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RESEARCH ARTICLE

Peat extraction sites providing cavities and large areas of open soil favour a threatened songbird

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Abstract

1. The northern wheatear (*Oenanthe oenanthe*) is a songbird that is considered threatened with extinction in both the German federal state of Lower Saxony and Germany. Today, in the mainland of Lower Saxony (NW Germany), industrial peat extraction sites are the most important breeding habitat for the species. However, our knowledge regarding the detailed habitat requirements of the northern wheatear in these mining sites is still scarce.
2. In this study, we aimed to identify the environmental drivers of nest site selection by the northern wheatear in its last distribution stronghold in the mainland of Lower Saxony. In three different raised bogs, where peat was still exploited and the northern wheatear was still breeding, we systematically surveyed wheatear nests and environmental parameters at 26 randomly selected plots with an area of 45 ha each.
3. Our study confirmed that peat extraction sites were an important breeding habitat for the northern wheatear. However, this was only true if they provided a combination of (i) regular availability of suitable cavities for nesting and (ii) vast open areas that guaranteed easy access to arthropod prey and increased detectability of potential predators. By far, the most important structures for nesting were the cavities within the rows of cross- and lengthwise stacked peat sods. The availability of large open areas was particularly ensured by regular milling of the peat.
4. *Practical implication*. Based on our findings, peat extraction sites used as a breeding habitat for the northern wheatear would benefit from a combination of sod cutting and peat milling to create both the required (i) nesting structures and (ii) open soil for foraging and early predator recognition. To avoid nest losses, re-stacking of peat sods is best carried out before the breeding season starts (until mid-April) and harvesting of the sods after the breeding season from the end of July onwards.

KEYWORDS
anthropogenic habitat, biodiversity conservation, farmland bird, land use change, northern wheatear (*Oenanthe oenanthe*), raised bog

1 | INTRODUCTION

Mire ecosystems are globally the main terrestrial carbon store and provide multiple other ecosystem services, such as climate regulation, water purification and storage (Loisel & Gallego-Sala, 2022; Rydin & Jeglum, 2013; Tanneberger et al., 2024). Moreover, they harbour many highly specialised and often threatened species (Guilfoyle et al., 2025; Krieger et al., 2019; Šigutová et al., 2025; Sushko & Novikova, 2024). The northern hemisphere holds by far the most mires with a global share of at least 80% (Rydin & Jeglum, 2013). Here, particularly in the temperate and boreal zone, a cool climate and relatively high precipitation had over millennia fostered the development of peat bogs (Bragg & Lindsay, 2003; Joosten & Clarke, 2002; Spitzer & Danks, 2006).

However, especially due to land use change, the area of mires has decreased dramatically. Across Europe, drainage of mires for agriculture, forestry and peat cutting started already in medieval times (van Dam, 2001), but the most severe losses occurred from the 1950s onwards (European Commission (EC), 2007). Particularly in Central Europe, the decrease has been dramatic; here, only 1% of the previous area of peat-accumulating mires has remained (Succow & Joosten, 2001). In Germany, today, 80% of the original mires are used for agriculture (DGMT—Deutsche Gesellschaft für Moor- und Torfkunde e.V, 2016) and 8% for peat mining (Deutscher Bundestag, 2016). Consequently, these mires now emit carbon and no longer fulfil their original ecosystem services.

In Germany, peat is mined in drained mires either with (arable land or grassland) or without previous agricultural use (Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (NLWKN), 2006). This peat is nowadays exclusively used to produce potting soil (Deutscher Bundestag, 2016). In 2040, peat mining is estimated to end in the federal state of Lower Saxony, which is the last stronghold of peat extraction in Germany (Hirschler & Thrän, 2023). After cessation of peat extraction, mire ecosystems have to be restored (NLWKN, 2006). To ensure successful mire restoration, mining must be stopped when a minimum thickness of 0.5 m of the raised bog peat layer has been reached. Then the drainage ditches are blocked to raise the water level and to foster the regrowth of peat mosses and the colonisation of characteristic bog species in general on the former extraction sites.

Birds are highly sensitive indicators of environmental change (Gregory & van Strien, 2010; Newton, 2017). The northern wheatear (*Oenanthe oenanthe*) is a songbird of very open habitats with short and sparse vegetation, which additionally exhibit cavities for nesting (Conder, 1989; Cramp, 1988; Kämpfer & Fartmann, 2019; Suter, 1988; Figure 1). Due to the severe loss of such habitats in our landscapes, the species has strongly declined in recent decades (Gedeon et al., 2014; Kämpfer & Fartmann, 2019). Consequently, it is today considered threatened with extinction in Lower Saxony (Krüger & Sandkühler, 2022) and in Germany (Ryslavy et al., 2020). Nowadays, in the mainland of Lower Saxony, industrial peat extraction sites are the most important habitat of the species (Blüml & Schönheim, 2006). However, our knowledge regarding the detailed habitat requirements of the northern wheatear in peat extraction sites is still scarce.

FIGURE 1 Male northern wheatear (*Oenanthe oenanthe*). Photo credit: Thomas Fartmann.

