Extensive dune grasslands largely lacking human disturbance are an important refuge for a vole-dependent raptor

Steffen Kämpfer [a],[*],[1], Florian Fumy [a],[2], Thomas Fartmann [a],[b],[3]

[a] Department of Biodiversity and Landscape Ecology, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany
[b] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157 Münster, Germany

ABSTRACT

Agricultural intensification and abandonment have led to a dramatic decrease of semi-natural grasslands such as low-intensity pastures and hay meadows. The Short-eared owl (*Asio flammeus*) is a ground-nesting raptor of open grasslands that has severely suffered from these changes. We studied the habitat preferences of this umbrella species of open grasslands in its last permanent breeding area in Germany (East Frisian Islands, southern North Sea). We analysed the breeding-territory preferences based on 576 territories on six of the islands. Moreover, we assessed nest-site preferences of 13 breeding pairs on the German abundance hot spot, the island of Spiekeroog. Our investigation revealed that the Short-eared owl strongly preferred open dunes for breeding, especially dune grasslands. By contrast, built-up areas and small stands of trees were avoided. For nest-building, microhabitats with a high cover of the herb layer and litter resulting in tall vegetation were favoured. By contrast, the vegetation in the wider surrounding of the nest was characterised by more bare ground and shorter vegetation but still a high cover of the herb layer and litter. In conclusion, our study highlights the prime importance of extensive open grasslands with a pronounced litter layer and largely lacking human disturbance as breeding habitats for the Short-eared owl. At the nesting site, we suggest that tall and dense vegetation with a high cover of litter (i) might enhance concealment and (ii) causes a favourable microclimate by protecting fledglings against adverse weather conditions. In the wider surrounding of the nest, shorter vegetation with a pronounced litter layer (i) improves fledgling mobility, (ii) fosters vole abundance and (iii) increases prey accessibility.

1. Introduction

Grasslands cover more than 20% of the EU-28 land surface and are among the most species-rich ecosystems in Europe (Chytrý et al., 2015; Feurdean et al., 2018; EC 2019; Fartmann, 2024). Besides some natural grasslands such as coastal dunes, most grasslands on the European continent have been shaped by human agricultural activities (Veen et al., 2009; Feurdean et al., 2018). However, agricultural intensification and abandonment have led to a dramatic decrease of these semi-natural grasslands (Bonari et al., 2017;

Fartmann, 2024). This loss has been associated with a strong decline of species that depend on such grasslands, including many birds (Donald et al., 2006; Marques et al., 2020). Among grassland birds, in particular ground-nesting species have suffered from these changes (Donázar et al., 1997; Heldbjerg et al., 2018; Kamp et al., 2021).

The Short-eared owl (*Asio flammeus flammeus*) is a ground-nesting raptor of open grasslands in the Holarctic (Keller et al., 2020). In the 19th and early 20th century, it was common in cultural landscapes across Western and Central Europe. The species has continually declined since suffering major range losses between 1970 and 1990 (BirdLife International, 2004; Keller et al., 2020). Today, the occurrence of the Short-eared owl is restricted to only a very few remaining strongholds in this part of Europe such as some low mountain ranges or coastal dunes (Tucker et al., 1994; Newton, 2017, Kämpfer & Fartmann 2019a). In Germany, the species is listed as 'threatened with extinction' in the national red data book (Ryslavy et al., 2020). Accordingly, the conservation status of the Short-eared owl in Central Europe gives cause for concern (Calladine et al., 2012). The same applies to other parts of its range such as Canada (Smith et al., 2019) or the United States of America (Booms et al., 2014; Gahbauer et al., 2021a). Although the Short-eared owl is still categorized as 'least concern' in the IUCN red list, its population is decreasing, also on a global scale (BirdLife International, 2021).

The main threats of the Short-eared owl population in Western and Central Europe are currently considered to be: (i) habitat loss due to agricultural intensification, particularly drainage of bogs, marshes and other wetlands, (ii) increased predation by mammalian mesopredators, (iii) reduced prey availability as a result of shrinking vole populations (*Microtus arvalis*) and (iv) nest destruction through agricultural activities (Bos et al., 2020; Fernández-Bellon et al., 2020; Kämpfer et al., 2022). Consequently, the Short-eared owl is exposed to similar threats and suffers from comparable population declines as many other ground-nesting grassland birds (e. g. the Hen harrier [*Circus cyaneus*] or many wader species) (Fernández-Bellon et al., 2020). Together with its status as a higher trophic-level predator, this makes it a charismatic umbrella species for the conservation of open grassland ecosystems (Booms et al., 2014; Kämpfer et al., 2022). Since the development of effective conservation strategies depends on precise knowledge of the species' habitat requirements (Fuller, 2013; Gahbauer et al., 2021b), there is an urgent need to identify the key drivers of territory establishment and nest-site preferences of the Short-eared owl (Fernández-Bellon et al., 2020).

Here, we studied the habitat preferences of the Short-eared owl as an umbrella species of open grasslands. The research was conducted in the last permanent breeding area in Germany, the East Frisian Islands (southern North Sea). The study area is part of the Wadden Sea National Park of Lower Saxony and characterised by vast natural dunes and marshes. The islands are (i) mostly free from predatory mammals, (ii) largely undisturbed by agricultural activities or humans (Niedringhaus et al., 2009) and (iii) exhibit a high breeding success of the Short-eared owl (Kämpfer et al., 2022). We investigated the breeding-territory preferences of the Short-eared owl between 1996 and 2019 on the basis of 576 territories with confirmed breeding on six of the East Frisian Islands. Moreover, in 2019, we assessed nest-site preferences of 13 breeding pairs on the island of Spiekeroog, the German abundance hot spot. Based on the results of this study, we make suggestions to improve future conservation measures for the Short-eared owl and other bird species of open grasslands.

2. Materials and methods

2.1. Study species

The nominate form of the Short-eared owl (*Asio flammeus flammeus*) has a large Holarctic breeding range (Keller et al., 2020). Breeding abundance, however, varies strongly across its distribution area. In most parts of Europe, the ground-nesting bird has a very local distribution and is quite rare. The majority of the European population breeds in Northern Europe and Russia. By contrast, in Central Europe, higher breeding densities are strongly dependent on an exceptionally high local abundance of voles (*Microtus* spp.) (Korpimäki and Norrdahl, 1991; Krüger, 2019). Across its European range, a large variety of open habitats are used for nesting. They
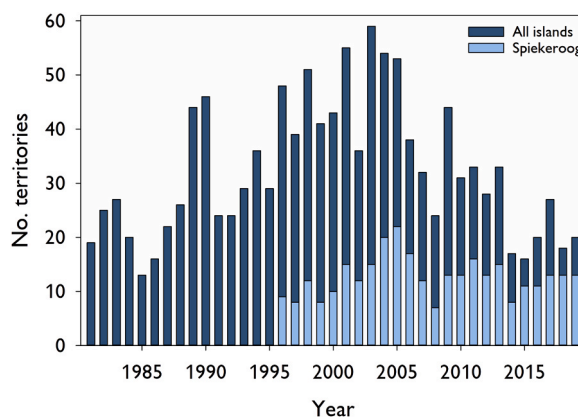

Fig. 1. Population development of Short-eared owls breeding on the East Frisian Islands (1981–2019, dark blue) and on the island of Spiekeroog (1996–2019, light blue). Data provided by M. Schulze-Dieckhoff, NLWKN 2020.

comprise natural habitats such as bogs, coastal dunes, marshes, steppes or tundra but also semi-natural ones such as heathlands or young plantations and even agricultural land (Keller et al., 2020).

