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Wind energy facilities affect resource selection of capercaillie *Tetrao urogallus*

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The recent increase in wind energy facilities (WEF) has led to concerns about their effect on wildlife. While the focus of most studies has mainly been on increased mortality of birds and bats due to collision, indirect effects, such as behavioural responses, are currently gaining attention. Indeed, effects of WEF on the behaviour of forest dwelling wildlife still remain largely unknown. Using GPS-tracking of 16 individuals, we studied how seasonal resource selection of the capercaillie *Tetrao urogallus*, a forest grouse species known as sensitive to disturbance by human presence and infrastructure, was related to wind turbines and other environmental covariates in a wind farm in Sweden. During the lekking season, the probability of site-selection by capercaillie decreased with increasing turbine noise, turbine visibility and turbine shadow. During summer, we found reduced resource selection with increasing proximity to the turbines (up to 865 m), turbine density, noise, shadow and visibility. Furthermore, we found an avoidance of turbine access roads. Due to the high collinearity of the wind turbine predictors it was not possible to identify the specific mechanism causing turbine avoidance. Our study reveals that forest dwelling species with known sensitivity to other forms of human disturbance (i.e. recreation) are also likely to be affected by wind turbine presence. In addition, we provide proximity thresholds below which effects are likely to be present as a basis for conservation planning.

Keywords: avoidance, capercaillie, forest grouse, GPS telemetry, resource selection, wind energy

Renewable energy sources are increasingly being exploited to counter anthropogenic climate change, with on-shore wind power being the fastest developing sector (Renewable Energy Network 2018). However, the construction of infrastructure in previously unused or scarcely used landscapes can have considerable impacts on biodiversity and species abundance (Lior 2008, Miller et al. 2014). Negative effects of wind energy facilities (WEF) have been demonstrated for various taxa, such as insects, birds and bats (Kunz et al. 2007, Pearce-Higgins et al. 2009, Helldin et al. 2017, Hötker 2017), but effects are species specific (De Lucas et al. 2007, Pearce-Higgins et al. 2012) and might differ between individuals as well (Winder et al. 2014a). Furthermore, effects of WEF on wildlife can differ depending on weather conditions influencing e.g. visibility or seasonal changes in behaviour (Breuer 2001). Direct effects, such as collisions of birds and bats with the turbines, have been the main focus of research and intervention planning in the past years (Arnett et al. 2008, Loss et al. 2013, De Lucas and Perrow 2017). However, apart from direct mortality, WEF may also have indirect effects through construction and maintenance work, turbine visibility as well as shadow and noise (Pruett et al. 2009, Hötker 2017). Consequently, WEF have been shown to affect vigilance behaviour (Rabin et al. 2006), vocalizations (Zwart et al. 2016, Whalen et al. 2019) and temporal or spatial habitat use of wildlife (Hötker 2017), with reduced use of habitats effectively causing habitat loss (Plumb et al. 2018). Avoidance or reduced use of habitats affected by WEF can negatively impact the exploitation of energy resources, and thus negatively affect populations (Hoover and Morrison 2005, 2017).
Material and methods

Study area and species

The study was conducted in forests at elevations of 65–465 m a.s.l. in Dalarna and Gävleborg County, Sweden (Fig. 1). The study area encompassed approx. 10,000 ha, including the Jädraäls wind farm with 68 Vestas V112 turbines, operational since 2013, and the Mönbässen wind farm with 10 Vestas V126 turbines, operational since 2016. The dominant tree species in the study area is Scots pine *Pinus sylvestris*, followed by Norway spruce *Picea abies* interspersed with small amounts of silver birch *Betula pendula*. Most parts of the forest covering the study area are managed with regular thinnings, clearcuttings and replantation for timber production. Ornithological surveys preceding our study in 2015 (i.e. two years after construction of the WEF) revealed capercaillie occurrence and lekking sites with up to five capercaillie males in the central parts of the study area (E. Ringaby, unpubl. report 2015). These surveys were however too superficial to deliver suitable data for assessing the habitat use or density of capercaillie in the study area in the first years after the construction of the WEF.

The capercaillie is a large ground nesting forest grouse species (Johnsgard 1983). The species is highly sexually dimorph, with females with an inconspicuous plumage and the males being twice the size of the females with a conspicuous plumage (Johnsgard 1983). Capercaillie have a polygynous mating system where males gather at display arenas, from here on referred to as lekking sites, where they produce visual and acoustic signals to attract females (Johnsgard 1983). Whereas the females only visit the leks for a short time period, the males stay close to the lekking site from late winter to the end of the lekking season (Wegge and Larsen 1987, Gjerde and Wegge 1989). With a diet mainly composed of buds and berries in summer and conifer needles in winter, and the chicks highly dependent on insect food, capercaillie prefer semi-open to open forests with a rich ground vegetation, including bilberry *Vaccinium myrtillus* (Storch 1993, Summers et al. 2004, Bollmann et al. 2008, Graf et al. 2009). The species is considered an indicator for structurally diverse and species-rich conifer dominated forests (Suter et al. 2002, Pakkala et al. 2003). Although they occur over a wide geographical range across Eurasia (Klaus et al. 1989, Coppes et al. 2015), many local populations are decreasing or have gone extinct (Storch 2007, Jahren et al. 2016), which is why the capercaillie is red listed in many countries and included as a specially protected species in the EU Birds Directive, Annex I (Bauer et al. 2005). Several studies have shown that capercaillie are affected by human recreational activities in their habitats, resulting in increased stress hormones levels (Thiel et al. 2011, Coppes et al. 2018a) or reduced use of habitats close to human recreational infrastructure (Summers et al. 2007, Moss et al. 2014, Coppes et al. 2017, 2018b). Habitat deterioration related to human disturbance is even considered to negatively affect local capercaillie populations in central Europe (Coppes et al. 2017) and there are indications that WEF can have a negative effect on capercaillie occurrence (González and Ena 2011, González et al. 2016) and habitat use (Coppes et al. 2020b).