In this study, we aimed to identify the environmental drivers of nest site selection of the northern wheatear in its last distribution stronghold in the mainland of Lower Saxony (NW Germany). In three different raised bogs, where peat was still exploited and the northern wheatear was still breeding, we systematically surveyed wheatear nests and environmental parameters at 26 randomly selected plots with an area of 45 ha each. Statistical analyses were conducted at four spatial scales (plot, home range, territory and nest site). Based on our findings, we make recommendations for the management of wheatear habitats.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located in the south-western part of the German federal state of Lower Saxony (NW Germany, Figure 2). It is characterised by a suboceanic climate. From the west to the east, mean annual temperature increases from 9.3 to 9.6°C and mean annual precipitation decreases from 862 mm to 661 mm (meteorological stations: west—Alfhausen; east—Hannover airport; long-term mean 1981–2010; Deutscher Wetterdienst (DWD), 2018). After the last ice age, the humid climatic conditions and the mostly smooth relief have resulted in a large scale development of bog ecosystems (Grosse-Brauckmann, 1997). Within the study area, three different raised bogs, where peat was still exploited, were studied: Campemoor, Uchter Moor and Totes Moor (Figure 2). The Campemoor in the west of the study area was mainly used for agriculture and peat extraction (own observation). Here, peat exploitation mainly took place on former agricultural land. Extraction intensity was fairly high with frequent milling of the uppermost peat layer. The Uchter Moor is located about 40 km further east. In contrast to the former, agriculture played only a minor role here. Hence, peat extraction mainly occurred on drained bogs that had

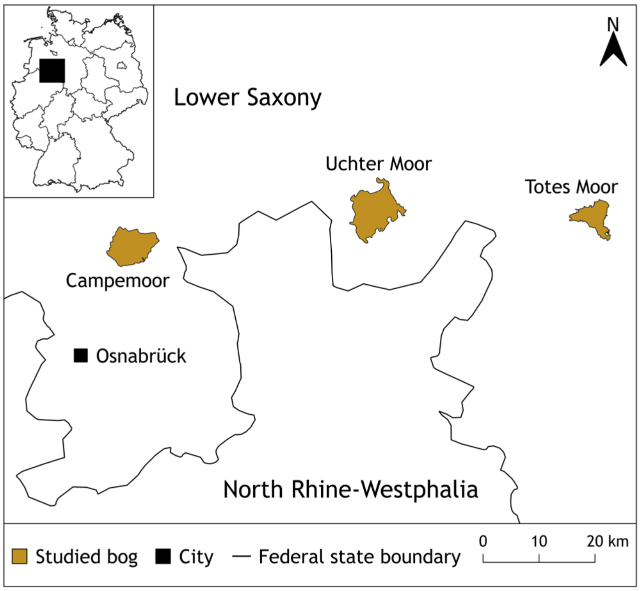

FIGURE 2 Location of the study area and the three studied raised bogs in Germany. Delimitation of the bogs is based on a peat layer of ≥30 cm (source: Niedersächsisches Ministerium für Umwelt, Energie, Bauen und Klimaschutz (NMUEBK), 2018).

never been used for farming. The peat layer was rarely milled and the overall intensity of peat exploitation was comparatively low. As a result, later successional stages dominated, including scrubland and forest. The Totes Moor is situated another 35 km east. Although the area of intensive peat extraction was pretty large, there were also patches that exhibited a slightly lower exploitation intensity. The main difference compared to the other two bogs was the larger grassland area. Consequently, a considerable proportion of the extraction sites were former grasslands.

Access to the study sites was granted by the nature conservation authorities of the counties of Osnabrück, Vechta and Nienburg and the Hannover Region, as well as by the respective peat extraction companies. The study involved non-invasive observational fieldwork only and required no additional permits.

2.2 | Peat extraction procedure

The peat is mined in drained mires either with (arable land or grassland) or without previous agricultural use (NLWKN, 2006). For peat extraction on former agricultural land, the top soil is removed to reduce the surface's nutrient content and the risk of weed contamination (pers. com. L. Große Holthaus, peat plant Warmsen). Two different methods are applied for peat extraction: (i) peat milling and (ii) peat cutting (pers. com. L. Große Holthaus, peat plant Warmsen). In the former procedure, a milling machine mills the uppermost centimetres of the peat layer. After the peat has dried, a peat hoover suctions the milled peat. In the latter procedure, peat sods are cut along a drainage ditch and stacked next to the ditch. Initially, the peat sods are tightly stacked to rows with a length of up to 500 m or more (Figure 3a). At this stage, they usually rarely provide cavities that could potentially be used for breeding by the northern wheatear. The tightly stacked peat sods remain at the extraction site over winter. This allows an initial coarse drying and freezing. Freezing modifies the structure of the peat, resulting in better air ventilation and higher water capacity. After winter, the sods are re-stacked in order to create cavities that accelerate further drying of the peat sods. Sometimes there is a second re-stacking and drying process. When the desired dryness is achieved—the time depends on weather conditions—the sods are harvested. Two different re-stacking methods are applied. In the first one, all sods are stacked loose crosswise to the cutting ditch. As a result, tunnels are created that are open to two sides (Figure 3b). However, cavities for breeding are usually lacking. In the second method, the peat sods are stacked cross- and lengthwise to the cutting ditch (Figure 3c). Consequently, a complex labyrinth of cavities with many hidden chambers appears. The area between the rows of stacked peat sods is either used for peat milling or is left fallow, so that vegetation develops.