Germany has only a very small population, which is estimated at 50–180 territories (2005–2009) (Gedeon et al., 2014). In most years, the population size is even at the lower end of this estimate. However, in years with vole outbreaks, the number of territories can strongly increase. The last outbreak was observed in 2019, when more than 200 territories were found mostly in intensively-used pastures and meadows (Krüger, 2019; Jödicke and Lemke, 2020). However, the breeding success was close to zero since most nests were destroyed and fledglings were killed by mowing (Krüger, 2019).

Apart from such exceptional years, the occurrence of the Short-eared owl in Germany is mainly restricted to the North Sea coasts of Schleswig-Holstein and Lower Saxony and its Wadden Sea Islands (Gedeon et al., 2014). In recent years, the only permanent breeding area was the East Frisian Islands. Despite typical fluctuations, the number of Short-eared owls breeding on these islands is relatively constant and ranged between 13 and 59 with an average of 32 territories between 1981 and 2019 (Schulze-Dieckhoff, NLWKN 2020). With 10–15 breeding pairs per year, the island of Spiekeroog is the abundance hot spot (Fig. 1).

2.2. Study area

The study area comprised the East Frisian Islands Borkum, Juist, Norderney, Baltrum, Langeoog and Spiekeroog in the southern North Sea (Lower Saxony, Germany). The islands cover an area of about 120 km^2 and are sandy barrier islands, influenced by tides. They are characterised by a mild Atlantic climate with a mean annual temperature of 9.6 °C and a mean precipitation of 752 mm (weather station: Norderney; long-term mean: 1981–2010) (Deutscher Wetterdienst, 2020).

The islands are dominated by beaches (24%), mudflats (20%), marshes (15%), built-up areas (11%) and dune grasslands (10%) (Petersen and Pott, 2005; Petersen et al., 2014). Further habitats that cover smaller areas are semi-natural grasslands (6%), small woodlots (4%), white dunes (patchy vegetation without a closed canopy, 4%), shrubs (3%), dune heathlands (1%), dune slacks (1%), reeds (1%) and transition zones between marshes and dune grasslands called salty dunes (1%). For more details on habitats, see Petersen et al. (2014). The East Frisian Islands are part of the Wadden Sea National Park of Lower Saxony (Dudley, 2013) and the Wadden Sea World Heritage site (Baird and Asmus, 2020). During the breeding season, human access is prohibited in most areas except on designated roads and paths and in small parts of the so called 'recreational zone'. Generally, dogs must be taken on a leash. Disturbance in protected areas occurs rarely thanks to visitor management, intensive public relations work and the use of National Park rangers and volunteers to control entry bans. Only small parts of the islands, primarily salt marshes, are grazed by livestock. Principally, the islands are free of mammalian predators except for Domestic cats (*Felis catus*) (Niedringhaus et al., 2008). However, in recent years, Red foxes (*Vulpes vulpes*) were present on the island of Norderney (Andretzke et al., 2016). 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 sizes of these introduced mammals has been carried out on the islands of Borkum, Norderney and Langeoog (Andretzke et al., 2016).

Since the island of Spiekeroog is the German abundance hot spot (Fig. 1), detailed analyses of the vegetation structure at nesting sites were conducted there. Spiekeroog is about 2 km wide and 10 km long and covers an area of 18 km^2 (Petersen and Pott, 2005).

2.3. Sampling design

2.3.1. Breeding-territory preferences

To identify breeding-territory preferences of the Short-eared owl on the East Frisian Islands, we used data from the annual breeding bird monitoring report between 1996 and 2019 provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (NLWKN, M. Schulze-Dieckhoff). Territory mapping was carried out according to Südbeck et al. (2005), with six visits between March and June (cf. Bibby et al., 2000). At each visit, alle parts of the islands were systematically surveyed with two to four people walking through with 100–200 m between routes. Territories were determined based on observed behaviours interpreted as possible/probable breeding (courtship display, constant perching during daylight periods, repeated observations of pairs) or confirmed breeding (repeatedly carrying prey to a area, giving alarm calls, mobbing potential predators, active nest or young located) (Calladine et al., 2010; Hardey et al., 2013). Since territories based on possible/probable breeding are associated with greater inaccuracies concerning actual nest location, they were excluded from further analyses, resulting in a data set of 576 territories based on confirmed breeding. The mean (± SE) annual number of located nests was 23.5 ± 1.8.

To determine preferred breeding areas on the islands and to show spatial clustering of breeding owls in the study area, i.e. areas which were repeatedly and most frequently used for breeding despite potential variation in environmental conditions or interannual variation between 1996 and 2019, we conducted a kernel density analysis applying a 100 m × 100 m grid in ArcGIS 10.8 (Silverman, 1986). Because the minimum distance between neighbouring breeding pairs was 300 m, we used this as the search radius distance for the calculation of kernel density.

To identify habitat preferences of breeding Short-eared owls at the landscape level, we calculated the area of each habitat within a buffer of 300 m (see above) around the nest/territory centres in ArcGIS 10.8 (cf. Kämpfer et al., 2022). To compare the habitat composition in the territories with that of the surrounding landscape, we randomly selected control samples using the 'create random points' tool in ArcGIS 10.8 and excluded areas that were unsuitable for breeding (beaches, built-up areas, forest, low marsh and mudflats). The number of control samples was adjusted to the number of Short-eared owl territories on each island resulting in a ratio of 1: 1. Subsequently, the resulting buffers were intersected with habitat data available from the Trilateral Monitoring and Assessment Program (TMAP) (Wadden Sea National Park of Lower Saxony, 2004) and the proportion of different habitats within each

territory/control was calculated. We used habitat data from 2004 since this was the middle of the period under study. Since the vegetation is assumed to change only slowly due to environmental stress (dry, nutrient-poor, sandy soils) and the low competitive power of the dominant perennial plants (cf. Kämpfer and Fartmann, 2022b), these data are assumed to be a good proxy for the complete study period.

2.3.2. Nest-site preferences

We conducted a detailed analysis of the preferred vegetation structure for nesting on the island of Spiekeroog. We searched for nests of Short-eared owls from March to July in 2019 in all thirteen territories with confirmed breeding (see Section 2.3.1). All nests were marked using a GPS device.

