Ecological Engineering 140 (2019) 105592

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer

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ARTICLE INFO

Keywords:
Dune grassland
European rabbit (*Oryctolagus cuniculus*)
Habitat preference
Land-use change
Northern wheatear (*Oenanthe oenanthe*)
Vegetation structure

ABSTRACT

In recent decades, numerous farmland birds have experienced considerable population declines. The loss of nutrient-poor habitats with short vegetation due to land-use intensification, abandonment or nitrogen deposition helps account for this decrease. Soil-disturbing ecosystem engineers can naturally create short and sparsely vegetated swards with beneficial effects for biodiversity.

The aim of this study is to examine the influence of the European rabbit (*Oryctolagus cuniculus*) as an ecosystem engineer on breeding populations of the severely declining northern wheatear (*Oenanthe oenanthe*) on the East Frisian Islands (Lower Saxony, northern Germany). Rabbits were found to have had a considerable influence on the structure of the dune grassland, the main breeding habitat of the wheatear: high rabbit abundance resulted in greater burrow density and more bare ground. Wheatears were also more abundant on islands with larger rabbit populations. At the plot level, wheatear abundance increased with burrow density and the cover of potential foraging habitats (short vegetation). In addition, the likelihood of nest-building increased with burrow density and decreased with vegetation height.

We thoroughly investigated the dependence of the northern wheatear on large populations of the ecosystem engineer European rabbit. Through their digging and grazing activities, rabbits create two key resources for breeding wheatears: (i) sufficient burrows as potential nesting sites and (ii) the availability of short vegetation as foraging habitats.

1. Introduction

Biodiversity loss in the Anthropocene constitutes a global concern (Rockström et al., 2009). Indeed, current extinction rates are 1,000 times higher than the natural background rate (De Vos et al., 2014). For terrestrial biomes, land-use change is assumed to be the main driver of species loss (Sala, 2000; Foley et al., 2005). Although most of Europe's biodiversity is associated with agricultural land (Donald et al., 2006; Henle et al., 2008; Kleijn et al., 2009), farmlands exhibit the largest decrease in biodiversity across different taxa such as plants, insects or birds (Donald et al., 2006; Flohre et al., 2011; Vickery et al., 2001). Two contrasting processes have been identified as the primary reasons for the recent loss of farmland flora and fauna: (i) the intensification of land use in productive areas; and (ii) the abandonment of marginal land (Foley et al., 2005; Henle et al., 2008; Kleijn et al., 2009). Both processes work alongside atmospheric nitrogen deposition (Bobbink et al., 2010; Wallis De Vries and Bobbink, 2017) to instigate a loss of nutrient-poor habitats with short vegetation, an important factor behind the steep decline of numerous farmland birds (Butler and Gillings, 2004; Devereux et al., 2004; Stillman and Simmons, 2006).

For grasslands, it has been shown that soil-disturbing ecosystem engineers can naturally create short and sparsely vegetated swards (Davidson et al., 2012; Streitberger et al., 2017). Ecosystem engineers are generally defined as organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials (Jones et al., 1994). Research on ecosystem engineers has particularly focused on soil-disturbing animals in the steppe and desert ecosystems of North America and Asia (Davidson et al., 2012). Nevertheless, in Central European grasslands, certain animal species also act as ecosystem engineers (e.g., ants, mole or wild boar) (Seifan et al., 2010; Streitberger et al., 2014; Streitberger and Fartmann, 2016; Streitberger et al., 2017; de Schaetzen et al., 2017). Due to their burrowing and mound-building activities, they can create small-scale patches of open and short vegetation with beneficial effects for less competitive plant species or threatened butterfly species. Another example of an ecosystem engineer occurring in European grasslands is the European

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https://doi.org/10.1016/j.ecoleng.2019.105592
Received 20 March 2019; Received in revised form 5 August 2019; Accepted 1 September 2019

rabbit (*Oryctolagus cuniculus*), which is known to promote lizard diversity and density through its borrowing activities (Bravo et al., 2009; Grillet et al., 2010). Yet, systematic studies regarding the effects of rabbits on bird species in open landscapes have not been conducted.

The northern wheatear (*Oenanthe oenanthe*) was formerly a widespread breeding bird of open habitats with sparse and short vegetation in Europe (Cramp, 1988; Bauer et al., 2012). However, due to the loss of such habitats, wheatear populations have declined in many European countries (Burfield and Van Bommel, 2004; BirdLife International, 2015). In Germany, the decrease has been estimated at 21–50% for the period 1985–2009 (Gedeon et al., 2014; Birdlife International, 2015). Several authors perceive that wheatears benefit from grazing by European rabbits through the creation of short vegetation for foraging (Brooke, 1979; Tye, 1980; Conder, 1989; Wilson et al., 2009; Newton, 2017). Furthermore, it has been shown that rabbit burrows are regularly used for nesting (Conder 1989; Blüml and Schönheim, 2006; Van Turnhout et al., 2018). Interestingly, in the Netherlands wheatear decline appears to have followed rabbit population trends with a delay of five to ten years (Van Turnhout et al., 2007). However, a thorough investigation of the relationship between the occurrence of European rabbit and the northern wheatear has yet to be undertaken.