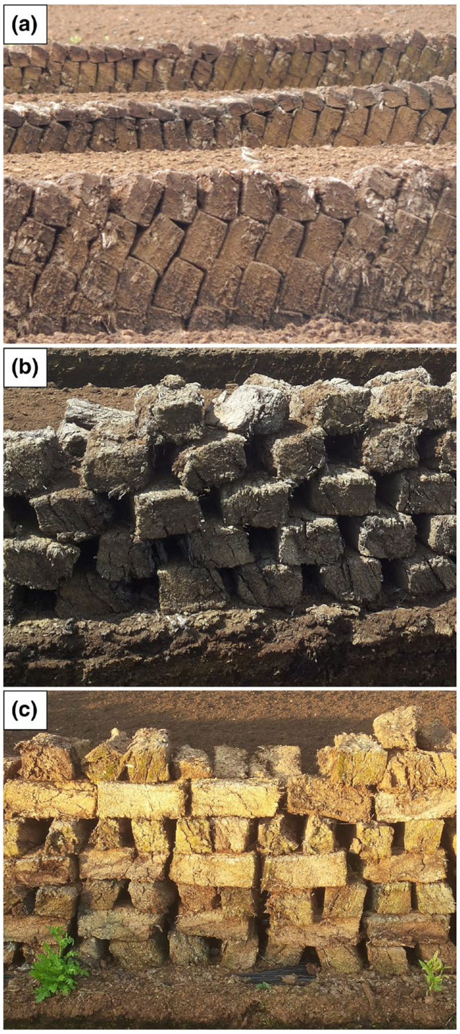

FIGURE 3 The three different peat stacking methods performed in the study area: Tightly stacked peat sods (a), crosswise stacked peat sods—all point to the cutting ditch (b) and cross- and lengthwise stacked peat sods (c).

2.3 | Study species

The northern wheatear (*Oenanthe oenanthe*) is an insectivorous breeding bird of the Palearctic and N/NW Nearctic (Gedeon et al., 2014; Suter, 1988). As a long-distance migrant, birds of all breeding populations overwinter in sub-Saharan savannahs in Africa. For territory establishment, very open habitats with short and sparse vegetation are used (Cramp, 1988; Kämpfer & Fartmann, 2019; Suter, 1988). For nesting, the species relies on burrows, clearance cairns, crevices, walls or other cavities. In the Central European lowland, breeding northern wheatears mainly occur in man-made habitats, for instance clear-cuts, military training areas, surface-mining areas and vineyards (Bauer et al., 2012). In Lower Saxony, however, industrial peat extraction sites are the most important anthropogenic habitat of the species (Blüml & Schönheim, 2006). The current population of the northern wheatear in this federal state is estimated to be 420 breeding pairs (Krüger & Sandkühler, 2022). Due to severe declines in recent decades, the species is today considered threatened with extinction in both Lower Saxony (Krüger & Sandkühler, 2022) and Germany (Ryslavy et al., 2020).

2.4 | Sampling design

2.4.1 | Environmental parameters

Environmental parameters were analysed at four spatial scales, grouped into a broader plot scale and a finer habitat scale (home range, territory and nest site).

Plot scale

At the plot scale, we randomly selected 26 quadratic plots with an area of 45 ha in the three bogs using the tool create random points in ArcGIS 10.2.2 (ESRI Inc.). Each plot contained at least 25% potential northern wheatear breeding habitat, which was defined as peat extraction sites with stacks of peat sods (cf. Blüml & Schönheim, 2006). The plots covered all potential breeding habitats within the three studied bogs. Its number corresponded to the total area of potential breeding habitat per bog (Campemoor: $n=11$, Uchter Moor: $n=8$, Totes Moor: $n=7$). Habitat composition of each plot was mapped according to von Drachenfels (2016) and digitised using ArcGIS 10.2.2 (ESRI Inc.). Former land use has strong effects on the nutrient content of the peat (cf. Krieger et al., 2019). Accordingly, peat extraction sites were distinguished into those that were formerly used as arable land, grassland or had never been managed for farming. The former was the most nutrient-rich, which favoured the establishment of vegetation (own observation). Consequently, intensive measures to remove vegetation were applied, such as mechanical removal of the vegetation in the cutting ditches, mowing of vegetated peat, herbicide application and more regular peat milling between the rows of stacked peat sods. Furthermore, we differentiated the area between the stacks of peat sods into those that were (i) still regularly milled and therefore exhibited much bare ground (vegetation cover: <2.5%) and those that were no longer milled and had a (ii) low vegetation cover (2.5%–30%; ruderal peat extraction site) or (iii) high vegetation cover (>30%; overgrown peat extraction site). Additionally, the cover of cutting ditches and stacks of peat sods was quantified. The latter was subdivided into the following three types: Tightly stacked ones (Figure 3a), those that were re-stacked loose crosswise to the cutting ditch (Figure 3b) and those that were re-stacked cross- and lengthwise to the cutting ditch (Figure 3c) (see Section 2.2).