After adults and fledglings had left the nest, we determined the cardinal direction of the nest entrance (0–360°) and measured vegetation characteristics in an area of 2 m × 2 m (fine scale), representing the direct surrounding of the nest, and 10 m × 10 m (coarse scale), representing the surrounding vegetation structure in the breeding habitat. For both spatial scales, we recorded the dominant plant species, measured the mean vegetation height (cm) with an accuracy of 1 cm using a ruler and estimated the cover of bare ground, herbs, mosses, shrubs and litter. Furthermore, we measured vegetation height at the nest in all four cardinal directions by placing a ruler in the nest and measuring vegetation height in north, east, south and west directions. The same parameters were also recorded at randomly selected control sites (hereinafter referred to as 'control'), which were again selected by using the function 'Create random points' in ArcGIS 10.8. For the selection of controls, areas that were unsuitable for breeding (see above) were excluded. The ratio between nests and controls was 1:2 to cover the entire range of available vegetation structure.

2.4. Statistical analysis

All statistical analyses were conducted using the software R 4.0.4. (Development Core Team, 2020). Vegetation structure data were not normally distributed. Accordingly, differences between nest and control on both spatial scales were analysed using Mann-Whitney *U* test and those between nests on the two different scales by Wilcoxon test since they were not independent from each other. Differences in vegetation height between the four cardinal directions of the nests were tested using ANOVA with Tukey post-hoc test. Mean direction and standard error of nest entrance were calculated using the 'circular' (Agostinelli and Lund, 2017) and 'std.error. circular' functions (Flávio and Baktoft, 2020).

To evaluate which habitats were preferred for breeding on the islands, we used generalised linear mixed-effects models (GLMMs) with binomial error structure using the 'lme4' package of Bates et al. (2015). Within the habitat models, presence/absence was used as binomial response variable, the area of different habitats within buffers as fixed effects and island as a random effect to account for data variation between islands. To assess the effects of vegetation structure on nest-site selection, we conducted generalised linear models (GLMs) with binomial error distribution (nest vs. control) and vegetation parameters as predictors. Predictors were standardised (centred and scaled) to make their effect size comparable (cf. Border and Calladine, 2021). 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. Kämpfer & Fartmann, 2022b). Multicollinearity was low for all predictors in all models ($|r_s| < 0.6$) (Graham, 2003), but calculated variance inflation factor (VIF, Zuur et al., 2010) was high in models containing tidal habitats (beaches, mudflats and low marsh). Therefore, these variables were excluded from the performed models to avoid multicollinearity (VIF < 2). To increase the robustness of models with multiple predictors and to identify the most important variables, we conducted model averaging (full average) based on an information-theoretic approach (Burnham and Anderson, 2002; Grueber et al., 2011). Model averaging was performed using the 'dredge' function (R package MuMIn;
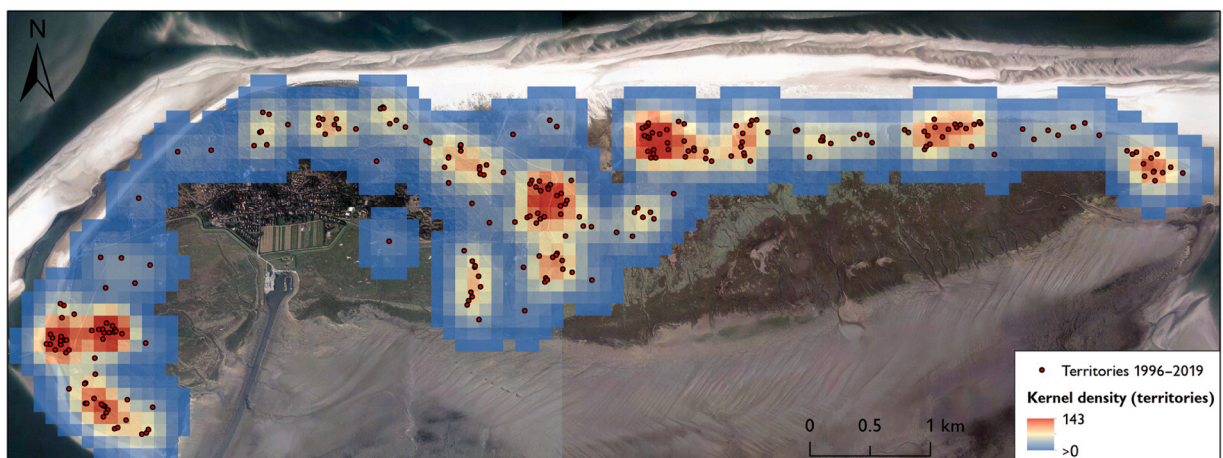

Fig. 2. Kernel density of confirmed breeding territories of the Short-eared Owl between 1996 and 2019, exemplarily shown for the island of Spiekeroog.

Barton, 2020) and included only top-ranked models with ΔAICc < 2 (cf. Grueber et al., 2011). When only one model was within ΔAICc < 2, the best individual model was used.

For binomial models, we calculated the area under the curve (*AUC*) as a measure of model accuracy (Fielding and Bell, 1997). Moreover, we calculated the variance explained by the models applying McFadden's pseudo *R*-squared (R_{MF}^2) for GLMs and marginal *R*-squared (R^2_m = variance explained by fixed effects only) and conditional *R*-squared (R^2_c = variance explained by both fixed and random effect) for GLMMs by using the function 'r.squaredGLMM' (Nakagawa et al., 2017). For model validation and diagnostics, we used the 'DHARMa' (Hartig, 2022) package and tested dispersion, uniformity, and temporal and spatial autocorrelation (functions 'testDispersion', 'testUniformity', 'testTemporalAutocorrelation', 'testSpatialAutocorrelation'). No violations of the model assumptions or difficulties caused by potential temporal or spatial autocorrelation were identified in the models (see supplementary material I for results).

3. Results

3.1. Breeding territory preferences

Short-eared owl territories were strongly clumped on the islands (cf. the island of Spiekeroog as an example; Fig. 2). The 576 confirmed breeding territories between 1996 and 2019 were located in only 2.5% of all grid cells (*n* = 447). Accordingly, the calculated kernel density was zero in the remaining 97.5% of the grid cells (*n* = 17,850). Since values of kernel density were high in very few grid cells (maximum 143), these cells can be considered as the breeding hot spots, i.e. they were frequently used and, hence, preferred for breeding (Fig. 2). Based on the GLMM analysis the likelihood of breeding territory establishment increased especially with the area of dune grassland, salty dunes and reeds, and to a lesser extent with those of white dunes, semi-natural grassland and dune heath. By contrast, small woodlots and built-up areas reduced the probability of occurrence of Short-eared owl territories (Fig. 3, see supplementary material II for model output tables).

3.2. Nest-site preferences

In 2019, seven of the 13 nests found on the island of Spiekeroog—more than 50%—were in dune grassland. Of the remaining six, two nests were found in each of white dunes and dune heath. The two remaining nests were situated in salty dune and high marsh, respectively. As a result, the dominant plant species at nests were *Ammophila arenaria* (*n* = 10), *Empetrum nigrum* (*n* = 2) and *Juncus maritimus* (*n* = 1). The direct vicinity of the nest (fine scale) was characterised by high cover of the herb layer (mean ± SE: 80 ± 5%) and litter (55 ± 5%) as well as the nearly complete absence of bare ground (1 ± 1%) (Table 1). The vegetation was tall with a mean height (± SE) of 40 ± 2 cm. Compared to control, the cover of the herb layer and litter were higher, the vegetation was taller, and the cover of bare ground was lower. On the coarse scale, the herb layer and litter also covered large parts. In comparison to the fine scale, however, the cover of bare ground was higher, and the vegetation was less tall (mean ± SE: 30 ± 2 cm). As has been shown for the fine scale, the cover of bare ground was lower adjacent to nests in comparison to control.