The aim of this study is thus to examine the influence of European rabbits on breeding populations of the rapidly declining northern wheatear. We selected the East Frisian Islands (Lower Saxony, northern Germany) for our study location, because the islands vary considerably in rabbit abundance. The influence of rabbit abundance on habitat structure and wheatear populations was analysed by considering all eight East Frisian Islands. Detailed studies on the habitat preferences of breeding wheatear were conducted on the Lower Saxonian abundance hotspot of the species, the island of Norderney.

2. Materials and methods

2.1. Study species

The northern wheatear (*Oenanthe oenanthe*) is an insectivorous passerine bird with a Palaearctic and north Nearctic breeding range (Bauer et al., 2012). The wintering grounds of the European breeding population of this long-distance migrant are the sub-Saharan savannahs in Africa (Schmaljohann et al. 2012). The species breeds in open habitats with sparse and short vegetation (Cramp, 1988). For nesting the northern wheatear relies on cavities such as rock crevices, niches and burrows (Conder, 1989). In the Central European lowland, breeding wheatears mainly occur in human-made habitats, for instance clear-cuts, peat cuts, military training areas, surface-mining areas and vineyards (Bauer et al., 2012). In contrast, on the coastal islands of the North Sea the species primarily occurs in natural dune grasslands (Blüml and Schönheim, 2006). Due to steep declines the northern wheatear is considered critically endangered in Lower Saxony (1990–2014: > 50%) and Germany (1985–2008: > 50–75%) (Grüneberg et al., 2015; Krüger and Nipkow, 2015, Sudfeldt et al. 2013).

2.2. Study area

The study area comprised the East Frisian Islands in the southern North Sea (Lower Saxony, Germany; Fig. 1). An Atlantic climate with a mean annual temperature of 9.6 °C and a mean precipitation of 752 mm characterises the study area (weather station: Norderney; long-term mean: 1981–2010) (Deutscher Wetterdienst, 2018). The East Frisian Islands are sandy barrier islands and are influenced by tides. The main habitats on the islands are beaches, dunes, dry and wet dune slacks as well as salt marshes and tidelands. The most important habitats colonised by wheatears are dune grasslands typically dominated by *Agrostis capillaris*, *Carex arenaria* and *Corynephorus canescens* as well as different mosses and lichens. Saltmarshes, which are flooded only by high tides, are dominated by *Agrostis stolonifera*, *Festuca rubra*, *Juncus gerardii* and further salt tolerant plants. All eight East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony and the Wadden Sea World Heritage.

The two most intensively studied islands, Norderney and Spiekeroog, have a width of about 2 km. Norderney is approximately 14 km long, with an area of about 25 km^2 (Petersen and Pott, 2005). Spiekeroog is situated 20 km further east and has a length of 10 km and an area of 18 km^2. Norderney is the most important stronghold of the wheatear in Lower Saxony. In 2015, a total of 179 wheatear territories were detected on Norderney (Schulze-Dieckhoff, pers. comm., Lower Saxonian Water Management, Coastal Defence and Nature Conservation Agency [NLWKN]), approximately one third of the breeding population of Lower Saxony (Krüger et al., 2014) and more than two thirds of those of the East Frisian Islands (Schulze-Dieckhoff, pers. comm., NLWKN). With an assumed population size of 5000 individuals, the island is densely populated by European rabbits (*Oryctolagus cuniculus*) (Walter and Kleinekuhle, 2008). In contrast, on Spiekeroog wheatears breed very rarely and rabbits have been extinct since 1889 (Meyer-Deepen and Meijering, 1979; Schulze-Dieckhoff, pers. comm., NLWKN). The presence/absence of rabbits on Norderney and Spiekeroog is reflected in the vegetation structure with much more open soil on Norderney (Fig. 2, Isermann et al., 2010).

2.3. Sampling design

2.3.1. Influence of rabbit abundance on habitat structure and wheatear populations

Rabbit abundance on the East Friesian Islands was classified into two categories: high (> 1 rabbits/ha island area) and low (< 0.1 rabbits/ha or even uncolonised) (data source: Peters and Pott, 1999; Hahn, 2006; Walter and Kleinekuhle, 2008). The effects of rabbit abundance on habitat structure were analysed on a representative island for the categories high (Norderney: 1.9–13.4 individuals/ha; Peters and Pott, 1999) and low abundance (Spiekeroog: uncolonised; Walter and Kleinekuhle, 2008). On both islands we randomly selected 15 plots each within the dominant and main breeding habitat of the wheatear on the East Frisian Islands: dune grassland (cf. Section 2.1). In August 2018 we counted the number of burrows within a radius of 5 m around the centre of each plot. Furthermore, we measured vegetation height (cm) at an accuracy of 2.5 cm using a ruler and estimated the cover (%) of bare ground, herbs, mosses, shrubs and litter in an area of 3 m × 3 m (Table 1). Data on wheatear territory densities on the East Frisian Islands in 2015 were based on territory mapping (Bibby et al., 2000; Fischer et al., 2005) and provided by Schulze-Dieckhoff (pers. comm., NLWKN).