Habitat scale (home range, territory, nest site)

At the habitat scale, all environmental parameters were analysed in radii of 80 m (home range; 2 ha), 40 m (territory; 0.5 ha) and 5 m (nest site; 78.5 m^2) around each wheatear nest and around the same number of random control points (Berg, 2008; Suter, 1988). Control points were selected by using the tool create random points in ArcGIS 10.2.2 (ESRI Inc.). Moreover, the distance between nests or control points and the next forest, tree, path and building was ascertained. For all spatial analyses we used ArcGIS 10.2.2 (ESRI Inc.). To avoid any disturbance, all environmental parameters were collected after the young birds had left the nest.

2.4.2 | Bird surveys

From the beginning of May until the end of June 2017, we searched for northern wheatear nests in all 26 plots by observing adults carrying food (Südbeck et al., 2005). Surveys started at sunrise and ended before sunset. Per plot, four surveys were conducted with a distance of at least 7 days between each visit. Each survey started from a different point, moving in loops through the plot with an overview of 100 m to both sides.

2.5 | Statistical analysis

All statistical analyses were performed using R 4.3.2. (R Development Core Team, 2025). For statistical comparisons between two or more groups, we used generalised linear mixed-effects models (GLMMs). To account for potential spatial autocorrelation, 'bog' was set as a random factor. Furthermore, we calculated Moran's *I* using the R package lctools to test for spatial autocorrelation in model residuals (Kalogirou, 2020). To assess the influence of previous land use of the peat extraction sites on nest site selection, we calculated Jacobs index: $D=(r-p)/(r+p-2rp)$, where r is the proportion of nests on peat extraction sites with a certain previous land use and p the overall proportion of peat extraction sites with this previous land use in the study area (Jacobs, 1974).

We compared environmental parameters on different spatial scales (occupied vs. unoccupied plots, home range vs. control, territory vs. control, nest site vs. control; binomial error structure) by

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using univariable GLMMs. For pairwise comparisons we applied Tukey contrasts (glht function, R package multcomp; Hothorn et al., 2021). We reduced overdispersion (>3) within the models by adding observation level random effects (Harrison, 2014, 2015).

We further performed multivariable GLMMs to detect environmental parameters that explain plot occupancy and the number of nests per occupied plot, as well as the selection of home ranges, territories and nest sites (binomial error structure, except for the number of nests per occupied plot: Poisson error structure) (Crawley, 2007). We excluded intercorrelated variables from multivariable analysis (Spearman rank correlation $|r_s|>0.6$) to avoid multicollinearity (Graham, 2003; Table A1).

In order to increase model robustness and identify the most important environmental parameters, we performed model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al., 2011). We conducted model averaging using the dredge function (R package MuMIn; Bartón, 2016) and included only top-ranked models within $\Delta AIC_C <3$ (cf. Grueber et al., 2011). For all top-ranked models, we calculated the range of conditional R^2 (variance explained by fixed effects; $R^2{}_c$) and marginal R^2 (variance explained by both fixed and random effects; $R^2{}_m$; Nakagawa et al., 2017). To compare the effect size, significant predictors were centred and scaled (cf. Kämpfer et al., 2023).

3 | RESULTS

Overall, 13 plots were occupied and 13 unoccupied by the northern wheatear. In the occupied plots, we detected a total of 28 breeding pairs (nests). Mean (±SE) density in the occupied plots varied between the three bogs from 0.22 ± 0.00 (Totes Moor) to 0.57 ± 0.13 (Campemoor) nests per 10 ha. The average density across all occupied plots was 0.48 ± 0.10 nests per 10 ha. The vast majority of nests (20; 71.4%) were found in cross- and lengthwise stacked peat sods. The rest was located in tightly stacked peat sods (8; 28.6%). However, all nests found in this type of peat sods had been created by one particular company (Gramoflor). They used a different cutting machine that created slightly larger gaps between the sods every few meters and thus potential cavities for breeding.

On average, more than 60% of the plots were covered by different types of peat extraction sites (Table 1). Those that were formerly used as grassland were common in both occupied and unoccupied ones. In contrast, occupied plots were dominated by peat extraction sites that were formerly used as arable land and unoccupied ones by those that had never been used for farming. In general, plots with a larger area of arable land and grassland were preferred and those that had a larger area of scrubland and forest were avoided for nesting. The area of arable land was positively correlated with peat extraction sites that were used in the past for arable farming (Table A1). The area of grassland was positively correlated with peat extraction sites that were formerly used as grassland and negatively with peat extraction sites that had never been used for agriculture.

TABLE 1 Mean (±SE) area (ha) of habitat types in occupied ($n=13$) and unoccupied ($n=13$) plots (45 ha).

Parameters	Occupied	Unoccupied	p
Peat extraction site			
Former land use			
Arable land	12.8 ± 4.2	4.0 ± 2.7	n.s.
Grassland	11.5 ± 4.1	10.4 ± 4.0	n.s.
Bog	3.8 ± 2.6	13.3 ± 4.1	n.s.
Restored peatland	3.9 ± 1.2	3.8 ± 1.2	n.s.
Agricultural land			
Arable land	2.3 ± 0.7	1.4 ± 1.3	**
Grassland	4.2 ± 1.5	1.8 ± 0.6	**
Scrubland	0.1 ± 0.1	2.0 ± 0.8	*
Hedge and tree line	1.2 ± 0.2	0.8 ± 0.2	n.s.
Forest	4.0 ± 1.5	7.0 ± 2.0	***
Path	0.6 ± 0.1	0.3 ± 0.1	n.s.
Other habitat types[a]	0.6 ± 0.3	0.2 ± 0.1	n.s.

