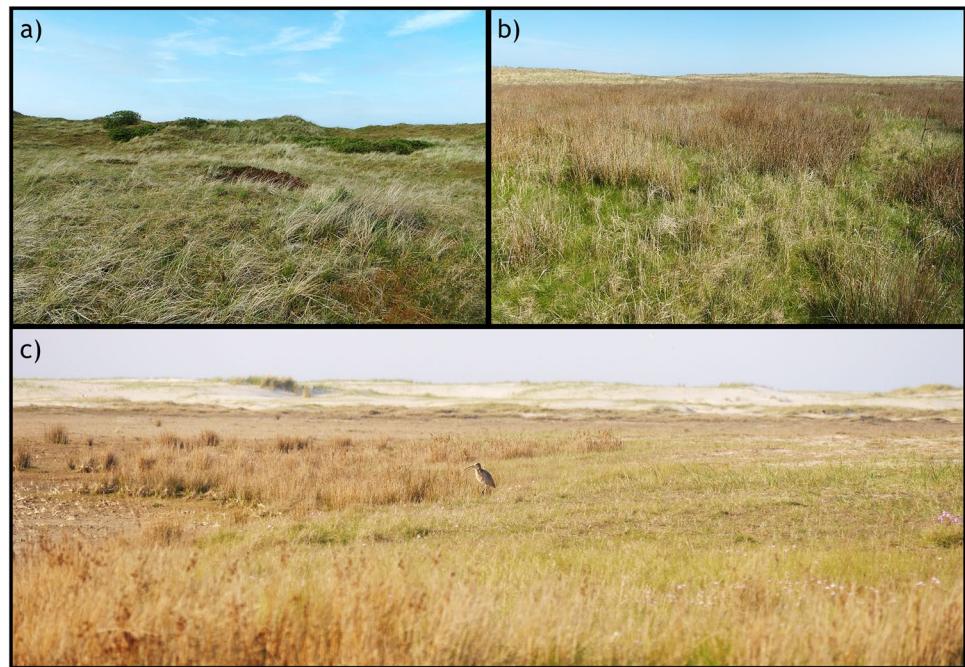


Fig. 2 Photos of typical breeding habitats of the Curlew on the East Frisian Islands: a) dune grassland, b) high marsh, c) salty dune: transition zone between high marsh and dune grassland providing heterogeneous vegetation including areas of short vegetation and bare ground as well as high and dense vegetation



Schulze-Dieckhoff (pers. comm., NLWKN 2018). For the identification of territories, we paid special attention to repeated observations of territorial behaviour (at least twice seven days apart) such as territory marking by flights as well as copulating, breeding or warning adults or pairs (suspected breeding). Special attention was paid to simultaneous observations for separating different territories situated close to each other. Furthermore, we paid special attention to the observation of breeding adults, distraction display, mobbing of potential avian predators and adults guiding young (confirmed breeding) (Südbeck et al. 2005). Where nests were not found, territory centres were defined as the centre where these behavioural signs were concentrated.

After Bauer et al. (2012), minimum territory size of Curlews in north-west Germany is 7 ha. This is in line with the results of five GPS tagged birds breeding on the East Frisian Islands in 2020 (unpublished data 2020, Movebank ID 1126572166). Accordingly, we analysed the habitat composition of an area with a radius of 149 m around each territory centre using the function “Buffer” in software ArcGIS 10.2 (ESRI Inc.) (Kämpfer and Fartmann 2019). In total, we analysed 88 (from all seven islands) and 20 (Spiekeroog) territories, respectively (Fig. 3).

For all territories where nest location has been identified (confirmed breeding) ($N=46$), we compared habitat-type composition within a radius of 149 m around each Curlew nest with those of randomly selected control territories (without nests) of the same size ($N=46$). Selection of controls was performed using the function “Create random points” in ArcGIS 10.2 and excluded areas that were

unsuitable for breeding (beaches, built-up areas, forest, low marshes, and mudflats). Moreover, the Shannon index of habitat types served as a measure of habitat heterogeneity, H' (Fartmann et al. 2018; Schwarz et al. 2018) and was calculated by:

$$H' = - \sum_i p_i \ln p_i \text{ with } p_i = \frac{n_i}{N}$$

where N is the total area of the territory, and n_i is the area of each habitat type in the territory.