Data collection

Capture and tracking

Capercaillie were caught in 2017 and 2018 by placing walk-in nets at lekking sites while lekking took place in April and May and around sand baths in May. We selected capture...
locations as close as possible to wind turbines, with distances to the nearest wind turbine between 250 m and 800 m. Birds were tagged within a handling time of maximum 10 min and released. The capturing and handling protocol was approved by the Swedish Animal Ethics Committee (permit DNR C 40/16). We equipped birds with backpack-transmitters, as these remain close to the birds’ centre of gravity for impairing the animals as little as possible. The GPS-3D-acceleration transmitters (Bird 1AA2, Bird 1A-light, Bird Solar and Bird 2AA2, E-obs digital telemetry, Munich, Germany) weighed 38–48 g for females and males respectively, which is up to 2% of the birds’ bodyweight. A 5% limit is commonly seen as a maximum device payload that should be added to a flying animal (Cochran 1980). However, since this 5% limit is seen to be essentially arbitrary more recently a 3% criterion (Casper 2009) has been recommended. We used teflon and silicon band for fitting the transmitter to prevent excoriation. To maximize sampling duration and minimize the sampling interval we used both solar and battery tags. The solar tags (38 g, both sexes) enabled high-resolution GPS measurements every 5 min when batteries were charged completely, whereas below a certain voltage threshold sampling was reduced to 3 GPS locations/24 h on cloudy days. Battery tags enabled a constant sampling of 3 GPS locations/24 h, which could provide data for at least one year for males (transmitter weight 48 g) or 7 months for females (38 g), respectively. The data was downloaded at a regular interval of two to four weeks using a handheld device, at a distance of several hundred meters. When the GPS points clustered and the acceleration data indicated no movement, the bird was expected to be dead, the tags were retrieved and the situation on site recorded. Identification of the cause of death was carried out according to Smith and Willebrand (1999).

Data preparation
To avoid a bias relating to different sampling regimes, we subsampled the data set of the birds with solar-tags (i.e. with bursts of locations taken at a 5-min interval) to a sampling regime of 3 GPS locations/24 h, thus matching the sampling regime of battery tags. We divided the GPS locations into two biologically distinct seasons: the lekking season for males (n = 8) and the summer season for males (n = 11) and females (n = 4). The lekking season was defined individually for each male by the period the individual attended the lek at night and nearby feeding areas during the day (Storch 1997) until the male eventually left the lek (end of May to beginning of June) and did not return in the same year. In addition, three out of four females were caught at road sites at the
end of the lekking season, but since they did not attend the leks anymore, they were excluded from the lekking season analysis. In contrast to Storch (1993) our defined summer season covered the period June to October as only data from few transmitters were received during this time. Although the females started to breed, the breeding season was not analysed separately because the nests were abandoned or preyed upon, therefore the females were included in the summer season analysis. We did not consider GPS locations taken during the first 72 h after capture in order to minimize the impact of the tagging and handling process on the data.

Accuracy filtering
We performed accuracy filtering of GPS locations to assess the potential effect of location error on the estimated resource selection of capercaillie. For this purpose, a test data set was generated by deploying stationary GPS-tags in different habitat types (i.e. closed and open canopy). The deviation of the locations estimated by the tag from the tag's actual location were used to evaluate the internal accuracy estimate provided by the tags which is based on the number of satellite connections at a given fix. We fitted both linear and piece-wise linear regressions to the data and proceeded with a linear model as there was no evidence for a segmented relationship. The increase in spread of the residuals around the linear model estimate with increasing location error was used to select a threshold beyond which the internal accuracy estimates were considered unreliable. The resulting threshold in the internal values (value '25') was equivalent to approximately 12 m real location error and classified 30% of the test data as potentially ‘unreliable’. We used this threshold value to split the capercaillie dataset into a ‘full dataset’ (containing all locations) and a ‘reduced dataset’ (containing only ‘reliable’ locations).

Environmental variables

Predictor variables potentially related to resource selection of capercaillie were obtained from topographic and land cover maps (as of 2018), as well as forestry inventory data recorded in 2010/2011 (Lantmäteriet 2017a, b, SLU Skogsstyrelsen 2017, Skogsstyrelsen 2018). All environmental variables (Table 1) were processed at a resolution of 25 × 25 m. Forest land cover data was processed in four different classes to distinguish between pine or spruce dominated forest if the raster cell included ≥ 75% of either tree species, mixed forest if pine and spruce included < 75% of either species in a raster cell and ‘other forest’ if a raster cell included less abundant tree species like birch or unknown forest types. As clearcutting affects capercaillie habitat use (Rolstad and Wegge 1989, Storch 1995, Mikolàš et al. 2015) we complemented the forest inventory data with two different categories of clear-cuts, depending on the time since the clearcutting was performed: < 5 years old and > 5 years old, with a maximum age of 20 years using 2018/2019 as reference year. Final categorical land cover types consisted of eight classes: pine forest, spruce forest, mixed forest, other forest, open bog, forest bog, clear-cut < 5 years and clear-cut > 5 years. Clear-cut < 5 years was treated as the intercept. In addition, we calculated Euclidean distances to bogs located in forests and to bogs located in open areas. Forest structures were characterized using mean basal area to characterize stand density and the mean tree diameter at breast height based on the average values per stand provided by the forest inventory data.