Note: Statistical comparisons between occupied and unoccupied plots were done by generalised linear mixed-effects models (GLMMs). For further information, see Section 2.5. Statistical significances are indicated as follows: n.s. = not significant; $*p \le 0.05$, $**p \le 0.01$, $***p \le 0.001$.

[a]Building, heathland.

In the multivariable GLMM, none of the variables explained plot occupancy (Table 2). By contrast, nest densities in occupied plots increased with the area of peat extraction sites that were formerly used as arable land.

Milled peat extraction sites were the dominant habitat type in both the home range and territory. On average, they covered 70% and 80%, respectively. Overall, the differences between home range and territory, respectively, and control were very weak (Table 3). Solely, the area of ditches was lower in the home range than in the controls. By contrast, the multivariable GLMMs revealed that in the home range milled peat extraction sites as well as cross- and lengthwise stacked peat sod were preferred, whereas forests and cutting ditches were avoided (Figure 4). Moreover, within the territories, milled peat extraction sites, ruderal peat extraction sites and cross- and lengthwise stacked peat sods were preferred.

Open soil covered more than 70% of the close vicinity around the nest and its area was larger than in the controls (Table 4). In addition, nests were located further away from forests than the controls were. The multivariable GLMM revealed that larger areas of open soil as well as cross- and lengthwise stacked peat sods favoured the probability of nesting (Figure 4). Furthermore, previous land use had a strong effect on nest site selection (Figure 5). Although the availability of peat extraction sites that were formerly used as arable land, grassland or had never been used for farming was roughly the same, more than two-thirds of all nests were found on sites that were previously used as arable land (Figure 5A). The clear preference for former arable land and avoidance of former grasslands and bogs without any land use is also reflected by the Jacobs index (Figure 5B).

TABLE 2 Model-averaging results (GLMM): Relationship between occupancy (binomial response variable) and number of nests per occupied plot (Poisson response variable), respectively, of northern wheatear and environmental predictors at different spatial scales (plots, occupied plots, home range, territory and nest site).

Parameter	Estimate	SE	*z*	*p*
(a) Plot occupancy (R^2_m = 0.00–0.19, R^2_c = 0.13–0.23; Moran's *I*: 0.03, n.s.)				
(Intercept)	−0.09	0.63	0.13	n.s.
Former bog	−0.80	0.60	1.26	n.s.
Former arable land	0.68	0.50	1.31	n.s.
Forest	−0.23	0.48	0.46	n.s.
Restored peatland	0.03	0.44	0.06	n.s.
(b) No. nests per occupied plot (R^2_m = 0.00–0.48, R^2_c = 0.20–0.48; Moran's *I*: −0.12, n.s.)				
(Intercept)	0.67	0.21	2.75	**
Former arable land	0.48	0.20	2.12	*
Restored peatland	0.33	0.19	1.47	n.s.
(c) Home range (R^2_m = 0.69–0.78, R^2_c = 0.69–0.78; Moran's *I*: 0.01, n.s.)				
(Intercept)	−0.36	0.50	0.71	n.s.
Peat cross−/lengthwise stacked	1.43	0.61	2.28	*
Cutting ditch	−1.45	0.51	2.76	**
Forest	−2.26	0.94	2.35	*
Milled peat extraction site	2.21	0.81	2.66	**
Ruderal peat extraction site	1.04	0.60	1.71	n.s.
Grassland	0.37	0.39	0.94	n.s.
Path	0.87	0.50	1.70	n.s.
Hedge and tree line	0.79	0.56	1.38	n.s.
(d) Territory (R^2_m = 0.38–0.47, R^2_c = 0.38–0.47; Moran's *I*: 0.06, n.s.)				
(Intercept)	−0.15	0.36	0.41	n.s.
Peat cross−/lengthwise stacked	1.22	0.45	2.63	**
Ruderal peat extraction site	0.99	0.44	2.21	*
Milled peat extraction site	1.78	0.56	3.08	**
Grassland	0.31	0.35	0.86	n.s.
Cutting ditch	−0.80	0.44	1.78	n.s.
Hedge and tree line	−0.56	0.45	1.23	n.s.
(e) Nest site (R^2_m = 0.41–0.59, R^2_c = 0.41–0.59; Moran's *I*: 0.02, n.s.)				
(Intercept)	−1.13	0.61	1.80	n.s.
Peat cross−/lengthwise stacked	0.24	0.11	2.09	*
Open soil	1.35	0.53	2.51	*
Cutting ditch	−0.65	0.61	1.05	n.s.
Distance forest	0.75	0.42	1.74	n.s.
Distance path	−0.86	0.45	1.85	n.s.
Distance tree	−0.30	0.37	0.81	n.s.
Distance building	−0.15	0.32	0.44	n.s.

Note: To make predictors effect sizes comparable we standardised them (centred and scaled). Model-averaged coefficients were derived from the top-ranked models ($\Delta AIC_C < 3$). For further information, see Section 2.5. Statistical significances are indicated as follows: n.s. = not significant; $^*p \leq 0.05$, $^{**}p \leq 0.01$.