2.3.2. Habitat preferences of the wheatear on its abundance hotspot

2.3.2.1. Breeding-pair survey. On Norderney, the density stronghold of Lower Saxony, we randomly selected 71 quadratic plots with a size of 250 m × 250 m (area: 6.25 ha) within the main breeding habitat of dune grassland (total survey area: 443.75 ha). In these plots we surveyed breeding pairs and habitat characteristics. To determine the number of wheatear breeding pairs per plot, three surveys from the end of May to the end of June 2018 were conducted on all 71 plots (Bibby et al., 2000; Andretzke et al., 2005). During each survey we systematically searched for wheatear displaying territorial behaviour by following linear transects covering the entire plot. Transect lines were set about 60 m apart from each other. Due to late migrants and a high proportion of unmated, singing males (Currie et al., 2000), the number of wheatear breeding pairs is often overestimated when conducting regular territory mapping (Bibby et al., 2000; Andretzke et al., 2005). Consequently, in this study the number of breeding pairs was determined only when clear evidence of breeding was available, i.e., the observation of warning or feeding adults. For each breeding territory where warning wheatears were observed and the nesting site

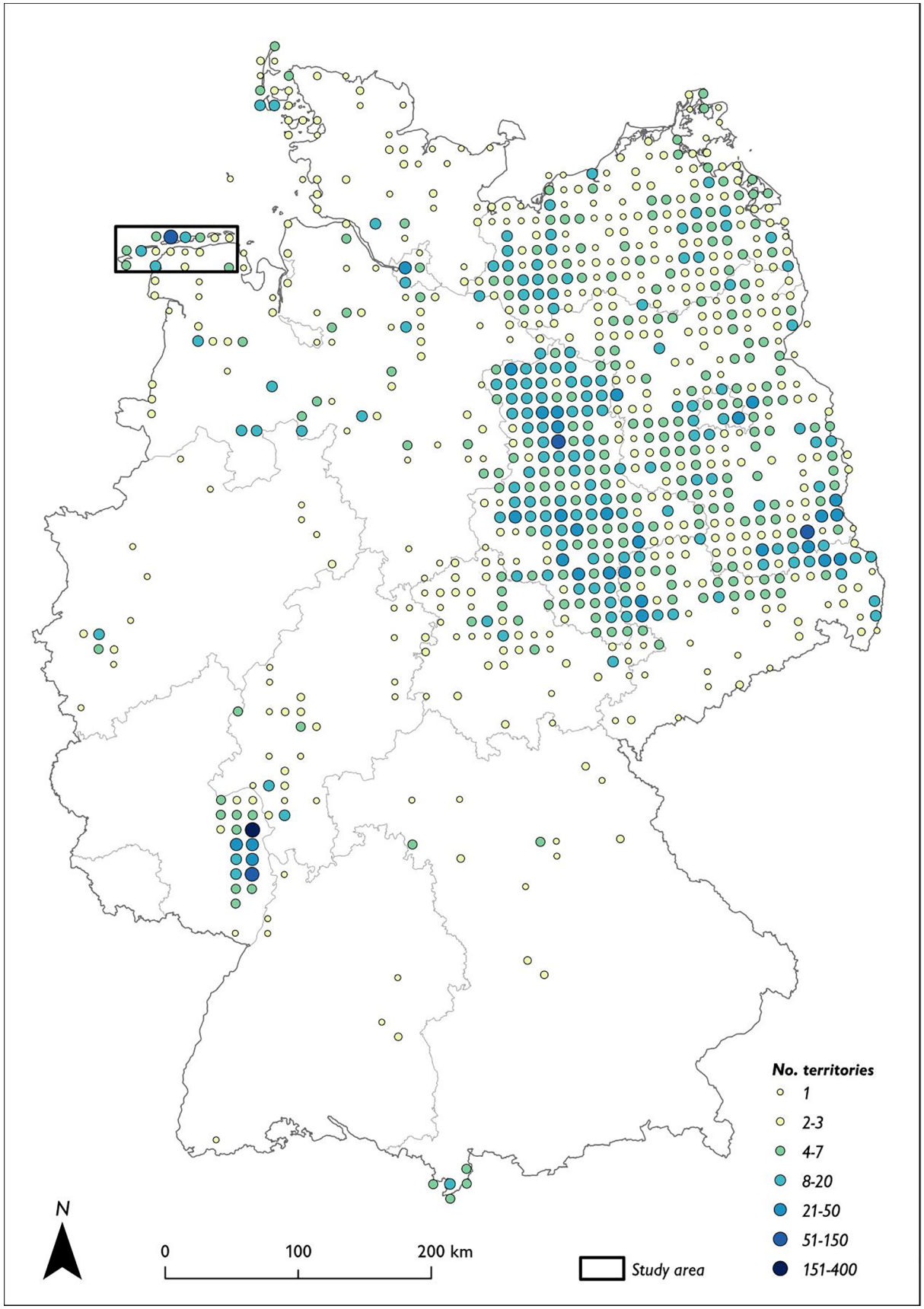

Fig. 1. Location of the study area as well as the distribution and number of territories of the northern wheatear (*Oenanthe oenanthe*) in Germany based on 10′ × 6′ geographic minute grids. Data Source: Gedeon et al. (2014).