Further predictor variables were the closest distance to areas that were frequented by humans (buildings, paths, streets), as a proxy for anthropogenic disturbance, and wetlands (mudflats, standing water, wet dune slacks, tidal creeks), as a measure of proximity to the nearest foraging habitat. Both variables were determined using the function “Nearest” in ArcGIS 10.2.

Nest-site preferences

To assess the vegetation structure at Curlew nesting sites, we searched for nests on the island of Spiekeroog in April and May 2017. Nest sites were identified through observations of territorial behaviour from elevated dunes that indicated confirmed breeding (see above) and a subsequent systematic search for nests. In total, 14 nests out of 20 breeding pairs on Spiekeroog were found and recorded using a GPS device. Vegetation characteristics on the East Frisian Islands are assumed to change only slightly from the breeding period to

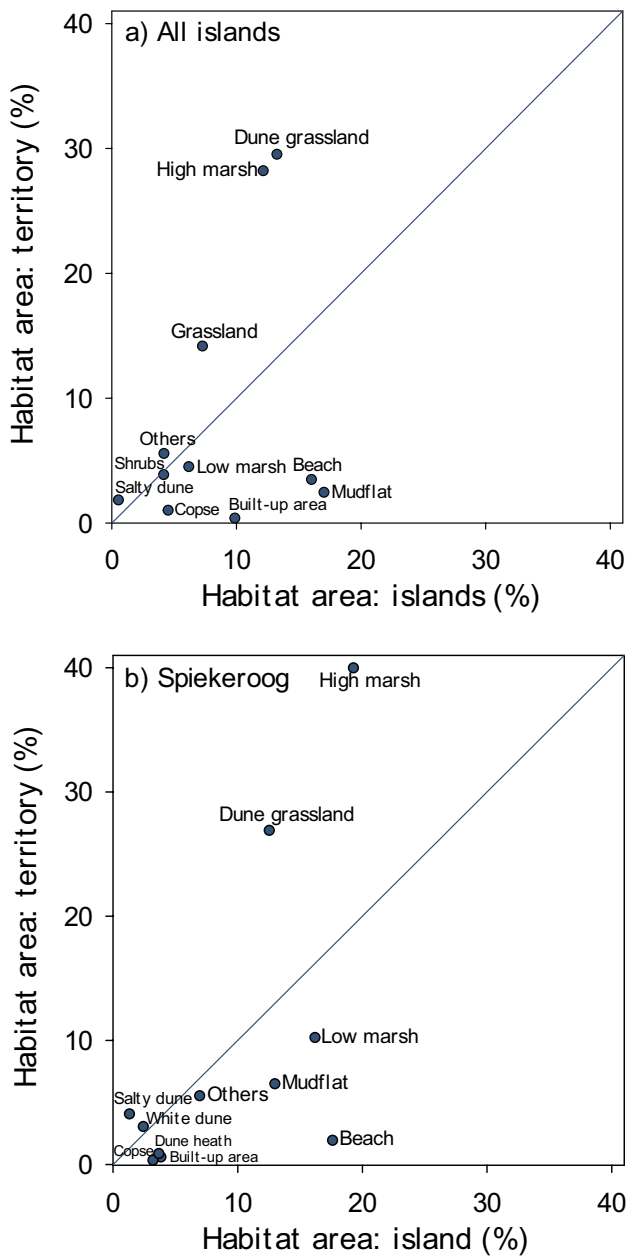


Fig. 3 Proportion of different habitat types within Curlew territories and on the islands, for all East-Frisian Islands (a) and Spiekeroog (b), respectively. All islands (a): others=dune heath, dune slack, open water, white dune, ruderal, and reed; Spiekeroog (b): others=dune slack, grassland, open water, reed, ruderal, and shrubs. All islands (a) and Spiekeroog (b): Fisher’s Exact Test <0.001

summer due to (i) environmental stress (dry, nutrient-poor sandy soils), (ii) low competitive power of the perennial plants and (iii) mild climate with early start of the growing season (own observation). To avoid unnecessary disturbance of numerous scarce and threatened breeding birds in the core zone of the national park, vegetation characteristics were, therefore, measured after the breeding season in August/