Wind turbine effects were represented by six predictors, of which the first three were described by Coppes et al. (2020b): 1) we modelled the expected meteorologically plausible yearly amount (hours) of turbine shadow across the study area in the software WindPRO 3.1 (EMD International A/S 2018). This approach accounts for the location of turbines within the study site, the typical weather patterns, site topography, latitude, turbine height and rotor diameter. 2) We calculated the distance of each location to the closest wind turbine in meters. 3) We modelled the expected turbine noise emission (in decibel) across the study area based on the ISO 9613-2 method, using the maximum noise volume

| Category     | Description                      | Unit       | Type     | Model lek | Model summer |
|--------------|----------------------------------|------------|----------|-----------|--------------|
| Land cover   | Land cover types                 | Pine *Pinus sylvestris* forest | cat.     | ✓         | ✓            |
|              |                                  | Spruce *Picea abies* forest     |          | ✓         |              |
|              |                                  | Mixed forest                      |          | ✓         |              |
|              |                                  | Other forest                       |          |           |              |
|              |                                  | Open bog                           |          | ✓         |              |
|              |                                  | Forest bog                         |          | ✓         |              |
|              |                                  | Clear-cut < 5 years                |          | ✓         |              |
|              |                                  | Clear-cut > 5 years                |          | ✓         |              |
| Forestry     | Distance to open bog             | m          | cont.    | ✓         | ✓            |
|              | Distance to forest bog           | m          | cont.    | ✓         | ✓            |
|              | Mean stand density               | m² ha⁻¹    | cont.    | ✓         | ✓            |
|              | Mean tree diameter               | cm         | cont.    | ✓         | ✓            |
|              | Distance clear-cut < 5 years     | m          | cont.    | ✓         | ✓            |
|              | Distance clear-cut > 5 years     | m          | cont.    | ✓         | ✓            |
| WEF          | Turbine shadow                   | h year⁻¹   | cont.    | ✓         | ✓            |
|              | Turbine noise                    | dB         | cont.    | ✓         | ✓            |
|              | No. of turbines < 800 m          | m          | cont.    | ✓         | ✓            |
|              | Distance to turbine              | m          | cont.    | ✓         | ✓            |
|              | No. of visible turbines          | m          | cont.    | ✓         | ✓            |
|              | Distance to access road          | m          | cont.    | ✓         | ✓            |
levels (at 95% turbine capacity) for each turbine model as stored in the WindPRO database. These values are based on empirical measurements for each turbine type. 4) We modelled the number of visible wind turbines from each ground-location in the study area using landscape (digital elevation model) and vegetation heights derived from high resolution aerial LiDAR data (Lantmäteriet 2018), which was validated using in situ observations (i.e. by validating whether wind turbines were visible or not). 5) We calculated the distance of each location to the closest turbine access road (i.e. enlarged gravel forest roads that provide access to the turbine sites). 6) Finally, we calculated the number of wind turbines within 800 m, based on the results of Coppes et al. (2020b) for each location.

**Resource selection analysis (RSF)**

We estimated capercaillie resource selection by contrasting capercaillie GPS locations to a set of random locations (i.e. RSF ‘sampling protocol A’ in a use-available design, Manly et al. 2002). We generated random locations (i.e. random coordinate pairs, as described in Urban and Cagnacci 2014) separately for the two seasons considered (i.e. lekking and summer) and per individual within each individuals’ seasonal home ranges (home range as 100% minimum-convex polygon around GPS locations from the respective season). The number of random locations per presence location is known to affect parameter estimates, implying that estimated selection coefficients may be biased or unstable dependent on the number and spatial position of random locations (Roberts et al. 2017, Ciuti et al. 2018). We followed Ciuti et al. (2018) and performed a sensitivity analysis to determine the minimum number of required random points to obtain stable parameter estimates. We fitted generalized linear mixed models (GLMM, R package lme4, Bates et al. 2015) with varying sample sizes of random locations (stepwise increasing from a ratio of 1:1 to 1:30 relocations to random locations). The GLMM contained all predictors considered in the analysis. Stability of parameter estimates was assessed by iterating the process 30 times. Estimates were stable at a ratio of 1:15 relations to random locations (Roberts et al. 2017). Owing to our limited sample size (i.e. n = 8 and n = 12 animals, lekking and summer season) we assigned CV-folds by leaving out single animals to ensure model convergence. We refitted all final models in both seasons on each fold and extracted beta values and associated p-values.

We obtained selection scores \( w(x) \) for all models in each season by plugging the estimated model coefficients into the resource selection function (RSF), omitting the model intercept. We assumed the RSF to take the exponential form:

\[
w(x) = \exp(\beta_1 \times x_1 + \beta_2 \times x_2 + \ldots + \beta_n \times x_n),
\]

where \( \beta_n \) represents model coefficients that are associated with the environmental data \( x_n \) (Manly et al. 2002, Lele et al. 2013). The resulting score \( w(x) \) reflects the relative strength of the selection effect on a positive scale.

To determine overall thresholds up to which effects of wind turbine predictors affected capercaillie resource selection we determined the point at which the response curve for each selection score \( w(x) \) diverged from local maxima or minima (i.e. the point beyond which effects were detectable). We determined thresholds numerically by obtaining the point where the first order derivative of the response curves (i.e. the slope) changed sign. We likewise applied this approach to each CV-fold and calculated the 95% quantile range across CV-folds as a measure of uncertainty. Thresholds for the number of visible turbines were obtained using the model including the number of wind turbines within a radius of 800 m around each location, because it consistently had the lowest AIC in both summer and lekking season (Table 3, 4).