Fig. 2. Aerial photographs of dune grassland on Norderney with high abundance of rabbits (left) and Spiekeroog without occurrence of rabbits (right).

Table 1
Mean values (± SE) of environmental parameters in dune grassland on an island with high rabbit abundance (High Abundance; Norderney, $n = 15$) and uncolonised by rabbits (Uncolonised; Spiekeroog, $n = 15$). For further explanations see Section 2.3.1. Differences between the island with high abundance and the uncolonised island were tested using Mann-Whitney U test. Significance levels are indicated as follows: n.s. $P > 0.5$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Parameter	Dune grassland		*P*
	High Abundance	Uncolonised	
Burrow density (burrows/100 m^2)	5.6 ± 0.8	0 ± 0	***
Vegetation height (cm)	11.6 ± 1.8	10.9 ± 1.1	n.s.
Cover (%)			
Bare ground	12.8 ± 4.3	3.4 ± 1.1	*
Herbs	54.1 ± 6.3	47.7 ± 4.3	n.s.
Mosses	43.2 ± 7.2	72.1 ± 7.8	**
Shrubs	0.9 ± 0.9	0.9 ± 0.9	n.s.
Litter	19.1 ± 4.5	31.8 ± 5.9	n.s.

remained unknown, we sought to locate the nests through observing feeding adults. Data on breeding pairs were used for analyses of the habitat preferences of the wheatear on two different spatial scales: (i) the plot level representing large-scale habitat conditions affecting the breeding density of wheatears and (ii) the breeding territory level representing small-scale habitat conditions at nest sites.

2.3.2.2. Environmental conditions at the plot level. At each of the 71 breeding-pair survey plots we measured the vegetation height (cm) and estimated the cover (%) of bare ground and short vegetation (height < 5 cm) as potential foraging habitats (cf. Conder, 1989; Low et al., 2010; Van Oosten et al., 2014) on nine systematically arranged subsamples covering the whole plot. Moreover, we counted the number of burrows within a radius of 10 m around the centre of each subsample (Table 2). For further analyses we used the sum (burrow density) and mean values (all other variables), respectively.

2.3.2.3. Environmental conditions at the breeding territory level. At the breeding territory level environmental conditions were sampled within the (i) breeding territories and controls as well as within (ii) nesting sites and controls. Breeding density within the plots was high and the lowest distance between two nests was only 46 m (mean ± SE: 185.6 ± 9.6). As a result, we analysed the environmental conditions within a radius of 40 m around nests and the centre of controls. This corresponded to a territory size of 0.5 ha, which is the minimum

Table 2
Results of the GLM (Poisson) analysis (model-averaging): relationship between the abundance of wheatear breeding pairs per plot and environmental parameters. Model-averaged coefficients (conditional average) were derived from top-ranked models (ΔAICc < 3). R^2_{MF} = McFadden's Pseudo R^2 of averaged model. Significance levels are indicated as follows: n.s. $P > 0.5$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. $R^2_{MF} = 0.21$.

Parameter	Estimate	SE	Z	P
Intercept	–0.86	0.31	0.32	*
Burrow density	0.02	0.01	1.96	*
Short vegetation	0.04	0.01	2.72	**
Bare ground	0.02	0.02	1.42	n.s.
Vegetation height	–0.04	0.04	0.13	n.s.

territory size on Central European coasts (Bauer et al., 2012). Controls were randomly selected within the plots using the function "Create random points" in ArcGIS 10.2. Their number was identical to those of the detected nests ($N = 49$). Analysis of environmental conditions of the breeding territories and controls was conducted according to Berg (2008) using the function "Buffer" in ArcGIS 10.2. We calculated the area of the different habitat types using habitat data from the Trilateral Monitoring and Assessment Programme (TMAP) (Wadden Sea National Park of Lower Saxony [WCNPLS] 2004; cf. Table 3). For further

Table 3
Mean (± SE) area of habitat types and habitat heterogeneity at breeding territories ($n = 49$) and control ($n = 49$). For further explanations see Section 2.3.1. Differences between breeding territories and controls were tested using Mann-Whitney U test. Significance levels are indicated as follows: n.s. $P > 0.5$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Parameter	Breeding territory	Control	*P*
Habitat type (m^2)			
Dune grassland	2,474.6 ± 1,977.4	1,732.5 ± 197.0	***
High salt marsh	887.1 ± 153.9	1,445.0 ± 224.5	n.s.
White dune	641.9 ± 145.1	796.8 ± 151.9	n.s.
Salt dune	287.7 ± 70.6	151.9 ± 54.4	*
Built-up area	226.8 ± 87.9	342.2 ± 123.2	n.s.
Shrub	165.3 ± 55.3	124.8 ± 30.5	n.s.
Open dune	102.5 ± 34.0	72.4 ± 22.7	n.s.
Dune slack	85.0 ± 45.3	69.4 ± 26.0	n.s.
Reed	48.5 ± 20.9	15.7 ± 7.6	n.s.
Dune heath	37.6 ± 21.9	35.3 ± 15.2	n.s.
Copse	14.9 ± 7.6	83.5 ± 37.2	n.s.
Habitat heterogeneity *H'* (Shannon index)	0.8 ± 0.1	0.8 ± 0.0	n.s.