September. We measured the mean vegetation height (cm), at an accuracy of 1 cm using a ruler, and estimated the percentage cover of bare ground, the herb layer, mosses, shrubs, and litter in an area of 2 m×2 m (finer scale) and 10 m×10 m (coarse scale) around each nest. All parameters were also recorded at control sites, which were randomly selected within the potential breeding area (see above) using the function “Create random points” in ArcGIS 10.2. To obtain representative controls that cover the entire range of available vegetation structures, we chose a ratio between nest-sites and controls of 1:2.

Statistical analysis

Habitat composition (TMAP) (Petersen et al. 2014) within the territories was compared with the available habitat on the islands, by using Fisher’s exact test (McDonald 2009). Differences in habitat-type composition and vegetation structure (territory vs. control, nest-site vs. control) were analysed using the Mann–Whitney *U* test, because the data were not normally distributed. The effects of habitat-type composition and distance to relevant habitats on breeding-territory occupancy were analysed by generalised linear mixed-effect models (GLMM) with binomial error distribution (response variable: nest vs. control, predictors: see Table 1) and island as a random factor (cf. Crawley 2007).

To assess the drivers of nest-site occupancy at finer and coarse scale we used generalized linear models (GLM) with binomial error distribution (nest vs. control) and parameters of vegetation structure as predictors (see Table 2) (cf. Crawley 2007). If graphical inspections of the data suggested unimodal rather than linear relationships between the response variable and predictor variables, centred and squared values of the predictors were entered into the full model in addition to the untransformed values (cf. Johnstone et al. 2017). To increase model robustness and identify the most important environmental parameters, we performed model averaging based on an information-theoretic approach (Burnham and Anderson 2002; Grueber et al. 2011). Top-ranked models are presented in supplementary Table 1. Model averaging was performed using the ‘dredge’ function (R package MuMIn; Barton 2019) and included only top-ranked models with $\Delta AIC_c < 2$ (cf. Grueber et al. 2011). To avoid overfitting, maximum number of predictors to be included in a single model was limited to 1/10 of sample (Harrell et al. 1996). To avoid multi-collinearity in the GLM(M), Spearman’s rank correlations (r_s) were used to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (Grueber et al. 2011). Because the cover of the herb layer was negatively correlated with moss cover both within a radius of 2 m and 10 m around

Table 1 Mean area (\pm SE) of habitat types, habitat heterogeneity, distance to human-frequented areas and wetlands for breeding territories ($n=46$) and controls ($n=46$) on the East Frisian Islands

Parameter	Territory	Control	<i>P</i>
Habitat type (ha)			
Dune grassland	2.24 \pm 0.24	1.66 \pm 0.23	n.s.
High marsh	1.83 \pm 0.26	1.56 \pm 0.30	n.s.
Grassland	0.65 \pm 0.27	0.71 \pm 0.27	n.s.
Shrub	0.34 \pm 0.07	0.45 \pm 0.10	n.s.
Mudflat	0.31 \pm 0.08	0.14 \pm 0.07	n.s.
White dune	0.27 \pm 0.08	0.18 \pm 0.07	n.s.
Beach	0.24 \pm 0.10	0.26 \pm 0.11	n.s.
Dune slack	0.20 \pm 0.07	0.11 \pm 0.05	n.s.
Ruderal	0.17 \pm 0.08	0.09 \pm 0.05	n.s.
Salty dune	0.17 \pm 0.03	0.08 \pm 0.04	*
Low marsh	0.15 \pm 0.06	0.42 \pm 0.13	n.s.
Dune heath	0.11 \pm 0.06	0.25 \pm 0.10	n.s.
Reed	0.10 \pm 0.06	0.12 \pm 0.05	n.s.
Open water	0.10 \pm 0.04	0.09 \pm 0.02	n.s.
Copse	0.08 \pm 0.03	0.60 \pm 0.15	**
Built-up area	0.03 \pm 0.01	0.22 \pm 0.08	**
Habitat heterogeneity (H')	1.15 \pm 0.06	1.12 \pm 0.05	n.s.
Distance to wetland (m)	157.7 \pm 20.9	271.2 \pm 49.4	n.s.
Distance to human-frequented area (m)	484.7 \pm 77.5	439.3 \pm 49.3	*