On both spatial scales, less bare ground and more litter were favoured for nesting (Fig. 4, see supplementary material II for model output tables). Additionally, on the fine scale, taller vegetation was preferred and a higher cover of shrubs was avoided for nesting. On the coarse scale, an intermediate vegetation height of around 30 cm had a positive effect. Model accuracy (*AUC*: 0.91–0.97) and explained variance in the data set (R^2: 0.43–0.70) were high in both models.

The nest entrance was mainly oriented to the east (mean ± SE: 90.3 ± 0.5°). Vegetation height in the four main cardinal directions differed at nests (Fig. 5). It increased from the eastern over the northern to southern and finally the western side. By contrast, there was no difference in vegetation height between the four cardinal directions at control.
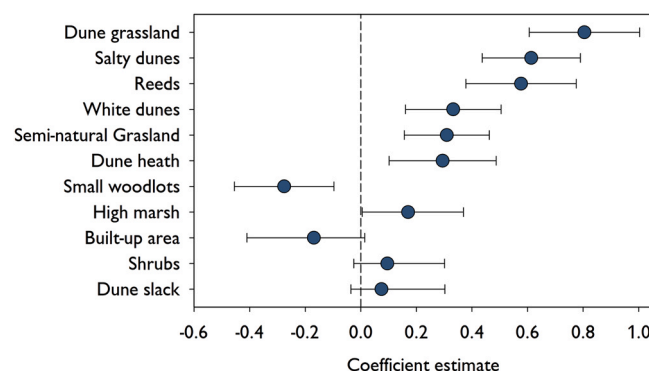

Fig. 3. Relationship between the probability of occurrence of Short-eared owl territories (presence vs. absence) and different habitats on the East-Frisian Islands based on model averaging of models with ΔAICc < 2. Predictors were standardised (centred and scaled) to make their effect size comparable. The effect size of the coefficients ± 95% confidence interval (CI) of the weighted model is shown. Variables whose 95% CI do not intersect the value 0 on the y-axis are significant. AUC: 0.78, R^2_m = 0.28, R^2_c = 0.29–0.30.

Table 1

Mean values (± SE) of vegetation structure at nests ($n = 13$) and controls ($n = 26$) on (a) fine scale (2 m × 2 m) and (b) coarse scale (10 m × 10 m), on Spiekeroog and comparison of both scales (F vs. C). F = fine scale, C = coarse scale. Differences between nests and controls were tested using the Mann-Whitney U test and those between nests on the two different scales by Wilcoxon test since they were not independent from each other. Significance levels are indicated as follows: n.s. $P > 0.05$, * $P < 0.05$, * * $P < 0.01$, * ** $P < 0.001$.

Parameter	Fine scale (2 m × 2 m)			Coarse scale (10 m × 10 m)			F vs. C
	Nest	Control	P	Nest	Control	P	P
Cover (%)							
Bare ground	0.9 ± 0.5	12.6 ± 3.7	* *	5.5 ± 1.4	14.0 ± 2.8	*	* *
Mosses	28.1 ± 9.2	36.6 ± 8.4	n.s.	43.5 ± 9.8	31.4 ± 7.5	n.s.	n.s.
Litter	55.4 ± 4.9	30.9 ± 4.2	* *	45.0 ± 5.0	33.5 ± 3.3	n.s.	n.s.
Herb layer	80.4 ± 5.1	68.2 ± 4.1	n.s.	69.2 ± 5.3	72.5 ± 3.6	n.s.	n.s.
Shrubs	0.5 ± 0.4	2.5 ± 1.7	n.s.	2.1 ± 1.1	5.6 ± 2.4	n.s.	n.s.
Vegetation height (cm)	39.6 ± 2.3	26.3 ± 3.8	* *	29.5 ± 2.2	32.5 ± 3.1	n.s.	* *

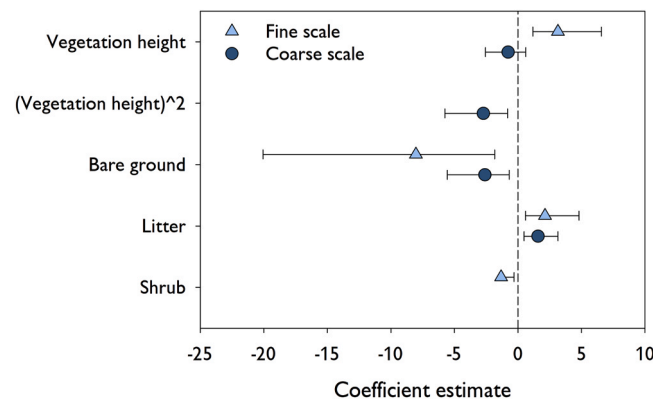**Fig. 4.** Relationship between the probability of Short-eared Owl nest-building and vegetation structure on fine scale (2 × 2 m) ($R^2_{MF} = 0.70$, $AUC = 0.97$) and coarse scale (10 × 10) ($R^2_{MF} = 0.43$, $AUC = 0.91$) based on model averaging (see supplementary material II for model output tables). Predictors were standardised (centred and scaled) to make their effect sizes comparable.

4. Discussion

Our analysis of the long-term data set from the only permanent breeding area of the Short-eared owl in Germany, the East Frisian Islands, revealed that the ground-nesting bird strongly preferred open dunes for breeding, especially dune grasslands and interlinked habitats such as salty dunes, reeds, white dunes semi-natural grasslands and dune heath. By contrast, built-up areas and small woodlots
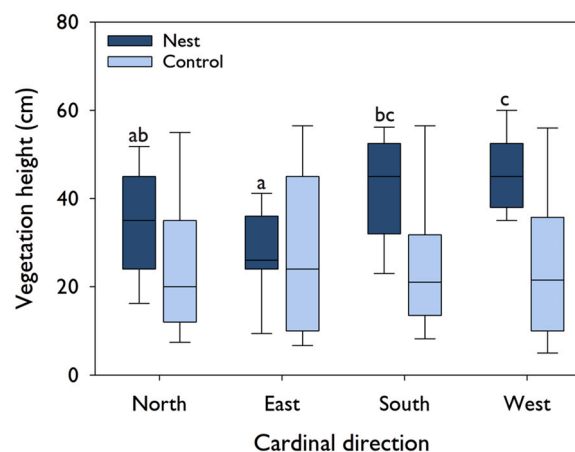

Fig. 5. Vegetation height at the four main cardinal directions at nests ($n = 13$) and controls ($n = 26$). Difference between the directions was tested using ANOVA. Nest: $F = 7.76$, $df = 3$, $P < 0.001$; Control: $F = 0.05$, $df = 3$, $P = 0.98$. Different letters indicate significant differences of pairwise comparisons (Tukey test, $P < 0.05$).

were avoided. For nest-building, microhabitats with a high cover of the herb layer and litter resulting in tall vegetation were favoured (fine scale). By contrast, the vegetation in the wider surrounding of the nest was characterised by more bare ground and shorter vegetation but still a high cover of the herb layer and litter (coarse scale).