Table 4
Mean values (± SE) of environmental parameters at nest sites (n = 49) and control (n = 49). For further explanations see Section 2.3.1. Differences between nest and control were tested using Mann-Whitney U test. Significance levels are indicated as follows: n.s. $P > 0.5$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Parameter	Nest site	Control	P
Burrow density (burrows/100 m²)	8.4 ± 0.6	4.5 ± 0.3	***
Vegetation height (cm)	5.8 ± 0.7	12.3 ± 1.3	***
Distance to foraging habitat (m)	9.0 ± 1.3	14.1 ± 1.0	***
Cover (%)			
Bare ground	25.0 ± 2.9	11.2 ± 2.5	***
Herb layer	52.9 ± 2.9	65.5 ± 4.2	*
Moss	37.8 ± 3.8	26.2 ± 4.4	**
Shrubs	2.1 ± 1.1	3.0 ± 1.5	n.s.
Litter	8.7 ± 1.2	21.5 ± 3.0	**

information concerning the habitat types see Petersen et al. (2014). Moreover, habitat data formed the basis for the calculation of habitat heterogeneity (H') using the Shannon Index (O'Neill et al., 1988).

In order to assess the environmental conditions at the nesting sites, we measured the vegetation height (cm) and cover (%) of the bare ground, as well as the herb layer, mosses, shrubs and litter in an area of 3 m × 3 m around each nest (Table 4). We also counted the number of burrows within a radius of 5 m around the nest and measured the distance to the next potential foraging habitat with a vegetation height of less than 5 cm (see above). To document the range of available nesting sites within the breeding-pair survey plots studied, we analysed the same parameters at control samples of equivalent size using the same methods as described for the breeding territories and controls (see above).

2.4. Statistical analysis

Differences in environmental conditions between two groups (high vs. low rabbit abundance, breeding territory vs. control and nest site vs. control) were analysed using Mann-Whitney U test, because data were not normally distributed (Tables 1, 3 and 5). At the plot level, we assessed the influence of the sampled environmental parameters (Table 2) on wheatear abundance (breeding pairs/plot) by conducting a generalised linear model (GLM) with Poisson error distribution (cf. Crawley, 2007). At the breeding territory level, we analysed the effects of the sampled environmental parameters (Table 4) on breeding territory occupancy and nest-site occupancy, respectively, via generalised linear mixed-effect models (GLMM) with plot as a random factor (Crawley, 2007). To increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson, 2002; Grueber et al., 2011). Model averaging was conducted using the 'dredge' function (R package MuMIn; Barton, 2016) and included only top-ranked models within ΔAICc < 3 (cf. Grueber et al., 2011). To avoid multi-collinearity in the GLMM, Spearman's rank correlations (r_s) were conducted to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (Dormann et al., 2013). The area of salt marsh was negatively correlated with those of dune grassland ($r_s = -0.57$, $P < 0.001$) and the cover of mosses was negatively correlated with the cover of the herb layer ($r_s = -0.52$, $P < 0.001$). Therefore, the variable of salt marsh was excluded from the breeding territory occupancy and moss from the nest-site occupancy analysis. All statistical analyses were performed using R 3.5.1 (R Development Core Team, 2018).

Table 5
Results of the GLMM (Poisson) analyses (model-averaging): relationship between breeding territory (a) and nest site occupancy (b) and environmental parameters. Plot was used as a random factor. Model-averaged coefficients (conditional averaged) were derived from top-ranked models (ΔAICc < 3). R^2_{GLMMc} = variance explained by fixed effects, R^2_{GLMMm} = 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). Significance levels are indicated as follows: n.s. $P > 0.5$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Parameter	Estimate	SE	Z	P
(a) **Breeding territory**				
R^2_{GLMMc} = 0.09–0.34, R^2_{GLMMm} = 0.13–0.37, AUC = 0.78				
Intercept	–0.79	0.47	1.66	n.s.
Dune grassland	0.29	0.14	2.07	*
Salt dune	0.93	0.44	2.08	*
Dune shrub	0.32	0.53	0.61	n.s.
Open dune	1.04	0.83	1.25	n.s.
White dune	0.05	0.18	0.28	n.s.
Bare sand/mud	–0.396	2.87	1.37	n.s.
Dune slack	0.199	0.64	0.31	n.s.
Built-up area	–0.03	0.23	0.13	n.s.
(b) **Nest site**				
R^2_{GLMMc} = 0.57–0.62, R^2_{GLMMm} = 0.57–0.64, AUC = 0.91				
Intercept	–0.481	0.817	0.58	n.s.
Burrow density	0.455	0.135	3.64	***
Vegetation height	–0.162	0.064	2.51	*
Distance foraging habitat	–0.065	0.047	1.36	n.s.
Bare ground	0.023	0.015	1.53	n.s.
Herb layer	0.008	0.013	0.59	n.s.
Shrubs	0.048	0.043	1.11	n.s.
Litter	–0.039	0.024	1.56	n.s.