**Results**

We captured twelve capercaillie males and six females from mid-April until end of May in 2017 and 2018 (Table 2). On average a capture site was 587 m away from the nearest wind turbine (ranging between 325 m and 950 m). Due to defective transmitters, migration or predation events, the periods over which GPS locations were available varied between individuals (between 50 and 400 days; Table 2). Two females died within 30 days after capture (predation by mammals, presumably red fox *Vulpes vulpes*) and were therefore excluded from the analysis due to insufficient data.
Table 2. Overview of the capercaillie included in the analysis. The column ‘Type’ indicates the tag type: solar or battery. Days tracked and numbers of GPS locations are given per individual and per season. Minimum convex polygons (MCP) contain 100% of GPS locations included for the analysis per season in hectares. The check marks indicate which individuals were included in the RSF models for the lekking and summer season, respectively.

| Sex | Type | Days lek | Locations lek | MCP lek | Days summer | Locations summer | MCP summer | Model lek | Model summer |
|-----|------|----------|--------------|--------|-------------|-----------------|------------|-----------|-------------|
| m   | Solar| 43       | 127          | 30     | 167         | 446             | 457        | ✓         | ✓           |
| m   | Solar| 44       | 130          | 19     | 139         | 272             | 454        | ✓         | ✓           |
| m   | Battery| 45      | 133          | 19     | 26          | 74              | 136        | ✓         | ✓           |
| m   | Solar| 31       | 89           | 46     | 139         | 409             | 526        | ✓         | ✓           |
| m   | Battery| 33      | 98           | 36     | 92          | 272             | 454        | ✓         | ✓           |
| m   | Solar| –        | –            | –      | –           | –               | –          | –         | –           |
| f   | Solar| –        | –            | –      | 106         | 312             | 116        | ✓         | ✓           |
| f   | Battery| –      | –            | –      | 54          | 158             | 260        | ✓         | ✓           |
| f   | Solar| –        | –            | –      | 69          | 201             | 82         | ✓         | ✓           |
| f   | Solar| –        | –            | –      | 51          | 151             | 74         | ✓         | ✓           |
| m   | Solar| 39       | 113          | 7      | 105         | 311             | 475        | ✓         | ✓           |
| m   | Solar| –        | –            | –      | 88          | 258             | 131        | ✓         | ✓           |
| m   | Battery| 29     | 83           | 63     | 73          | 215             | 243        | ✓         | ✓           |
| m   | Solar| 18       | 52           | 18     | 123         | 358             | 622        | ✓         | ✓           |
| f   | Solar| –        | –            | –      | 147         | 433             | 1284       | ✓         | ✓           |
| m   | Battery| –      | –            | –      | 173         | 512             | 1166       | ✓         | ✓           |

were sufficient (≥ 45 days tracked per season) for RSF analysis for eight males in the lekking season and 15 individuals (4 females, 11 males) in the summer season (Table 2). For the lekking season the average MCP home range size of the eight males was 30 ± 17 ha. For the summer season the average home range size of the 11 males (504 ± 301 ha) was more than twice as large as those of the four females (133 ± 75 ha). The home ranges of the birds were located around the lekking sites during the lekking season, but moved away from the lekking sites during the summer season. During both seasons the home ranges were located both within and surrounding the wind park.

**Turbine effects in the lekking season**

Of the three models compared (Table 3) the model containing the number of turbines within 800 m best explained resource selection (i.e. lowest AIC) of capercaillie males (Table 3c). However, the model containing turbine shadow was most competitive (Table 3a; ΔAIC = 2.6), followed by the model containing turbine noise (Table 3b; ΔAIC = 8.3). Marginal and Conditional R² ranged between 0.221 and 0.249 and 0.310 and 0.411 respectively, with both values highest for the model including turbine noise (Table 3). Blocked cross-validation led to considerable variation in the size of the estimated beta coefficients, but all wind turbine effects had a constant sign and support for higher-order polynomial terms was stable (Supplementary information).

The following effects of wind turbines on resource selection were found: the probability of selection by capercaillie males during the lekking period decreased with turbine shadow of approx. ≥ 14 h year−1 (0.14–24.5 h; Fig. 2a, Table 3a) and with increasing noise emission (Fig. 2b, Table 3b). Also, the probability of selection declined with high turbine density (Fig. 2c, Table 3c) and in areas with more than four (4.5) visible turbines (1.3–5.2 turbines; Fig. 2d). The magnitude of effects (i.e. the selection score) was highly variable and larger for all wind turbine predictors in the lekking period models than in the summer models (compare Fig. 2, 3). In addition, a strong negative effect of turbine access roads on resource selection of capercaillie males was prevalent in all three models (Table 3, Supplementary information).

**Turbine effects in the summer season**

Of the four models compared (Table 4), the model containing the number of turbines within 800 m best explained resource selection of capercaillie males and females (Table 4c). The second best model included distance to turbine (Table 4d; ΔAIC = 23.6), followed by the models containing turbine noise emissions (Table 4b; ΔAIC = 38.8) and turbine shadow (Table 4a; ΔAIC = 118.4). Marginal and conditional R² ranged between 0.195 and 0.205 and 0.199 and 0.211 respectively, with both values highest for the model including the number of wind turbines < 800 m (Table 4). Blocked cross-validation led to less variation in the size of the estimated beta coefficients as compared to the lekking season. Wind turbine effects had likewise a stable sign and higher-order polynomial terms were supported (Supplementary information).