The observed preference of Short-eared owls for dense and tall grassland vegetation rich in litter for nesting is in line with former studies from North America (Fondell and Ball, 2004; Gahbauer et al., 2021b; Holt, 1992; Keyes et al., 2016; Swengel and Swengel, 2014). According to the nest-concealment hypothesis, more concealed nests are less vulnerable to predation (Filliater et al., 1994; Kämpfer and Fartmann, 2022; Fartmann et al., 2022). However, support for the nest-concealment hypothesis has been equivocal due to morphological traits and methods used to measure concealment (Borgmann and Conway, 2015). Nevertheless, many studies have shown that concealed nests are less prone to predation, especially in ground-nesting birds (Wiebe and Martin, 1998; Møller, 2018). We assume that besides the dense and tall vegetation, the pronounced litter layer also enhances nest concealment. The litter layer was often made primarily by European beachgrass (*Ammophila arenaria*) and Sand sedge (*Carex arenaria*). The colour of this litter strongly matches those of the plumage of Short-eared owls (own observation). A recent study of Kämpfer et al. (2022) determined that a high litter cover fostered the survival of Short-eared owl fledglings and led to an increase in the number of fledged young per nest. The authors also explained this relationship by an improved concealment but additionally by a better shelter against adverse weather (see below) due to the dense litter layer. In contrast to other ground-breeding birds (e.g. species with deceptive behaviour; Smith et al., 2018), breeding Short-eared owls are known to leave their nests in case of approaching mammalian predators or humans usually only when the potential enemies have nearly reached the nest (Hardey et al., 2013). Consequently, Short-eared owls seem to rely on their high concealment within their nesting site, supporting the nest-concealment hypothesis as well.

Moreover, dense vegetation and litter can have positive effects on nest microclimate and, therefore, reproduction by providing shelter from extreme weather such as strong wind, heavy rainfall or intensive solar radiation (Heenan, 2013; Fartmann et al., 2022; Kämpfer et al., 2022). Vegetation height at nests was highest in west and south directions, representing both the main wind direction and the cardinal direction with the most intensive solar radiation in Central Europe (Bauer, 1999; Bürger, 2003). By contrast, the nest entrance was mostly oriented to the opposite direction (east). Kämpfer et al. (2022) observed that adverse weather, especially strong winds, affected fledgling survival of Short-eared owls. Consequently, we attribute the preference for tall vegetation in the west and south directions of the nest and the location of the nest entrance in the east as a strategy to cope with the negative effects of bad weather, in particular windy and rainy conditions (Miller et al., 2014; Holmes et al., 2020). Such weather conditions are known to affect coastal areas of the North Sea more regularly than most of the Central European mainland (Bürger, 2003).

In the wider surrounding of the nest, an intermediate vegetation height was preferred. Litter cover, however, was still high. Too high and dense vegetation might hamper the mobility of fledglings after leaving the nest (Devereux et al., 2004) and reduce the accessibility of voles for hunting adults (Baker and Brooks, 1981; Toland, 1987). By contrast, a high cover of litter is known to foster the abundance of voles, the most important prey of Short-eared owls (Amar and Redpath, 2005; Huang et al., 2010; Swengel and Swengel, 2014; Kämpfer et al., 2022).

A high food abundance may also explain the observed general preference for dune grasslands. In a recent two-year study on the East Frisian Island of Spiekeroog, Kämpfer et al. (2022) showed that dune grasslands were characterised by a relatively high vole abundance and the least fluctuating vole population within the investigated habitats. Additionally, dune grasslands usually surmount the surrounding habitats (e.g. dune slacks), which facilitates early predator detection (cf. Kämpfer and Fartmann, 2022b).

Based on our study, extensive open rough grasslands (long, thick, matted) are of prime importance as breeding habitats for the Short-eared owl. Similar observations have been made for North America (Wiggins et al., 2004; Swengel and Swengel, 2014; Miller et al., 2022). Such habitats do not only provide suitable habitat structures for breeding but also for foraging (Kämpfer et al., 2019a, 2019b, 2022a; see above). By contrast, small woodlots and built-up areas were avoided. Woodlots hamper access to small mammal prey. Additionally, they can serve as a perch for avian predators (e.g. Carrion crows [*Corvus corone*]), which may result in enhanced nest predation (Andersson et al., 2009). An avoidance of disturbance by human activity has already been shown by Calladine et al. (2010). In general, it can be assumed that the low frequency of human disturbance in the studied national park due to zoning, visitor management and the work of national park rangers favours the Short-eared owl breeding population. This assumption is supported by the findings of Kämpfer et al. (2022). Although the densities of avian predators (Herring gull [*Larus argentatus*], Lesser black-backed gull [*Larus fuscus*], Carrion crow and Marsh harrier [*Circus aeruginosus*]) were high on the island of Spiekeroog, they detected a very high nest survival rate of Short-eared owls. They explained this pattern by the highly effective defensive behaviour of adult Short-eared owls due to the widespread absence of human disturbance.

In conclusion, our study highlights the prime importance of extensive open rough grasslands largely lacking human disturbance as breeding habitats for the Short-eared owl. The main habitats in our study were dune grasslands and interlinked habitats that provided mosaics of tall and dense vegetation rich in litter for nesting and areas with shorter vegetation but also providing a pronounced litter layer for foraging. At the nesting site, tall and dense vegetation with a high cover of litter (i) enhances concealment and (ii) causes a favourable microclimate by protecting fledglings against adverse weather conditions. In the wider surrounding of the nest, by contrast, shorter vegetation with a pronounced litter layer (i) improves fledgling mobility, (ii) fosters vole abundance and (iii) increases prey accessibility. As a result, the described environmental conditions in the preferred habitats on both spatial scales generally favour higher reproduction rates in the Short-eared owl.

5. Implications for conservation

Kämpfer et al. (2022) detected a comparatively high reproduction rate of Short-eared owls (probability of nest survival: 0.9; hatched young per nest: 5.6) on the East Frisian Island of Spiekeroog. They explained the favourable conditions for reproduction on the

island by a combination of the following key factors: (i) absence of mammalian mesopredators such as the Red fox, (ii) relatively stable vole populations without cyclic variation, (iii) nearly no disturbance through agricultural measures and (iv) widespread lack of human disturbance due to legal regulations of the National Park. Our study confirmed the latter and, additionally, highlighted the prime importance of large and well-connected open rough grasslands for the establishment of breeding territories of the species. Since habitats meeting the described requirements are very rare in Central Europe due to the dominance of intensive agriculture (Ellenberg and Leuschner, 2010) and high density of mammalian mesopredators (Roos et al., 2018), we assume that the availability of suitable habitats is a decisive factor limiting the occurrence of the umbrella species Short-eared owl on the Central European mainland.