3. Results

3.1. Influence of rabbit abundance on habitat structure and wheatear populations

Rabbits had a significant influence on the habitat structure of the main breeding habitat of the wheatear on the East Frisian Islands, dune grassland (Table 1). Indeed, burrow density was significantly higher on the island with high rabbit abundance compared to those without rabbits. In addition, high rabbit abundance resulted in significantly greater bare-ground cover and a significantly lower cover of mosses. Moreover, wheatear abundance was significantly greater on islands with high rabbit abundance relative to those with low abundance (Fig. 3).

3.2. Habitat preferences of the wheatear on its abundance hotspot

3.2.1. Plot level

The habitat structure in the 71 plots was characterised by a high density of burrows (mean ± SE: 5.2 burrows/1000 m² ± 0.4), short turf (height: 11.4 cm ± 0.4), the availability of potential foraging habitats (cover: 11.9 ± 1.0) and some bare ground (cover: 9.5 ± 0.9).

In total, we detected 70 breeding pairs within the 71 plots, resulting in an abundance of 1.6 breeding pairs/10 ha. For 49 of these pairs, the nests were found. All nests, with the exception of one in a niche of an old bunker, were placed in rabbit burrows. Almost 40% of the plots (27 plots) were not occupied by the wheatear. Within the occupied plots, the number of breeding pairs varied from one to three. According to the GLM analysis, wheatear abundance at the plots increased with burrow density and cover of potential foraging habitats (Table 2, Fig. 4).

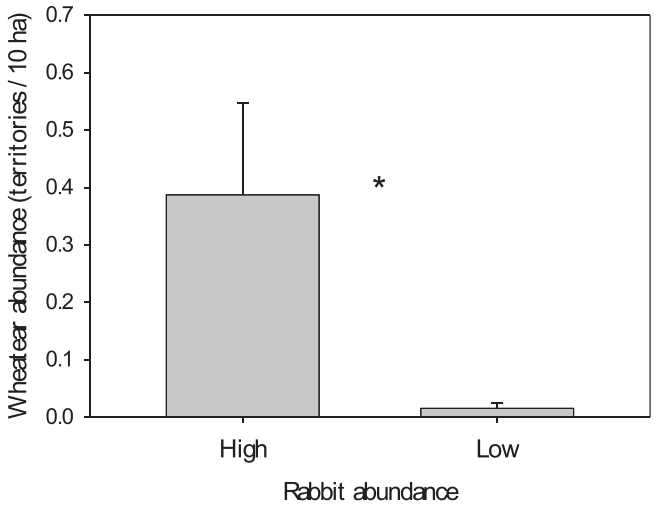

Fig. 3. Mean (± SE) wheatear abundance on the East Frisian Islands with high and low rabbit abundance. High abundance (> 1 rabbits/ha; $N = 3$): Baltrum, Borkum and Norderney; low abundance (< 0.1 rabbits/ha or even uncolonised; $N = 5$): Juist, Langeoog, Memmert, Spiekeroog and Wangerooge. For further information see Section 2.3.1. Differences between the two abundance categories were tested using Mann-Whitney U test: $U = 0.00$, $^*P < 0.05$.

3.2.2. *Breeding territory level*

The dominant habitat type within the wheatear breeding territories was dune grassland covering an average of 50% of the territories (Table 3). High salt marshes (18%) and white dunes (13%) also covered larger parts. Areas of dune grassland and salt dune were significantly higher within the wheatear breeding territories than at the control. In contrast, the areas of all other habitat types and the habitat heterogeneity did not differ between breeding territories and the control. Based on the GLMM analysis the likelihood of breeding territory establishment increased with the area of dune grassland and salt dunes, too (Table 5).

The direct vicinity of the nesting sites was characterised by the occurrence of some burrows, short vegetation, a short distance to potential foraging habitats, a high cover of bare ground and mosses, a herb layer with intermediate cover and low shrub and litter cover (Table 4, Fig. 4). Aside from shrub cover, all sampled environmental parameters significantly differed between nest site and control. For nest-building, habitats with a higher burrow density, shorter vegetation, shorter distance to potential foraging habitats, higher cover of bare ground and mosses and a lower cover of the herb layer and litter were preferred. The GLMM analysis revealed that the likelihood of nest-building increased with burrow density and decreased with vegetation height (Table 5).