Differences between breeding territories and controls were tested using the Mann–Whitney *U* test. Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

Table 2 Mean values (\pm SE) of vegetation structure at nest sites ($n=14$) and controls ($n=28$) at coarse scale (10 m \times 10 m) (a) and fine scale (2 m \times 2 m) (b), on Spiekeroog

Parameter	Nest	Control	<i>P</i>
a) Coarse scale (10 m \times 10 m)			
Cover (%)			
Bare ground	19.6 \pm 3.8	6.7 \pm 1.8	***
Mosses	17.9 \pm 4.4	20.6 \pm 6.2	n.s.
Litter	17.9 \pm 4.2	26.3 \pm 5.0	n.s.
Herb layer	57.5 \pm 6.0	74.9 \pm 4.3	*
Shrubs	0.2 \pm 0.2	0.1 \pm 0.0	n.s.
Vegetation height (cm)	18.1 \pm 2.5	21.2 \pm 2.2	n.s.
b) Fine scale (2 m \times 2 m)			
Cover (%)			
Bare ground	13.9 \pm 3.3	4.4 \pm 1.4	**
Mosses	11.2 \pm 5.7	17.5 \pm 6.0	n.s.
Litter	30.0 \pm 6.2	30.5 \pm 5.0	n.s.
Herb layer	59.6 \pm 6.5	72.2 \pm 5.2	n.s.
Shrubs	0.0 \pm 0.0	0.0 \pm 0.0	–
Vegetation height (cm)	19.3 \pm 2.2	22.6 \pm 3.0	n.s.

Differences between nest sites and controls were tested using the Mann–Whitney *U* test. Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

the nests ($|r_s|=0.69$ and 0.66 , respectively), we excluded moss cover from further analysis. All statistical analyses were performed using R 3.5.3 (R Core Team 2020).

Results

Breeding-territory preferences

Habitat composition within Curlew territories and on the islands overall differed significantly (Fig. 3). This was true for all the islands studied. Within Curlew territories on Spiekeroog, high marsh and dune grassland dominated and were overrepresented while, in contrast, low marsh, beaches and mudflats were clearly underrepresented. When considering the habitat composition of all the islands, besides high marsh, and dune grassland, also grasslands were overrepresented in Curlew territories, whereas built-up areas were underrepresented. In addition, despite small proportions of salty dunes on the islands, this type was overrepresented in the territories.

Comparisons between territories and controls provided deeper insights into breeding-territory preferences (Table 1). Dune grassland, high marsh and grassland were the dominant habitat types within Curlew territories. However, the proportion of these habitats did not differ between territories and controls. In contrast, Curlews preferred to establish territories in areas with higher proportions of salty dunes and a larger distance to areas that are frequented by humans. Copses and built-up area, however, were avoided. All the other parameters did not differ between territories and controls. Based on the GLMM analysis, the likelihood of territory establishment increased with the availability of dune grassland and decreased with those of copses and built-up area (Fig. 4). With an AUC value of 0.88 the model accuracy was high.

Nest-site preferences

The direct vicinity of the nest was almost covered by the herb layer (60%) and the vegetation was nearly 20 cm high (Table 2). Around the nest, at coarse scale, bare ground, mosses, and litter cover were very similar, with nearly 20% in each case. At fine scale, litter covered on average a further 30%, followed by bare ground with 14% and mosses with 11%. Habitats with a higher cover of bare ground were significantly preferred for nest-building, at both spatial scales. At coarse scale, in addition, the cover of the herb layer was significantly lower compared to control. The GLM analysis revealed that at both spatial scales the likelihood of nest-building was highest with increasing amounts of bare ground and an intermediate vegetation height (Fig. 5). The model accuracy was very high with AUC values of 0.87 and 0.89, respectively.