Consequently, to promote the species, conservation management should focus on the restoration of extensive und unfragmented rough grasslands and the reduction of human disturbance and predator pressure. Ecosystems where abundance of mammalian mesopredators is naturally low such as bogs, marshes or other wetlands (cf. Border and Calladine, 2021) and which are characterised by nutrient-poor soils with low successional speed therefore appear to be particularly suitable for conservation management. The latter is important since under such conditions the preferred vegetation exhibiting a high cover of litter and not too tall vegetation where shrubs are absent can be maintained for longer time periods without management. This assumption is confirmed by the fact that the nutrient-poor dune grasslands on the East Frisian Islands have already hosted strong populations of the Short-eared owl for decades (see section Study species), although they are only affected by weak natural disturbance (e.g. aeolian sand shifts). However, outside national parks, low intensity grazing and possibly clearing of shrubs are necessary from time to time to reset succession. Such measures are also known to increase habitat suitability for many other grassland species (Kämpfer and Fartmann, 2022b, Fumy and Fartmann, 2021). By contrast, intensive grazing should generally be avoided. It creates short swards that (i) have a low vole abundance due to the lack of litter (Amar and Redpath, 2005; Kämpfer et al., 2022) and (ii) are unsuitable for nesting (this study). Moreover, in farmland ecosystems, it must be ensured that neither nests nor young birds are harmed by agricultural activities such as mowing (Krüger, 2019).

Since human disturbance and predator pressure could impact habitat preferences, further studies in areas that differ in such conditions would be desirable. Due to strong competition for land in densely populated Central Europe (Fartmann et al., 2021), the implementation of large-scale habitat management is difficult to achieve and requires long-term approaches. Therefore, besides the development of suitable management measures at the mainland, the continuous protection of the few remaining refuges, such as the East Frisian Islands, should be given highest priority.

CRediT authorship contribution statement

Fartmann Thomas: Conceptualization, Funding acquisition, Supervision, Writing – review & editing, Methodology, Project administration. **Fumy Florian:** Formal analysis, Methodology, Writing – review & editing. **Kämpfer Steffen:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization, Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02758.

References

Agostinelli, C., Lund, U., 2017. R package 'circular': Circular Statistics (version 0.4–93). URL ⟨https://r-forge.r-project.org/projects/circular/⟩.

Amar, A., Redpath, S.M., 2005. Habitat use by Hen Harriers *Circus cyaneus* on Orkney: implications of land-use change for this declining population. Ibis 147, 37–47.

Andersson, M., Wallander, J., Isaksson, D., 2009. Predator perches: a visual search perspective. Funct. Ecol. 23, 373–379.

Andretzke, H., Oltmanns, B., 2016. What really helps breeding birds? Presentation and evaluation of protective measures in the National Park "Niedersächsisches Wattenmeer", exemplified by the East Frisian Island of Norderney. Vogelkundl. Ber. Niedersachs., 44: 195–215. (German with English abstract).

Baird, D., Asmus, R., 2020. ECSS Special Issue: Wadden Sea habitats: from single ecological interactions to holistic assessments of coastal habitats in the Wadden Sea. Estuar. Coast. Shelf Sci. 241, 106795.

Baker, J.A., Brooks, J., 1981. Distribution patterns of raptors in relation to density of meadow voles. Condor 83 (1), 42–47.

Barton, K., 2020. MuMIn: Multi-Model Inference: R Package. Version 1.43.17.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Bauer, M., 1999. Windverhältnisse an der niedersächsischen Nordseeküste. In: Nationalparkverwaltung Niedersächsisches Wattenmeer, Umweltbundesamt: Umweltatlas Wattenmeer. Wattenmeer zwischen Elb-. und Emsmündung. Stuttgart (Hohenheim): Ulmer.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird Census Techniques, 2nd edn. Academic Press, London.

BirdLife International, 2004. Birds in. Europe: Population Estimates, Trends and Conservation Status. BirdLife International, Cambridge.

BirdLife International, 2021. Asio flammeus. The IUCN Red List of Threatened Species 2021: e.T22689531A202226582. https://dx.doi.org/10.2305/IUCN.UK.20213.RLTS. T22689531A202226582.en Accessed on 24 July 2023.

Bonari, G., Fajmon, K., Malenovský, I., Zelený, D., Holuša, J., Jongepierová, I., Kočárek, P., Konvička, O., Uřičář, J., Chytrý, M., 2017. Management of semi-natural grasslands benefiting both plant and insect diversity: the importance of heterogeneity and tradition. Agric. Ecosys. Environ. 246, 243–252. https://doi.org/10.1016/j.agee.2017.06.010.

Booms, T.L., Holroyd, G.L., Gahbauer, M.A., Trefry, H.E., Wiggins, D.A., Holt, D.W., Johnson, J.A., Lewis, S.B., Larson, M.D., Keyes, K.L., Swengel, S., 2014. Assessing the status and conservation priorities of the Short-eared owl in North America. J. Wildl. Manag. 78 (5), 772–778. https://doi.org/10.1002/jwmg.719.

Border, J.A., Calladine, J., 2021. Sensitivities to land use change by breeding Short-eared owl (*Asio flammeus*) in Britain. Airo 29, 54–65.

Borgmann, K.L., Conway, C.J., 2015. The nest-concealment hypothesis: new insights from a comparative analysis. Wilson J. Ornithol. 127, 646–660.

, 2020Bos, J., Schaub, T., Klaassen, R., Kuiper, M. (Eds.), 2020. Book of abstracts. International Hen Harrier and Short-eared owl meeting 2019. Groningen, The Netherlands.

Bürger, M., 2003. Bodennahe Windverhältnisse und windrelevante Reliefstrukturen. Nationalatlas Bundesrepublik Deutschland, pp. 52–55.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York.

Calladine, J., du Feu, C., du Feu, R., 2012. Changing migration patterns of the Short-eared owl *Asio flammeus* in Europe: an analysis of ringing recoveries. J. Ornithol. 153, 691–698.

Calladine, J., Garner, G., Wernham, C., Buxton, N., 2010. Variation in the diurnal activity of breeding Short-eared Owls *Asio flammeus*: implications for their survey and monitoring. Bird. Study 57, 89–99.

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibík, J., Ujházy, K., Axmanová, I., Bernátová, D., Blanár, D., Dančák, M., Dřevojan, P., Fajmon, K., Galvánek, D., Hájková, P., Herben, T., Hrivnák, R., Janeček, S., Janišová, M., Jiráská, Š., Kliment, J., Kochjarová, J., Lepš, J., Leskovjanská, A., Merunková, K., Mládek, J., Slezák, M., Šeffer, J., Šefferová, V., Škodová, I., Uhlířová, J., Ujházyová, M., Vymazalová, M., 2015. The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). Preslia 87, 217–278 (with new world records). Preslia.