Selection decreased with increasing proximity to the wind turbine, levelling off at a distance of approx. 865 m (784–1025 m; Fig. 3d, Table 4d) and with increasing wind turbine density (Fig. 3c, Table 4c). The probability of selection also decreased with increasing noise emissions from 43 dB onwards (40–45 dB; Fig. 3b, Table 4b), below this value no effect could be demonstrated. Furthermore, the probability of selection was reduced in areas with more than 8 h of meteorologically probable shadow per year (2.25–22.47 h; Fig. 3a, Table 4a). Selection probability also decreased in areas where more than four (4.6) wind turbines were visible (3.2–5.2 turbines; Fig. 3e) as well as with increasing proximity to turbine access roads (Fig. 3f). The selection scores of the wind turbine predictors were similar between the models, although comparatively low (compare e.g. Fig. 2, 3, Supplementary information).
Environmental characteristics

In both seasons, capercaillie selected for areas further away from open bogs and clear-cuts > 5 years old, while the probability of selection was higher close to clear-cuts < 5 years old, although the selection against older clear-cuts was more pronounced than selection for more recent ones (Table 3, 4, Supplementary information). Stands with intermediate mean tree diameter were selected for during summer season (Supplementary information). During lekking season stands with smaller tree diameter were selected, although this effect was not significant for the model including turbine shadow (Table 3a) and turbine noise (Table 3b, Supplementary information). Capercaillie also selected for intermediate stand density during summer (Supplementary information). The probability of selection increased with increasing distance from forest bogs during the lekking season, while this effect was reversed during the summer season, when sites close to forest bogs were strongly selected for (Supplementary information). Finally, the probability of selection during summer was highest for young clear-cuts, followed by forest bogs and pine forests while the probability of selection was lowest for open bogs and spruce-dominated forest stands (Supplementary information).

Discussion

We show that resource selection of capercaillie is influenced by the presence of wind energy facilities and the associated infrastructure (i.e. access roads) during two seasons important for the species’ reproduction: spring and summer. We did not find absolute displacement (i.e. complete avoidance), but a reduced selection of areas with increasing turbine influence. Although we could not employ a before–after–control–impact design, resource selection of capercaillie in the wind farm was negatively affected by different turbine predictors included in the analyses. The majority of studies on displacement effects of WEF on birds are performed in open landscapes (Hötker 2017). Our results show that birds inhabiting forests can also be affected in their habitat selec-

Table 3. Results of the GLMMs estimating capercaillie resource selection during the lekking season in response to (a) turbine shadow, (b) turbine noise and (c) the number of turbines within 800 ms. AIC, Marginal R² and Conditional R² are provided for the models. Model coefficients (β), standard errors (SE) default p-values are provided for the predictors.

(a) Turbine shadow
AIC: 5886.6 (Δ2.6)

| Predictor             | β     | SE   | p-value |
|-----------------------|-------|------|---------|
| Intercept             | -2.888 | 0.258|         |
| Turbine shadow        | -0.271 | 0.112| 0.015   |
| Turbine shadow²       | -0.186 | 0.070| 0.008   |
| No. visible turbines  | -0.010 | 0.068| 0.879   |
| No. visible turbines² | -0.160 | 0.045| < 0.001 |
| Distance access road  | 0.617  | 0.103| < 0.001 |
| Mean tree diameter    | -0.119 | 0.065| 0.070   |
| Mean tree diameter²   | -0.064 | 0.034| 0.060   |
| Distance clear-cut < 5 y | -0.403 | 0.119| < 0.001 |
| Distance clear-cut > 5 y | 0.302  | 0.087| < 0.001 |
| Distance forest bog   | 0.079  | 0.110| 0.472   |
| Distance forest bog²  | 0.269  | 0.054| < 0.001 |
| Distance open bog     | 0.467  | 0.091| < 0.001 |
| Distance open bog²    | 0.156  | 0.042| < 0.001 |

(b) Turbine noise
AIC: 5894.3 (Δ8.3)

| Predictor             | β     | SE   | p-value |
|-----------------------|-------|------|---------|
| Intercept             | -3.191 | 0.358|         |
| Turbine noise         | -0.443 | 0.140| 0.002   |
| Turbine noise²        | 0.309  | 0.082| < 0.001 |
| No. visible turbines  | -0.052 | 0.068| 0.442   |
| No. visible turbines² | -0.181 | 0.046| < 0.001 |
| Distance access road  | 0.710  | 0.109| < 0.001 |
| Mean tree diameter    | -0.100 | 0.066| 0.129   |
| Mean tree diameter²   | -0.052 | 0.034| 0.120   |
| Distance clear-cut < 5 y | -0.221 | 0.126| 0.080   |
| Distance clear-cut > 5 y | 0.382  | 0.090| < 0.001 |
| Distance forest bog   | 0.233  | 0.113| 0.039   |
| Distance forest bog²  | 0.210  | 0.056| < 0.001 |
| Distance open bog     | 0.469  | 0.090| < 0.001 |
| Distance open bog²    | 0.101  | 0.045| 0.023   |