Fig. 4 Results of the GLMM analysis: relationship between occurrence of Curlew territories and area of different habitat types on the East-Frisian Islands (Appendix Table 3). Only significant parameters are shown. The regression slopes were fitted using multivariable GLMM. Marginal R^2 (variance explained by fixed effects) = 0.75–0.87, conditional R^2 (variance explained by both fixed and random effects) = 0.75–0.88, area under the curve (AUC) = 0.88

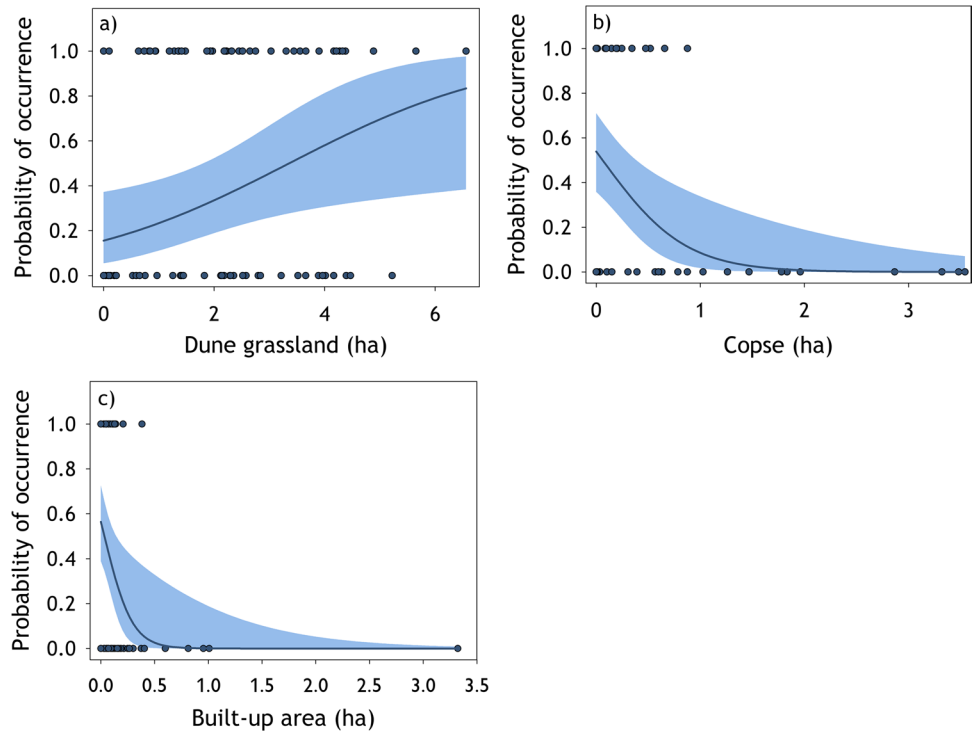
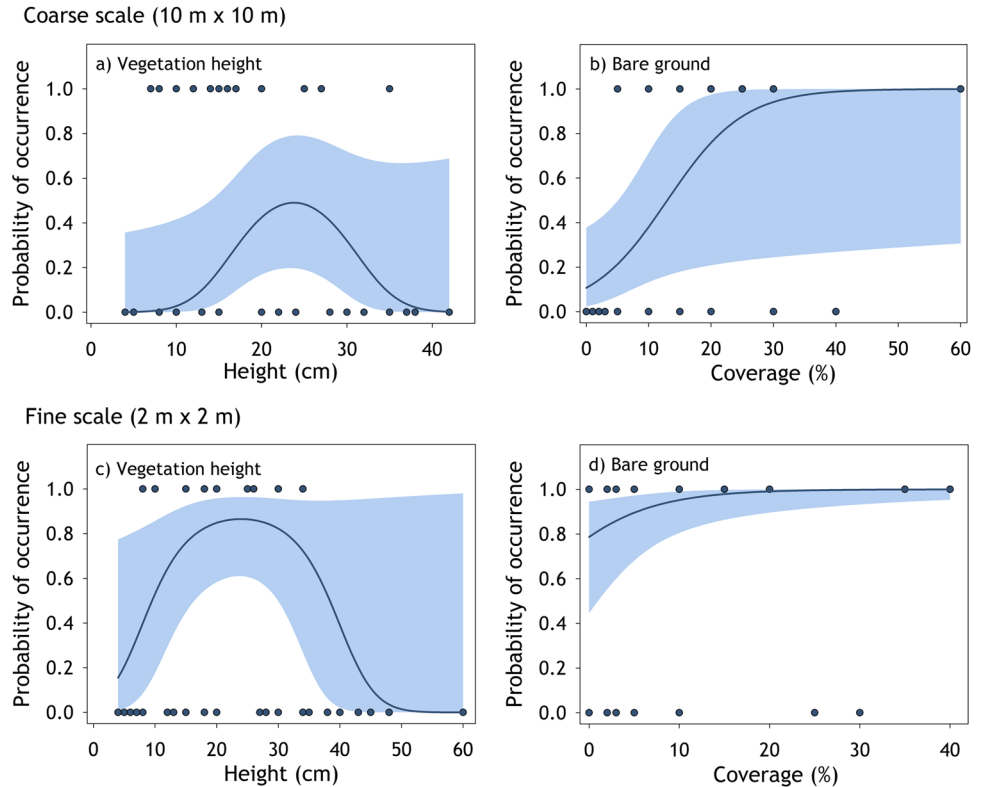