Development Core Team, R, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Devereux, C.L., Mckeever, C.U., Benton, T.G., Whittingham, M.J., 2004. The effect of sward height and drainage on Common Starlings *Sturnus vulgaris* and Northern Lapwings *Vanellus vanellus* foraging in grassland habitats. Ibis 146, 115–122.

Donald, P.F., Sanderson, F.J., Burfield, I.J., Van Bommel, I.J., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agr. Ecosyst. Environ. 116, 189–196.

Donázar, J.A., Naveso, M.A., Tella, J.L., Campión, D., 1997. Extensive grazing and raptors in Spain. In: Pain, D.J., Pienkowski, M.W. (Eds.), Farming and birds in Europe: The Common Agricultural Policy and its implications for bird conservation. Acad. Press, San Diego.

Dudley, N. (Ed.), 2013. Guidelines for applying protected area management categories including IUCN WCPA best practice guidance on recognising protected areas and assigning management categories and governance types. IUCN (Best practice protected area guidelines series, 21), Gland.

DWD (Deutscher Wetterdienst), 2020. Cliamte data Germany – monthly and daily values. Available under: https://www.dwd.de/DE/leistungen/klimadatendeutschland/klarchivtagmonat.html?nn=16102 (accessed 08 August 2020).

EC (European Commission), 2019. Eurostat – Land Cover/use Statistics (LUCAS). https://ec.europa.eu/eurostat/web/lucas/links. (Accessed 22 November 2018).

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen. 6th. Eugen Ulmer, Stuttgart.

Fartmann, T., 2024. Insect Conservation in Grasslands. In: Pryke, J., Samways, M.J., New, T., Cardoso, P., Gaigher, R. (Eds.), Routledge Handbook of Insect Conservation. Routledge, London.

Fartmann, T., Jedicke, E., Streitberger, M., Stuhldreher, G., 2021. Insektensterben in Mitteleuropa. Ursachen und Gegenmaßnahmen. Eugen Ulmer, Stuttgart.

Fartmann, T., Drung, M., Henning, O., Löffler, F., Brüggeshemke, J., 2022. Breeding-bird assemblages of calcareous grasslands and heathlands provide evidence for Common juniper (*Juniperus communis*) as a keystone species. Glob. Ecol. Conserv 40, e02315. https://doi.org/10.1016/j.gecco.2022.e02315.

Fernández-Bellon, D., Lusby, J., Bos, J., Schaub, T., McCarthy, A., Caravaggi, A., Irwin, S., O'Halloran, J., 2020. Expert knowledge assessment of threats and conservation strategies for breeding Hen Harrier and Short-eared owl across Europe. Bird. Conserv. Int 31 (2), 1–18. https://doi.org/10.1017/S0959270920000349.

Feurdean, A., Ruprecht, E., Molnár, Z., Hutchinson, S.M., Hickler, T., 2018. Biodiversity-rich European grasslands: ancient, forgotten ecosystems. Biol. Conserv. 228, 224–232. https://doi.org/10.1016/j.biocon.2018.09.022.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv 24, 38–49 doi.org/10. 1017/S0376892997000088.

Filliater, T.S., Breitwisch, R., Nealen, P.M., 1994. Predation on Northern Cardinal nests: does choice of nest site matter? Condor 96, 761–768.

Flávio, H., Baktoft, H., 2020. actel: Standardised analysis of acoustic telemetry data from animals moving through receiver arrays. Methods Ecol. Evol. 12, 192–203. https://doi.org/10.1111/2041-210X.13503.

Fondell, T.F., Ball, I.J., 2004. Density and success of bird nests relative to grazing on western Montana grasslands. Biol. Conserv. 117 (2), 203–213. https://doi.org/10.1016/S0006-3207(03)00293-3.

Fuller, R.J. (Ed.), 2013. Birds and Habitat: Relationships in Changing Landscapes. Cambridge University Press, Cambridge, New York.

Fumy, F., Fartmann, T., 2021. Climate and land-use change drive habitat loss in a mountain bird species. Ibis 163 (4), 1189–1206. https://doi.org/10.1111/ibi.12954.

Gahbauer, M.A., Miller, R.A., Paprocki, N., Morici, A., Smith, A.C., Wiggins, D.A., 2021a. Status and monitoring of Short-eared owls (*Asio flammeus*) in North and South America. Airo 29, 115–142.

Gahbauer, M.A., Booms, T.L., Novak, P.G., Schlesinger, M.D., Takats-Priestley, L., Keyes, K.L., 2021b. Movements and habitat selection of Short-eared owls (*Asio flammeus*) in North America. Airo 29, 95–114.

Gedeon, K., Grüneberg, C., Mitschke, A., Sudfeldt, C. (Eds.), 2014. Atlas Deutscher Brutvogelarten. Atlas of German breeding birds. Stiftung Vogelmonitoring Deutschland, Dachverband Deutscher Avifaunisten, Münster.

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84 (11), 2809–2815. https://doi.org/10.1890/02-3114.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evolution. Biol 24, 699–711.

Hardey, J., Crick, H., Wernham, C., Riley, H., Etheridge, B., Thompson, D., 2013. Raptors: A field guide for surveys and monitoring, Third edition. TSO.

Hartig, F. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6 2022.

Heenan, C.B., 2013. An Overview of the factors influencing the morphology and thermal properties of avian nests. Avian Biol. Res 6 (2), 104–118. https://doi.org/10.3184/003685013X13614670646299.

Heldbjerg, H., Sunde, P., Fox, A.D., 2018. Continuous population declines for specialist farmland birds 1987–2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. Bird. Conserv. Int. 28, 278–292. https://doi.org/10.1017/S0959270916000654.

Holmes, G.I., Koloski, L., Nol, E., 2020. Nest-site selection of a subarctic-breeding shorebird: evidence for tree avoidance without fitness consequences. Can. J. Zool. 98 (9), 573–580.

Holt, D.W., 1992. Notes on Short-eared owl, *Asio flammeus*, nest sites, reproduction, and territory sizes in coastal Massachusetts. Can. Field-Nat. 106 (3), 352–356.

Huang, K., Gauthier, P., Karpik, J., 2010. Short-eared owl (*Asio flammeus*) and Townsend's Vole (*Microtus townsendii*) Dynamics in grassland Set-asides. Fish, Wildlife & Recreation; British Columbia Institute of Technology.

Jödicke, K., Lemke, H., 2020. Sumpfohreule (*Asio flammeus*) 2019 in Dithmarschen. EulenWelt 2020, 31–38.

Kamp, J., Frank, C., Trautmann, S., Busch, M., Dröschmeister, R., Flade, M., Gerlach, B., Karthäuser, J., Kunz, F., Mitschke, A., Schwarz, J., Sudfeldt, C., 2021. Population trends of common breeding birds in Germany 1990–2018. J. Ornithol. 162 (1), 1–15. https://doi.org/10.1007/s10336-020-01830-4.

Kämpfer, S., Fartmann, T., 2019b. Breeding populations of a declining farmland bird are dependent on a burrowing, herbivorous ecosystem engineer. Ecol. Eng. 140, 105592 https://doi.org/10.1016/j.ecoleng.2019.105592.