4 | DISCUSSION

Our study confirmed that peat extraction sites were important breeding habitats for the northern wheatear. However, this was only true if they (i) exhibited rows of cross- and lengthwise stacked peat sods, (ii) contained large areas of milled peat extraction sites and (iii) had formerly been used as arable land.

Sufficient shelter against predators and adverse weather conditions is a key requirement for nest site selection in breeding birds (Fartmann et al., 2022; Götmark et al., 1995; Kämpfer et al., 2023). This is an

TABLE 3 Mean (±SE) area (m^2; except milled area: ha) of habitat types in northern wheatear ($n=28$) home ranges ($r=80$ m) and territories ($r=40$ m), respectively, and control sites of similar size ($n=28$).

Parameter	Home range	Control	*p*	Territory	Control	*p*
Peat-cutting site						
Peat sods						
Tightly stacked	226±54	434±118	n.s.	54±15	149±43	n.s.
Crosswise stacked	0±0	337±139	n.s.	0±0	90±37	n.s.
Cross−/lengthwise stacked	598±83	575±113	n.s.	188±28	144±31	n.s.
Peat sod pile	31±31	51±482	n.s.	20±20	0±0	n.s.
Cutting ditch	1023±87	1429±85	*	312±31	403±29	n.s.
Milled peat extraction site	1.4±0.1	0.7±0.1	n.s.	0.4±0.03	0.2±0.03	n.s.
Former peat extraction site						
Ruderal extraction site	1785±981	1811±871	n.s.	446±243	402±212	n.s.
Overgrown extraction site	1193±798	6312±1490	n.s.	311±216	1627±384	n.s.
Agricultural land						
Arable land	202±202	58±47	n.s.	17±17	0±0	n.s.
Grassland	381±122	444±210	n.s.	28±13	15±14	n.s.
Hedge and tree line	243±79	220±70	n.s.	8±7	38±20	n.s.
Forest	62±62	579±245	n.s.	3±3	6±6	n.s.
Path	234±61	99±41	n.s.	14±8	6±6	n.s.
Building	0±0	39±22	n.s.	0±0	0±0	n.s.
Water body	67±60	13±10	n.s.	0±0	0±0	n.s.

Note: Statistical comparisons between occupied and unoccupied plots were done by generalised linear mixed-effects models (GLMMs). For further information, see Section 2.5. Statistical significances are indicated as follows: n.s. = not significant; $^*p \leq 0.05$.

important reason why many bird species choose cavities for nesting (Fuller, 2012). The northern wheatear is such a cavity-breeding bird (Conder, 1989; Cramp, 1988; Suter, 1988). In our study, the species showed a strong preference for cross- and lengthwise stacked peat sods for nest site construction. The vast majority of nests (71%) were found in this type of peat sod. Moreover, in the multivariable GLMMs, cross- and lengthwise stacked peat sods were preferred at the home range, territory and nest scale. Morbach (1934) and Mildenberger (1943) had discovered that northern wheatears always establish their nests within hidden chambers in the cavities they use for breeding. In line with this, we detected no nests in peat sods that were stacked crosswise to the cutting ditch and, hence, were open to two sides. Notably, tightly packed peat sods were only used for nesting under certain circumstances. One company used, in comparison to the other ones, a different cutting machine that created slightly larger gaps between the sods every few meters and hence potential cavities for breeding. All nests detected in tightly packed peat sods occurred in these gaps.

The northern wheatear is a breeding bird of very open habitats with short and sparse vegetation (Cramp, 1988; Kämpfer & Fartmann, 2019; Suter, 1988). In line with this, both the home range and territory were dominated by milled peat extraction sites (cover: 70% and 80%, respectively). The multivariable GLMMs showed that milled peat extraction sites were preferred within the home range and territories. Moreover, in the territories, ruderal peat extraction sites, which had a cover of bare ground of at least 70%, were also preferred. In the vicinity of the nests the conditions were also very similar. More than 70% was covered by open soil and in the multivariable GLMM open soil was detected as a predictor of nest site selection. Additionally, occupied plots had a lower cover of scrubland and forest than unoccupied plots. Furthermore, the multivariable GLMM revealed that in the home range forests and cutting ditches were avoided. The latter were characterised by taller vegetation due to higher humidity and less regular management (own observation). Wheatears are morphologically adapted to foraging on the ground and thus require very short swards or bare ground (Brooke, 1979; Kaboli et al., 2007; Kämpfer & Fartmann, 2019). Such microhabitats guarantee easy access to arthropod prey and therefore foster reproductive success (Arlt & Pärt, 2007; Low et al., 2010). More bare ground also increases the detectability of potential predators favouring overall survival (Whittingham & Evans, 2004). As Pärt (2001) showed, nest predation was significantly higher in northern wheatear territories with more vegetation. The main predators, weasel (*Mustela nivalis*), stoat (*Mustela erminea*) and adder (*Vipera berus*), prefer foraging habitats that have a higher cover of vegetation. The same seems to be true for other potential predators such as red fox (*Vulpes vulpes*), badger (*Meles meles*), domestic cat (*Felis catus*) and rodents (Conder, 1989; Pärt & Wretenberg, 2002).