(c) No. of turbines < 800 m
AIC: 5886.0 (Δ0.0)

| Predictor             | β     | SE   | p-value |
|-----------------------|-------|------|---------|
| Intercept             | -3.181 | 0.304|         |
| No. turbines < 800 m  | -0.577 | 0.109| < 0.001 |
| No. turbines < 800 m² | 0.275  | 0.076| < 0.001 |
| No. visible turbines  | -0.056 | 0.068| 0.407   |
| No. visible turbines² | -0.176 | 0.046| < 0.001 |
| Distance access road  | 0.786  | 0.110| < 0.001 |
| Mean tree diameter    | -0.121 | 0.066| 0.066   |
| Mean tree diameter²   | -0.068 | 0.034| 0.048   |
| Distance clear-cut < 5 y | -0.314 | 0.121| 0.010   |
| Distance clear-cut > 5 y | 0.283  | 0.089| 0.002   |
| Distance forest bog   | 0.187  | 0.106| 0.080   |
| Distance forest bog²  | 0.212  | 0.056| < 0.001 |
| Distance open bog     | 0.479  | 0.091| < 0.001 |
| Distance open bog²    | 0.091  | 0.044| 0.040   |
tion by WEF. This is in line with the findings of a recent study, based on systematically sampled indirect presence data on capercaillie habitat use around WEF in six central European study regions, showing avoidance of wind turbines up to 650 m (Coppes et al. 2020b). In contrast to Coppes et al. (2020b), we were able to study two different seasons and also include additional variables linked to WEF and reveal that not only proximity to WEF, shadow flickering and WEF noise affect capercaillie, but that also the number of wind turbines around the animal and turbine access roads affect capercaillie resource selection. Coppes et al. (2020b) did not find significant effects of turbine visibility on the probability of presence, while we find a negative effect of turbine visibility on capercaillie resource selection. The estimated avoidance threshold in our study is somewhat larger than that estimated by Coppes et al. (2020b) (i.e. 650 m versus 865 m with CI). The exact shape of the predicted effect is, however, largely dependent on model formulation (i.e. the third-order polynomial term) and should thus be interpreted with care, but both the shape and magnitude of the effect in our study are strikingly similar to that presented in Coppes et al. (2020b). Accordingly, it appears likely that similar avoidance behaviour with regard to wind turbines could also be expected in other areas.

The reduced use of areas in close proximity to the wind turbines might explain the reduction in the number of indirect capercaillie signs linked to the construction of a wind farm in Spain (González et al. 2011, 2016). WEF have also been linked to lek displacement or a reduction in number of males at lekking sites in a different wind farm in Sweden (Rönning 2017) and also black grouse Lyrurus tetrix have been found to displace their lekking sites away from wind turbines in Scotland (Zwart et al. 2015). The high site fidelity that grouse are known for and their relative long life span could also result in a relatively slow displacement or extinction process of lekking sites close to wind turbines. We found capercaillie lekking sites with males and females present within the wind farm, however due to the lack of data from before the WEF construction, we cannot infer whether the location or number of males at the lekking sites was affected by the WEF in our study area.

Our results are in line with those of other studies studying resource selection of grouse under WEF influence. Winder et al. (2014a) found that females of the greater prairie chicken Tympanuchus cupido doubled their home range sizes during breeding seasons after the construction of WEF in Kansas. Also, LeBeau et al. (2017) found decreasing selection of brood and summer habitats by greater sage-grouse with an increase of surface disturbance associated with WEF. No negative effect of WEF has been found on female greater prairie-chicken survival (Winder et al. 2014b) or on nest site selection and survival of greater sage-grouse Centrocerus urophasianus (LeBeau et al. 2017). Columbian sharp-tailed grouse Tympanuchus phasianellus columbianus chick survival was found to decrease by 50% with more than 10 turbines within 2.1 km of the nest (Proett 2017), however this effect was not detected in a second study (Proett et al. 2019). Differences between studies may be linked to the goal...
of the study, e.g., focusing on resource selection or survival, which supports a multi-method approach when studying the impact of disturbances on grouse populations. The differences might also be explained by species specific characteristics, such as variation in predator avoidance behaviour or habitat (i.e. some of the studied grouse species occur in open prairie ecosystems whereas others in forests). Future studies should try to account for these factors, while studying long term effects of WEF on grouse, preferably using a before–after–control impact study design. These studies should focus on the effects of WEF on grouse reproductive success and mortality to study if the behavioural response we found results in reduced population sizes or even the extinction of local populations. A systematic replication with a larger sample size covering several study areas would further support extrapolation of our results to capercaillie worldwide. Because our study was limited to data of capercaillie which were caught close to wind turbines, it might be argued that these birds had habituated to the presence of the wind farm operational since 2013. Habituation to wind turbines has been shown for other bird species (Madsen and Boertmann 2008) and it is therefore possible that the effects of WEF on capercaillie might even be stronger, i.e. causing complete avoidance during the first years after construction (Pearce-Higgins et al. 2012).

WEF impact their environment through different means, such as construction, visibility of the spinning turbine blades, their noise and shadow flickering. Accordingly, it can be challenging to determine the exact mechanism that affects wildlife (Langston and Pullan 2003). Similar to previous studies (Coppes et al. 2020b), a high degree of collinearity of the WEF predictors (i.e. turbine proximity, shadow, noise) was also prevalent in our study. It was therefore impossible to identify the exact mechanisms causing the behavioural response of capercaillie towards WEF, but there are several plausible pathways. The movement of wind turbine blades and the shadow flickering, both changing in speed and turning angle over time, might provoke an anti-predatory response in capercaillie, corresponding to the response to raptors, and thus causing reduced use of habitats close to wind turbines. Capercaillie are known to be sensitive to disturbance by human presence, and areas close to recreational infrastructure are used less than areas further away (Summers et al. 2007, Moss et al. 2014, Coppes et al. 2017, 2018b). Therefore, maintenance work close to wind turbines might explain the reduced selection of these sites. Follow-up use of roads and turbine pads by humans might further contribute to the avoidance of access roads. Likewise, mammalian predators (i.e. red fox or pine marten Martes martes) may adapt their behaviour following the construction of access roads (Heldin et al. 2017, Sirén et al. 2017), which might increase predation risk close to linear features due to increased predator activity (Gómez-Catasús et al. 2018). Access roads are cleared of snow for maintenance work, which could additionally affect predator activity in otherwise remote and hardly accessible areas. How mamma-