Kämpfer, S., Fartmann, T., 2022. Natural coastal dunes on Wadden Sea islands as a refuge for an endangered wader species. J. Coast. Conserv. 26, 53 https://doi.org/10.1007/s11852-022-00897-w.

Kämpfer, S., Engel, E., Fartmann, T., 2022. Weather conditions determine reproductive success of a ground-nesting bird of prey in natural dune grasslands. J. Ornithol. 163, 855–865. https://doi.org/10.1007/s10336-022-01999-w.

Kämpfer, S., Löffler, F., Brüggeshemke, J., Fartmann, T., 2022. Untangling the role of a novel agro-ecosystem as a habitat for declining farmland birds. Ann. Appl. Biol. 181, 367–378. https://doi.org/10.1111/aab.12789.

Kämpfer, S., Fartmann, T.2019b Status and trend of the Short-eared owl in Germany. In: Bos, J., Schaub, T., Klaassen, R. and Kuiper, M. eds. Book of abstracts. International Hen Harrier and Short-eared owl meeting 2019. Groningen, The Netherlands.

Kämpfer, S., Engel, E., Hirschberg, M., Klock, M., Fartmann, T.2019a Breeding and feeding ecology of the Short-eared owl on the East Frisian Islands (NW Germany). In: Bos, J., Schaub, T., Klaassen, R. and Kuiper, M. eds. Book of abstracts. International Hen Harrier and Short-eared owl meeting 2019. Groningen, The Netherlands.

Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M.V., Bauer, H.-G., Foppen, R.P.B. (2020) European Breeding Bird Atlas 2: Distribution, Abundance and Change. European Bird Census Council & Lynx Edicions, Barcelona.

Keyes, K.L., Gahbauer, M.A., Bird, D.M., 2016. Aspects of the breeding ecology of Short-eared owls (*Asio flammeus*) on Amherst and Wolfe Islands. East. Ont. J. Raptor Res 50 (1), 121–124. https://doi.org/10.3356/rapt-50-01-121-124.1.

Korpimäki, E., Norrdahl, K., 1991. Numerical and functional responses of kestrels, Short-eared Owls, and long-eared owls to vole densities. Ecology 72, 814–826. https://doi.org/10.2307/1940584.

Krüger, T., 2019. Sumpfohreulen *Asio flammeus* als Brutvögel in Mähwiesen: Gefährdung und Schutz. Vogelwelt 139, 183–201.

Marques, A.T., Moreira, F., Alcazar, R., Delgado, A., Godinho, C., Sampaio, H., Rocha, P., Sequeira, N., Palmeirim, J.M., Silva, J.P., 2020. Changes in grassland management and linear infrastructures associated to the decline of an endangered bird population. Sci. Rep. 10, 15150.

Miller, R.A., Buchanan, J.B., Pope, T.L., Carlisle, J.D., Moulton, C.E., Booms, T.L., 2022. Short-Eared Owl land-use associations during the breeding season in the Western United States. J. Raptor Res. 56 (3), 273–286. https://doi.org/10.3356/JRR-21-19.

Miller, V., Nol, E., Nguyen, L.P., Turner, D.M., 2014. Habitat selection and nest success of the Upland Sandpiper (*Bartramia longicauda*) in Ivvavik National Park, Yukon, Canada. Can. Field-Nat. 128 (4), 341–349.

Møller, A.P., Thorup, O., Laursen, K., 2018. Predation and nutrients drive population declines in breeding waders. Ecol. Appl. 28 (5), 1292–1301.

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14: 1–11. dx. https://doi.org/10.1098/rsif.2017.0213.

Newton, I., 2017. Farming and birds. The New Naturalist Library, Harper Collins. Publishers, London.

Niedringhaus, R., Haseler, V., Janisch, P. (Eds.), 2008. Die Flora und Fauna der Ostfriesischen Inseln – Artenverzeichnisse und Auswertungen zur Biodiversität. 2. Aufl., 11. Schriftenr. Nationalp. Niedersächs. Wattenmeer, pp. 9–34.

Petersen, J., Pott, R., 2005. Ostfriesische Inseln. Landschaft und Vegetation im Wandel. Schrift. Heimatpfl. Niedersächs. Heimatb 15, 1–160.

Petersen, J., Kers, B., Stock, M., 2014. TMAP-Typology of Coastal Vegetation in the Wadden Sea Area. Common Wadden Sea Secretariat (CWSS), Wilhelmshaven.

Roos, S., Smart, J., Gibbons, D.W., Wilson, J.D., 2018. A review of predation as a limiting factor for bird populations in mesopredator-rich landscapes: a case study of the UK. Biol. Rev. 93 (4), 1915–1937. https://doi.org/10.1111/brv.12426.

Ryslavy, T., Bauer, H.-G., Gerlach, B., Hüppop, O., Stahmer, J., Südbeck, P., Sudfeldt, C., 2020. Rote Liste der Brutvögel Deutschlands – 6. Fassung, 30. September 2020. Berichte zum Vogelschutz 57, 13–112.

Silverman, B.W., 1986. Density Estimation for Statistics and Data Analysis. Chapman and Hall, New York.

Smith, A.C., Hudson, M.-A.R., Aponte, V., Francis, C.M., 2019. North American Breeding Bird Survey – Canadian Trends Website, Data-version 2017. Environment and Climate Change Canada, Gatineau, Quebec. K1A 0H3.

Smith, P.A., Edwards, D.B., 2018. Deceptive nest defence in ground-nesting birds and the risk of intermediate strategies, 10): e0205236 PLoS One 8 (13). https://doi.org/10.1371/journal.pone.0205236.

Südbeck, P., Andretzke, H., Fischer, S., Gedeon, K., Schikore, T., Schröder, K., Sudfeldt, C., 2005. Methodenstandards zur Erfassung der Brutvögel Deutschlands. Dachverband Deutscher Avifaunisten, Radolfzell.

Swengel, S.R., Swengel, A.B., 2014. Short-eared Owl abundance and conservation recommendations in relation to site and vegetative characteristics, with notes on Northern Harriers. Passenger Pigeon 76, 51–68.

Toland, B.J., 1987. The effect of vegetative cover on foraging strategies, hunting success and nesting distribution of American kestrels in central Missouri. J. Raptor Res. 21 (1), 14–20.

Tucker, G., Heath, M., Tomialojc, L., Grimmet, R., Socha, C.M., 1994. Birds in Europe: Their Conservation Status. BirdLife International,, Cambridge.

Veen, P., Jefferson, R., Smidt, J., de, Straaten, J. van der, 2009. Grasslands in Europe of High Nature Value. Koninklijke Nederlandse Natuurhistorische Vereniging Stichting Uitgeverij. Boston 1320.

Wiebe, K.L., Martin, K., 1998. Costs and benefits of nest cover for ptarmigan: changes within and between years. Anim. Behav. 56 (5), 1137–1144.

Wiggins, D., 2004. Short-eared owl (*Asio flammeus*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. Available: ⟨https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5182042.pdf⟩ (accessed 01 Oktober 2021).

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1 (1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.