Fig. 5 Results of the GLM analysis: relationship between occurrence of Curlew nests and vegetation structure on Spiekeroog (Appendix Table 4). Only significant parameters are shown. The regression slopes were fitted using multivariable GLM. McFadden’s pseudo R^2 = 0.40, area under the curve (AUC) = 0.87



Discussion

Our study revealed that Curlew territories consisted of large proportions of high marshes and dune grasslands, the two dominant habitat types on the East Frisian Islands. However, the most important predictors of territory establishment were a large area of dune grassland and a low extent of copses and built-up area. Microhabitats with an herb-layer characterised by intermediate cover and height as well as some bare grounds were preferred for nest-building.

Predation is regarded as one of the major drivers of reproductive failure in birds during the egg and nestling phase (Ricklefs 1969). One adaptation to reduce risk of nest predation is to maintain some view of the surroundings of the nest to facilitate early predator detection (Götmark et al. 1995). The two main habitats within Curlew territories, high marshes and, especially, dune grasslands, provide large areas of low-growing and not too dense vegetation (Petersen and Pott 2005). Such conditions may facilitate all-round visibility and early predator recognition (Götmark et al. 1995). However, in salty dunes, the panoramic view is probably even better. High marshes are mostly flat and dune grasslands have a pronounced relief. Despite the generally open habitat structure in both cases, such relief limits distance vision. In contrast, salty dunes usually form small-scale mosaics within high marshes and protrude from them by several decimetres allowing more distant views (Petersen and Pott 2005).

The extent of copses and built-up area were the two other main predictors for territory establishment on the islands. Poor visibility of potential predators is also the most likely explanation for the observed avoidance of copses. Several other studies observed that Curlews and other waders breed less likely near forest edges for the same reason (Berg 1992; Valkama et al. 1998; Douglas et al. 2014; Kaasiku et al. 2019). Many wader species are sensitive to disturbance by humans, especially near their nests (Hockin et al. 1992). This is also true for the Curlew (Haworth and Thompson 1990; Navedo and Herrera 2012); it is known to have very long escape distances (Smit and Visser 1993). In line with this, the amount of built-up area was lower and the distance to roads, paths and buildings was higher in territories than in controls. Additionally, the probability of nest establishment decreased with an increasing extent of built-up area (Fig. 4c).