\( \text{(a)} \quad \text{(b)} \quad \text{(c)} \quad \text{(d)} \quad \text{(e)} \quad \text{(f)} \)

Figure 3. Conditional effect plots for capercaillie resource selection during the summer season (expressed by the RSF selection score \( w(x) \)) in dependence of wind turbine predictors. All other covariates were held at their mean. Predictions for the number of visible turbines and the distance to access roads were obtained using the model containing the number of turbines < 800 m (i.e. model (c) in Table 4). Crossbars and shaded areas in the background denote estimated effect thresholds and associated uncertainty estimates (95% quantile range in cross-validation).
Table 4. Results of the GLMMs estimating capercaillie resource selection during the summer season in response to (a) turbine shadow, (b) turbine noise, (c) the number of turbines within 800 m and (d) the distance to the closest turbine. AIC, Marginal $R^2$ and Conditional $R^2$ are provided for the models. Model coefficients ($\beta$), standard errors (SE) and default p-values are provided for the predictors. Land cover types are compared with the intercept ‘clear-cut < 5 years’.

(a) Turbine shadow

| Predictor                  | $\beta$  | SE     | p-value |
|----------------------------|----------|--------|---------|
| Intercept                  | -1.954   | 0.087  |         |
| Shadow                     | -0.062   | 0.027  | 0.021   |
| Shadow$^2$                 | -0.066   | 0.016  | < 0.001 |
| No. visible turbines       | -0.004   | 0.027  | 0.879   |
| No. visible turbines$^2$   | -0.073   | 0.015  | < 0.001 |
| Distance access road       | 0.163    | 0.016  | < 0.001 |
| Mean tree diameter         | 0.417    | 0.027  | < 0.001 |
| Mean tree diameter$^2$     | -0.164   | 0.023  | < 0.001 |
| Distance clear-cut $>$ 5 years | 0.138   | 0.019  | < 0.001 |
| Distance forest bog $>$ 5 years | -0.219 | 0.028  | < 0.001 |
| Distance forest bog$^2$    | 0.024    | 0.012  | 0.037   |
| Distance open bog          | 0.052    | 0.023  | 0.022   |
| Distance open bog$^2$      | 0.034    | 0.013  | 0.006   |
| Mean stand density         | 0.077    | 0.028  | 0.006   |
| Mean stand density$^2$     | -0.050   | 0.017  | 0.004   |
| LU: clear-cut $>$ 5 years  | -0.760   | 0.120  | < 0.001 |
| LU: forest bog             | -0.459   | 0.091  | < 0.001 |
| LU: open bog               | -1.789   | 0.228  | < 0.001 |
| LU: mixed forest           | -0.789   | 0.073  | < 0.001 |
| LU: other forest           | -0.568   | 0.106  | < 0.001 |
| LU: pine forest            | -0.534   | 0.074  | < 0.001 |
| LU: spruce forest          | -1.203   | 0.123  | < 0.001 |

(b) Turbine noise

| Predictor                  | $\beta$  | SE     | p-value |
|----------------------------|----------|--------|---------|
| Intercept                  | -1.841   | 0.089  |         |
| Turbine noise              | -0.012   | 0.044  | 0.786   |
| Turbine noise$^2$          | -0.160   | 0.021  | < 0.001 |
| No. visible turbines       | 0.010    | 0.027  | 0.700   |
| No. visible turbines$^2$   | -0.070   | 0.016  | < 0.001 |
| Distance access road       | 0.166    | 0.016  | < 0.001 |
| Mean tree diameter         | 0.404    | 0.027  | < 0.001 |
| Mean tree diameter$^2$     | -0.165   | 0.024  | < 0.001 |
| Distance clear-cut $<$ 5 years | -0.042   | 0.020  | 0.037   |

(c) No. of turbines $<$ 800 m

| Predictor                  | $\beta$  | SE     | p-value |
|----------------------------|----------|--------|---------|
| Intercept                  | -1.938   | 0.088  |         |
| No. turbines $<$ 800 m     | -0.156   | 0.046  | < 0.001 |
| No. turbines $<$ 800 m$^2$ | -0.068   | 0.023  | 0.003   |
| No. visible turbines       | 0.024    | 0.026  | 0.356   |
| No. visible turbines$^2$   | -0.072   | 0.016  | < 0.001 |
| Distance access road       | 0.166    | 0.016  | < 0.001 |
| Mean tree diameter         | 0.404    | 0.027  | < 0.001 |
| Mean tree diameter$^2$     | -0.166   | 0.023  | < 0.001 |
| Distance clear-cut $<$ 5 years | -0.035   | 0.020  | 0.089   |
| Distance clear-cut $>$ 5 years | 0.133   | 0.019  | < 0.001 |
| Distance forest bog        | -0.190   | 0.028  | < 0.001 |
| Distance forest bog$^2$    | 0.031    | 0.012  | 0.008   |
| Distance open bog          | 0.078    | 0.023  | < 0.001 |
| Distance open bog$^2$      | 0.026    | 0.013  | 0.040   |
| Mean stand density         | 0.073    | 0.028  | 0.008   |
| Mean stand density$^2$     | -0.050   | 0.017  | 0.040   |
| LU: clear-cut $>$ 5 years  | -0.829   | 0.120  | < 0.001 |
| LU: forest bog             | -0.468   | 0.091  | < 0.001 |
| LU: open bog               | -1.826   | 0.228  | < 0.001 |
| LU: mixed forest           | -0.805   | 0.073  | < 0.001 |
| LU: other forest           | -0.597   | 0.106  | < 0.001 |
| LU: pine forest            | -0.557   | 0.074  | < 0.001 |
| LU: spruce forest          | -1.209   | 0.123  | < 0.001 |