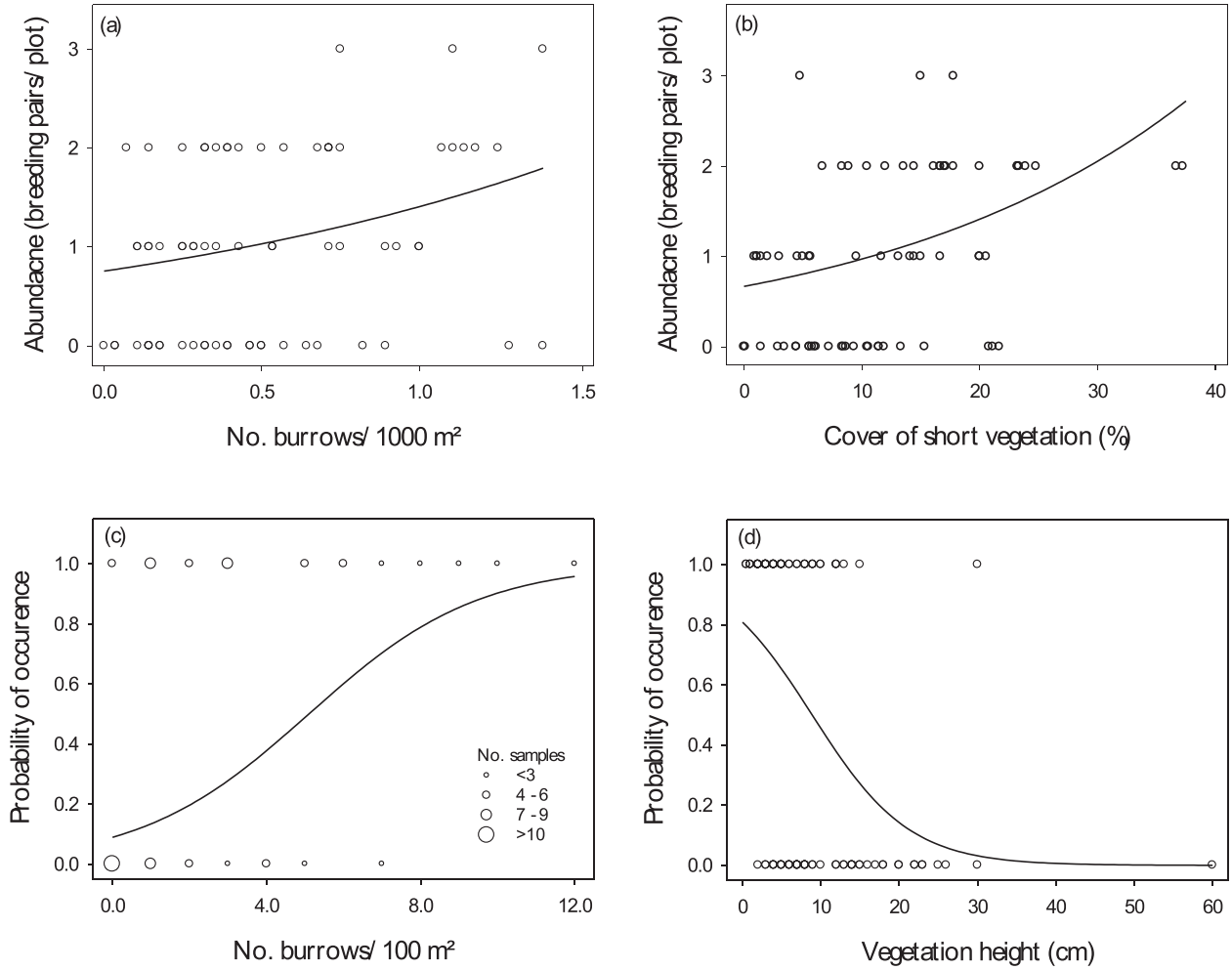

Fig. 4. Results of the GLMM analyses: relationship between abundance (a and b) and occurrence of wheatear breeding pairs (c and d) with significant predictor variables (see Table 5). The regression slopes were fitted using multivariate GLMM.

4. Discussion

Our study indicated that the occurrence of the northern wheatear on the East Frisian Islands was depending on large populations of the burrowing, herbivorous ecosystem engineer European rabbit. Rabbits were found to have had a considerable influence on the structure of the dune grassland, the main breeding habitat of the wheatear: high rabbit abundance resulted in greater burrow density and more bare ground. Wheatears were also more abundant on islands with larger rabbit populations. At the plot level, wheatear abundance increased with burrow density and the cover of potential foraging habitats (short vegetation). In addition, the likelihood of nest-building increased with burrow density and decreased with vegetation height.

The northern wheatear breeds in cavities near to the ground (Conder, 1989). In natural habitats above the timber line, potential nesting sites such as rock crevices are usually widespread (Bauer et al., 2012). In contrast, in lowlands the availability of suitable breeding places often constitutes a limiting factor. In our study, all wheatear nests except one were located within rabbit burrows. Rabbits dig extensive underground burrows ('warrens') for resting during the day as well as for shelter from predators (Wilson et al., 2016). They also create breeding burrows ('nurseries') days, weeks or even month before they are used. Large proportions of these nurseries become abandoned over time and are, hence, available for wheatears as nesting sites (Wilson et al., 2009; Wilson et al., 2016). Although some authors have reported on wheatears breeding in rabbit burrows (cf. Conder, 1989; Blüml and Schönheim, 2006), until now a detailed analysis of the importance of rabbit burrows for breeding wheatears was absent.