In Central Europe Curlews mostly nest on grasslands or arable fields in agricultural areas (Berg 1992, 1994; Valkama et al. 1998). On the East Frisian Islands, however, the role of improved and semi-natural grasslands differed between islands (cf. Figure 3a and b). Even on islands with larger areas of managed grasslands, they were only used for nesting when land-use intensity was low (own observation), which was the case on the islands of Borkum and Juist. On

Borkum, for example, most of the grasslands are grazed with low stocking rates (0.7–1 cattle/ha) and only partly subject to aftermath mowing, promoting the heterogeneous vegetation structure preferred for breeding (Andretzke and Oltmanns 2016).

The nest concealment hypothesis states that more concealed nests are less vulnerable to predation (Filliater et al. 1994). Indeed, several studies have shown that nest concealment usually reduces predation risk (Wiebe and Martin 1998; Møller et al. 2018), although other studies found, that this is not a universal pattern (e.g. Koivula and Rönkä 1998; Laidlaw et al. 2020). However, a well-hidden nest hampers all-round visibility and early detection of potential predators (Amat and Masero 2004). Hence, nest-site selection usually reflects a trade-off between sufficient concealment and a good view for the recognition of predators (Götmark et al. 1995). In line with this, we interpret the preference of Curlews for microhabitats with an herb-layer of intermediate cover and height, as found in our study, as such a trade-off. Other studies have also shown that Curlews preferred to nest in vegetation that is neither too short nor too high and dense (Valkama et al. 1998; Grant et al. 1999; Johnstone et al. 2017).

In addition, vegetation density and height influence the availability (Berg 1993) as well as the accessibility of invertebrate prey (Vickery et al. 2001; Butler and Gillings 2004; Atkinson et al. 2005). Short swards with patches of bare ground, are preferred foraging habitats of many insectivorous farmland birds (Atkinson et al. 2004; Schaub et al. 2010). While Curlews prefer ragworms outside of the breeding season, ground-dwelling invertebrates are an important food source for adult Curlews and their chicks during the breeding period (Berg 1993). Therefore, we also attribute the observed vegetation-structure preferences of breeding Curlews to food accessibility. Moreover, short, and scattered vegetation in combination with bare ground might enhance foraging efficiency. It (i) reduces the time needed for predator detection (Whittingham and Evans 2004), (ii) increases speed of movement during foraging (Butler and Gillings 2004) and (iii), finally, increases the food uptake of adult Curlews and their fledglings (Devereux et al. 2004).

In summary, on the East Frisian Islands Curlews preferred habitat mosaics dominated by high marshes and dune grasslands, far away from areas with human disturbance for breeding. Although salty dunes usually comprised a small share of breeding territories, they were preferred within breeding habitats. Salty dunes protrude above high marshes by several decimetres, allowing an excellent view into the distance and, hence, early predator detection. Heterogeneous microhabitats with intermediate vegetation cover and height and some bare grounds were preferred for nest-building. This reflects a trade-off between (i) sufficient shelter for nests and

fledglings, (ii) early recognition of predators and (iii) high levels of availability and accessibility of invertebrate prey. Such heterogeneous habitats, without mammalian predators and without destructive farming practices, are largely lacking in the intensively used agricultural landscapes of the European mainland (e.g. Berg 1992, 1994; Valkama et al. 1998). Consequently, Curlew populations on the mainland are mostly declining. In contrast, those on the East-Frisian Islands are stable and, therefore, of prime importance for the protection of the species.

In grasslands, the preferred habitat structures of intermediate vegetation height including areas of bare ground can be achieved by low intensity grazing or mowing (McCracken and Tallowin 2004). Moderate grazing especially by cattle, can represent a suitable tool in realising such habitats (Devereux et al. 2004). Additionally, small herbivores like hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) can significantly slow down dune succession and provide open areas of short vegetation (Kuijper and Bakker 2003; Kämpfer and Fartmann 2019). Moreover, spatial, and temporal mosaics of different sward heights can be achieved by selective grazing and mowing at different times of the year (Devereux et al. 2004; McCracken and Tallowin 2004) or through electric fencing in paddock grazing systems (Atkinson et al. 2005). To prevent nest and chick losses due to mowing or trampling by livestock, nests and chicks need to be located before mowing and paddock rotation. Afterwards, these areas must be excluded from agricultural practice until young are fully fledged or have left the area in question. Furthermore, Mandema et al. (2013) found horses to trample significantly more nests than cattle and suggest avoiding grazing by horses in areas with high densities of birds' nests.