Peat extraction sites that were previously used as arable land played a special role as a breeding habitat for the northern wheatear in our study. Nest densities in occupied plots increased with the area of this habitat type and former arable land was preferred for breeding while former grasslands and former bogs without any land

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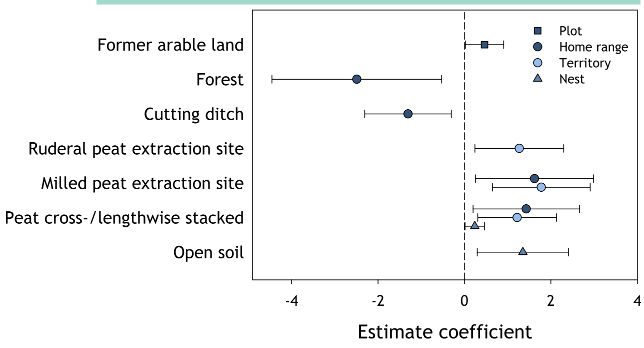

FIGURE 4 Model-averaging results (GLMM): Relationship between the probability of northern wheatear nest occurrence and significant predictors at different spatial scales (plot [nest density], home range, territory and nest site). Model-averaged coefficients (standardised estimates ±95% confidence intervals = CI) derived from the top-ranked models (ΔAICc <3) are shown. For detailed statistics see Table A1.

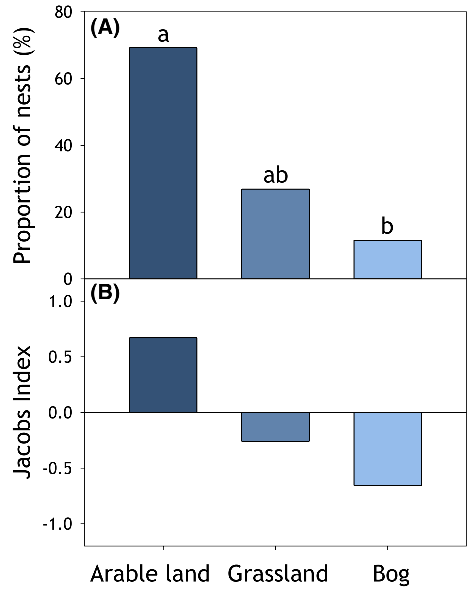

FIGURE 5 Frequency (%) of nests on peat extraction sites in relation to the former land use (A) and Jacobs index indicating preferences of different former land use types for nesting relative to total availability within the plots (zero line) (B). Differences in the frequency of nests between the three types were tested using generalised linear mixed-effects models (GLMM) with Tukey contrasts for pairwise comparisons. For further information, see Section 2.5. Different superscript letters indicate that parameters differ significantly between land use types (*$p \leq 0.05$).

TABLE 4 Mean values (±SE) of environmental parameters in northern wheatear nest sites ($n = 28$, $r = 5$ m) and controls ($n = 28$, $r = 5$ m).

Parameter	Nest	Control	p
Peat-cutting site (m^2)			
Peat sods			
Tightly stacked	2.6 ± 0.8	3.7 ± 1.0	n.s.
Crosswise stacked	0.0 ± 0.0	1.5 ± 0.6	n.s.
Cross-/lengthwise stacked	4.6 ± 0.7	3.5 ± 0.8	n.s.
Peat sod pile	1.9 ± 1.9	0.0 ± 0.0	n.s.
Cutting ditch	8.2 ± 0.4	8.3 ± 0.8	n.s.
Open soil	57.2 ± 2.2	45.0 ± 3.0	**
Distance (m)			
Forest	434.5 ± 51.4	255.4 ± 35.7	**
Tree	112.3 ± 11.0	126.2 ± 17.4	n.s.
Path	166.6 ± 24.5	272.3 ± 44.8	n.s.
Building	671.4 ± 62.3	867.1 ± 105.3	n.s.

Note: Statistical comparisons between nest sites and controls were done by generalised linear mixed-effects models (GLMMs). For further information, see Section 2.5. Statistical significances are indicated as follows: n.s. = not significant; **$p \leq 0.01$.

use were avoided. One might argue that the more nutrient-rich peat extraction sites on former arable land may foster arthropod abundance (cf. Siemann, 1998) and thus the availability of food resources for the wheatear. However, it has been widely shown that the northern wheatear can occur at high densities on nutrient-poor soils (Blüml & Schönheim, 2006; Kämpfer & Fartmann, 2019). Hence, we argue that a higher arthropod abundance was at best an additional driver of nest site selection. On the other hand, we assume that the much more intensive measures to remove vegetation, due to the higher successional speed on the more nutrient-rich sites (see Section 2.4.1 Environmental parameters), were the main cause of the preference for peat extraction sites on former arable land. All these measures created the preferred open soil (see above) on a large scale. This assumption is further supported by observations from the Uchter Moor, one of the three studied bogs. Here, peat extraction occurred mainly on drained bogs that had never been used for farming (see Section 2.1 Study area). Despite the very nutrient-poor conditions, 51 breeding pairs were present there between 2003 and 2005, which was an abundance of 2.1 nests/10 ha (Blüml & Sandkühler, 2015). By contrast, in the study year (2017), after cessation of milling and beginning revegetation of the peat, although suitable cavities for breeding were still present, we only detected three nests.