In general, information on rabbit burrows as a habitat for other animals remains scarce. In the case of southwestern Europe it has been shown that high rabbit burrow density fosters lizard diversity and density (Bravo et al., 2009; Grillet et al., 2010, Wouters et al. 2012). Furthermore, there appears to be a relationship between the abundance of further cavity-breeding bird species on the East Frisian Islands and rabbit burrow density. Those islands with greater abundance of rabbits have large populations of jackdaw (*Corvus mondula*), shelduck (*Tadorna tadorna*) and stock dove (*Columba oenas*), all of which regularly breed in rabbit burrows (Glue and Scott 1980, Krüger et al., 2014). Furthermore, the use of rabbit burrows as breeding sites has also been reported for the little owl *Athene noctua* (Patterson 1982).

Rabbits do not only create nesting sites for wheatears, but also shape the vegetation structure by digging and grazing (Wilson et al., 2016). In particular, they suppress succession, reduce herb-layer cover and increase the cover of bare ground, resulting in short and open swards (Foran et al., 1985; Leight et al., 1987; Norbury and Norbury, 1996; Eldridge et al., 2006, Isermann et al. 2010). The influence of rabbits on vegetation structure is also clearly visible when looking at aerial photographs of the two studied islands (Fig. 2). At the plot level, wheatear abundance increased with the cover of potential foraging habitats (short vegetation), while the likelihood of nest-building decreased with vegetation height due to decreased feeding activity of rabbits (cf. Isermann et al. 2010). In addition, the cover of bare ground and mosses was higher around nest sites compared to the control, while cover of the herb layer and litter as well as distance to foraging habitats was lower. All of these differences in habitat structure indicate breeding wheatears' preference for short and sparse vegetation. Being primarily a hopping or running bird that is morphologically adapted to foraging on the ground, wheatears require a fairly firm surface with sparse vegetation, bare ground or rocky terrain in order to move freely when pursuing arthropod prey (Brooke, 1979; Kaboli et al., 2007). Consequently, wheatears prefer short vegetation offering good access to prey (Low et al., 2010; Van Oosten et al., 2014) and, hence, pairs that establish their territories in habitats with permanently short swards exhibit superior reproductive performance (Arlt and Pärt, 2007). As a result, wheatear territory size is known to be negatively correlated with sward height and vegetation cover, implying an adjustment of territory size to hunting success (Tye, 1992; Exnerová et al., 2002).

In our study, wheatear breeding territory establishment was best explained by the area of dune grasslands and salt dunes. Rabbits prefer such dry, warm and sandy habitats (Wilson et al., 2016). On the East Friesian Islands, dune grasslands and salt dunes represent the main habitats of the European rabbit (Walter and Kleinekuhle, 2008). As a result, we can interpret the preference of the wheatear for these dune habitats by the high rabbit abundance.

Vegetation structure in the principal wheatear breeding habitat – dune grassland – differed considerably between the island with high rabbit abundance (Norderney) and its counterpart uncolonised by rabbits (Spiekeroog). Burrow density and cover of bare ground were greater, while cover of mosses was lower on the island with high rabbit abundance. Surprisingly, there was no difference in the vegetation height (Table 1). We assume that this is due to the fact that habitats on Norderney are structurally heterogeneous with short and tall swards (Van Oosten et al., 2014) so that also areas with tall vegetation were sampled. Given that aside from the occurrence of rabbits, the environmental conditions of the two islands were similar (cf. Section 2.2), such differences in habitat structure are very likely the result of the grazing and burrowing activities of the rabbits. This assumption is congruent with observations of dramatic changes in vegetation structure (taller vegetation and gradual encroachment by shrub and woodland) following the collapse of the United Kingdom's (UK) rabbit populations in the 1950s after the introduction of myxomatosis (e.g. Wilson et al., 2009; Newton, 2017). The same correlation was also described after a decline of the rabbit population in the Netherlands (Drees & van Manen 2005; Drees et al. 2006; Van Turnhout et al., 2018)

In summary, our study revealed the dependence of the northern wheatear on large populations of the burrowing, herbivorous ecosystem engineer European rabbit. Through their digging and grazing activities, rabbits create the two key resources for breeding wheatear: (i) sufficient burrows as potential nesting sites and (ii) availability of short vegetation as foraging habitats. With regard to conservation measures, our study showed that, in addition to the provision of burrows or niches for nesting, the availability of large patches with nutrient-poor, low-growing vegetation is of great importance.

Acknowledgements

The study was funded by a Ph.D. scholarship from the German Federal Environmental Foundation (DBU). We are grateful to the NLWKN, especially Martin Schulze-Dieckhoff and Josephin Erber, for the provision of data and general support. Furthermore, we thank Britta Stega, Martin Fuhse, Mareike Horst and Vera Gurniak (volunteers of NLWKN Norderney) for their assistance and accommodation during fieldwork. We would also like to thank the WSNPLS, particularly Peter Südbeck and Gundolf Reichert, for granting permission and providing support. Additionally, we would like to thank two anonymous reviewers for valuable comments on an earlier version of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2019.105592.

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