(d) Distance to the closest turbine

| Predictor                  | $\beta$  | SE     | p-value |
|----------------------------|----------|--------|---------|
| Intercept                  | -1.724   | 0.093  |         |
| Distance turbine           | 0.031    | 0.036  | 0.385   |
| Distance turbine$^2$       | -0.345   | 0.031  | < 0.001 |
| Distance turbine$^3$       | 0.118    | 0.014  | < 0.001 |
| No. visible turbines       | 0.006    | 0.027  | 0.820   |
| No. visible turbines$^2$   | -0.069   | 0.016  | < 0.001 |
| Distance access road       | 0.163    | 0.016  | < 0.001 |
| Mean tree diameter         | 0.402    | 0.027  | < 0.001 |
| Mean tree diameter$^2$     | -0.168   | 0.024  | < 0.001 |
| Distance clear-cut $<$ 5 years | -0.039   | 0.021  | 0.060   |
| Distance clear-cut $>$ 5 years | 0.133   | 0.020  | < 0.001 |
| Distance forest bog        | -0.185   | 0.028  | < 0.001 |
| Distance forest bog$^2$    | 0.027    | 0.012  | 0.022   |
| Distance open bog          | 0.065    | 0.023  | 0.005   |
| Distance open bog$^2$      | 0.026    | 0.013  | 0.043   |
| Mean stand density         | 0.073    | 0.028  | 0.008   |
| Mean stand density$^2$     | -0.042   | 0.017  | 0.016   |
| LU: clear-cut $>$ 5 years  | -0.866   | 0.121  | < 0.001 |
| LU: forest bog             | -0.506   | 0.091  | < 0.001 |
| LU: open bog               | -1.827   | 0.299  | < 0.001 |
| LU: mixed forest           | -0.821   | 0.074  | < 0.001 |
| LU: other forest           | -0.605   | 0.106  | < 0.001 |
| LU: pine forest            | -0.587   | 0.075  | < 0.001 |
| LU: spruce forest          | -1.208   | 0.123  | < 0.001 |
lian predators or raptor populations are affected by wind turbines and their infrastructure in our study area is, however, unknown. To date, studies on the effects of renewable energy infrastructure on wildlife show that they are also dependent on the size, type, number and location of the WEF (Lyon and Anderson 2003, Aldridge and Boyce 2007, Harju et al. 2010), but it was beyond the scope of our study to distinguish between different turbine types.

We assumed that capercaillie resource selection in the wind farm may differ between lekking period and summer season. Males gather around traditional leks and produce visual and acoustic signals to attract females, which may be masked by the noise of WEF and could influence mating success. Noise generated by wind turbines has been shown to affect vocalizations of lekking male greater prairie-chicken (Whalen et al. 2018, 2019), and also greater sage-grouse abundance at leks decreased with experimental intermittent noise created by gas rigs and their access roads (Blickley et al. 2012). Indeed, turbine noise had by far the strongest effects during the lekking season (Fig. 2), although the model for noise had considerably less support (i.e. lower AIC) than those for turbine density or shadow.

The magnitude of impact might also be dependent on habitat suitability or availability. Given a wide-ranging forest landscape with regularly distributed high-quality habitat patches, avoidance of WEF by capercaillie may be more likely than in low-quality areas, where the few attractive patches might be close to turbines (Percival 2005). Capercaillie selected for stands with intermediate mean tree diameter and intermediate density during summer (Supplementary information). Stand density and mean tree diameter reflect, amongst others, the canopy cover in a forest stand (Miettinen et al. 2010), and stands with low to intermediate canopy cover are an important component for capercaillie habitat suitability (Storch 1995). We found a preference for areas bordering forest bogs, which is in line with other studies highlighting the suitability of forest bogs as capercaillie habitat (Rolstad 1989, Wegge et al. 2005, Miettinen et al. 2010). That capercaillie select young clear-cuts was also found by Storch (1995) in the Bavarian Alps.

Average summer MCPs for males were larger (504 ± 301 ha) than reported for greater prairie-chicken (Winder et al. 2010), but it was beyond the scope of our study to distinguish between different turbine types.

Management implications

Our study indicates that capercaillie resource selection may be affected by the presence of wind turbines. We derived a distance threshold of 865 m (CI 784–1025 m) beyond which turbine effects appear negligible. This result can be easily applied in conservation and WEF planning, especially where capercaillie show distinct or patchy distribution patterns. For areas with a wide-ranging capercaillie distribution (as in Scandinavia), our distance threshold should at least be considered for those locations most important for species survival, such as brood summer habitats and lekking grounds. Although it remains unknown whether the detected effects bear actual fitness costs, particularly in small or threatened populations, e.g. those with unfavourable conservation status according to EU legislation, avoid WEF construction within 865 m from capercaillie habitats, to exclude the risk of negative population-level effects by the presence of wind turbines.

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Supplementary information (available online as Appendix wlb-00737 at <www.wildlifebiology.org/appendix/wlb-00737>).