In conclusion, breeding of northern wheatears in peat extraction sites depended on a combination of (i) regular occurrence of suitable cavities for nesting and (ii) vast open areas that guaranteed easy access to arthropod prey and increased detectability of potential predators. By far, the most important structures for nesting were the cavities within the rows of cross- and lengthwise stacked peat sods. The availability of large open areas was particularly ensured by regular milling of the peat.

4.1 | Implications for conservation

Based on our findings, peat extraction sites used as a breeding habitat for the northern wheatear would benefit from a combination of sod cutting and peat milling to create both the required (i) nesting structures and (ii) open soil for foraging and early predator recognition. The obligatory re-stacking of peat sods after winter (see Section 2.2 Peat extraction procedure) creates the most important nest sites for the northern wheatear in peat extraction sites, rows of cross- and lengthwise stacked peat sods with their suitable cavities. However, the timing of re-stacking and harvest of dry peat sods has strong effects on the reproductive success of the wheatear. If they occur during the nesting period, they cause the loss of eggs or young birds in the nest (Schumacher, 1999). Consequently, re-stacking is best done until mid-April, which is clearly before the start of the breeding season (Brooke, 1979; Suter, 1988). The cross- and lengthwise pattern is required to create suitable cavities for nesting. Harvesting peat sods after the breeding season, from late July onwards (Buchmann, 2001), is likely to reduce nest losses. Another cavity-breeding bird, the pied wagtail (*Motacilla alba*), which regularly uses the same rows of peat sods for nesting (own observation), will also benefit from these measures. In the last phase of peat extraction, only peat milling is applied to extract peat because the bottom peat layer is too decomposed to cut the peat (pers. comm. L. Gr. Holthaus). During this period, artificial nest boxes could provide an alternative nesting structure (cf. Robert, 2005).

Compared to peat extraction sites on former arable land, those with no prior land use had slower succession and lacked competitive weed species, due to the nutrient-poor conditions (own observation). Therefore, paradoxically, nutrient-poor peat extraction sites had a higher vegetation cover due to less regular peat milling (own observation and pers. comm. L. Gr. Holthaus). We have shown that the northern wheatear avoided such habitats. However, they were important breeding habitats for two other threatened species, meadow pipit (*Anthus pratensis*) and skylark (*Alauda arvensis*) (own observation; for threat status see Krüger & Sandkühler, 2022; Ryslavy et al., 2020). Accordingly, these peat extraction sites also provide valuable temporary habitats for species of conservation concern.

In Germany, peat extraction will come to an end in 2040 (Hirschler & Thrän, 2023), which is an important goal for climate and peatland conservation. However, if society and policy makers decide to continue the use of peat products, the risk of peat extraction shifting to intact peatlands in other regions such as the Baltic States is increasing (Hirschler & Thrän, 2023). Therefore, it would be preferable for peat extraction to focus on already degraded peatlands that are used for agriculture rather than on natural bogs. This may help to protect bog ecosystems with their highly specialised species assemblages and at the same time restore agriculturally used bogs after peat extraction. Moreover, peat extraction sites can be important temporary habitats for highly threatened species, such as the northern wheatear.

However, despite the planned cessation of peat extraction in Germany, this study provides valuable insights into the habitat requirements of the northern wheatear that can be applied to peat extraction sites in other regions and, potentially, to alternative habitats. Our results highlight the importance of a combination of suitable nesting structures and large areas of open soil for foraging and early predator detection (see also Kämpfer & Fartmann, 2019). Nevertheless, further research is needed to assess the effects of the decline and eventual cessation of peat extraction on the species, as well as on other breeding birds. In this context, potential management measures could be evaluated that may help to maintain suitable habitats. For example, the effectiveness of artificial nest boxes in sites without sod cutting could be evaluated. As peat extraction sites will ultimately disappear and, with them, large areas of suitable open habitat, it is essential to investigate whether and how similar habitat conditions can be maintained. Potential substitute habitats include open heathlands at the margins of peatlands, possibly enhanced with artificial nesting structures, as well as other surface-mining areas such as sand quarries, which are widespread in the study area. However, it remains unclear to what extent such habitats can compensate for the loss of peat extraction sites at the population level.

AUTHOR CONTRIBUTIONS

Marco Drung and Thomas Fartmann conceived the ideas and designed the methodology; Marco Drung collected and analysed the data; Marco Drung and Thomas Fartmann led the writing of the manuscript. All authors critically contributed to the draft.

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The authors declare no competing financial or personal conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data supporting this study are available at Zenodo: https://doi.org/10.5281/zenodo.20858502 (Drung & Fartmann, 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table A1. Overview of environmental parameters used for generalised linear mixed-effects models (GLMM) and their intercorrelations (Spearman correlation [r_s], $|r_s| > 0.6$). As a result, the following variables were excluded from the multivariable analyses: (a): arable land, former grassland, grassland; (b): arable land, former bog, grassland; (c): peat tightly stacked, overgrown extraction site, building; (d): peat tightly stacked, overgrown extraction site; (e): peat tightly stacked. Statistical significance is indicated as follows: $^{***}p < 0.001$.

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