Because tall, homogeneous, and dense vegetation is unsuitable for breeding, due to insufficient prey accessibility and restricted bird mobility (Vickery et al. 2001; Butler and Gillings 2004; Atkinson et al. 2005), the use of fertilizer should be avoided (e.g., McCracken et al. 2004). Due to the Curlew's sensitivity to disturbance, human activities should be reduced to a minimum during the breeding period, e.g., by closing paths and by promotion of nature related ecotourism (Davenport and Davenport 2006).

The apparently healthy population on the East Frisian Islands highlights the importance of natural habitats with low density of mammalian predators such as islands for threatened species. Since breeding productivity in habitats without mammalian predation is expected to be high, such populations may be important sources that reinforce populations on the mainland. This underlines the importance to retain or even intensify the protection of the Wadden Sea Islands not only in Germany, but also in the Netherlands and Denmark. Despite the great importance of adapted management systems to improve the habitat quality for Curlews breeding in

farmland habitats, the preservation and restoration of natural and near-natural habitats should be given high priority.

Appendix

Table 3 Results of the GLMM analysis (binomial response variable: presence [$n=46$] versus absence [$n=46$]): probability of Curlew territory establishment in relation to the area of different habitat types, habitat heterogeneity, distance to human-frequented areas and wetlands on the East Frisian Islands

Parameter	Estimate	SE	Z	P
Intercept	0.92	0.59	1.54	n.s
Built-up area	-9.02	3.71	2.40	*
Copse	-1.85	0.87	2.11	*
Dune grassland	0.67	0.27	2.44	*
$R^2_{GLMMm}=0.75-0.87, R^2_{GLMMc}=0.75-0.88$ AUC=0.88				

Island was used as a random factor. Model-averaged coefficients (conditional average) were derived from top-ranked models ($\Delta AIC_C < 2$). R^2_{GLMMm} = variance explained by fixed effects, R^2_{GLMMc} = variance explained by both fixed and random effects (Nakagawa et al. 2017), AUC Area under the curve; accuracy of model prediction (Fielding and Bell 1997). Low marsh, grassland, ruderal, shrub, open dune, dune slack, mudflat, wetland and distance to human-frequented area were not significant. Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$

Table 4 Results of the GLM analysis (binomial response variable: presence [$n=14$] versus absence [$n=28$]): probability of Curlew nest-building in relation to vegetation structure at coarse scale (10 m x 10 m) (a) and fine scale (2 m x 2 m) (b), on Spiekeroog

Parameter	Estimate	SE	Z	P
a) Coarse scale (10 m x 10 m)				
Intercept	-9.47	4.50	2.04	*
Vegetation height	0.83	0.41	1.96	*
Vegetation height (centred + squared)	-0.02	0.01	1.97	*
Bare ground	0.17	0.07	2.33	*
$R^2_{MF}=0.40, AUC=0.89$				
b) Fine scale (2 m x 2 m)				
Intercept	-3.96	2.48	1.57	n.s
Vegetation height	0.44	0.19	2.23	*
Vegetation height (centred + squared)	-0.01	0.00	2.23	*
Bare ground	0.12	0.06	2.14	*
$R^2_{MF}=0.40, AUC=0.87$				

Model-averaged coefficients (conditional average) were derived from top-ranked models ($\Delta AIC_C < 2$). R^2_{MF} = McFadden's pseudo R^2 , AUC Area under the curve; accuracy of model prediction (Fielding and Bell 1997). Litter was not significant (a); herb layer and litter were not significant (b). Significance levels are indicated as follows: n.s. $P > 0.05$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

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Declarations

Competing interests The authors declare that they have no competing interests.

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