Wind energy facilities affect resource selection of capercaillie Tetrao urogallus

Authors: Taubmann, Julia, Kämmerle, Jim-Lino, Andrén, Henrik, Braunisch, Veronika, Storch, Ilse, et al.

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

Julia Taubmann, Jim-Lino Kämmerle, Henrik Andrén, Veronika Braunisch, Ilse Storch, Wolfgang Fiedler, Rudi Suchant and Joy Coppes

J. Taubmann (https://orcid.org/0000-0002-8339-0184), J.-L. Kämmerle (https://orcid.org/0000-0002-5751-9757), V. Braunisch (https://orcid.org/0000-0001-7035-4662), R. Suchant (https://orcid.org/0000-0003-3600-7063) and J. Coppes (https://orcid.org/0000-0002-5295-8638) ✉ (joy.coppes@forst.bwl.de), Forest Research Inst. of Baden-Wuerttemberg FVA, Freiburg, Germany. VB also at: Conservation Biology, Inst. of Ecology and Evolution, Univ. of Bern, Bern, Switzerland. – H. Andrén (https://orcid.org/0000-0002-5616-2426), Grimsö Wildlife Research Station, Dept of Ecology, Swedish Univ. of Agricultural Sciences, Riddarhyttan, Sweden. – JT and I. Storch (https://orcid.org/0000-0002-3252-2036), Chair of Wildlife Ecology and Management, Univ. of Freiburg, Freiburg, Germany. – W. Fiedler (https://orcid.org/0000-0003-1082-4161), Dept of Migration and Immuno-Ecology, Max Planck Inst. of Animal Behavior, Radolfzell, Germany.

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,

1

Pearce-Higgins et al. 2009, Pruett et al. 2009, Winder et al. 2014b). Furthermore, fragmentation of forest landscapes by human land use may increase predator abundance (Kurki et al. 1998, Pasanen-Mortensen and Elmhagen 2015) for example infrastructures such as maintenance roads and buildings may concentrate fox activity (MacDonald 1980, Helldin et al. 2017, Hradsky et al. 2017). Accordingly, predation risk may be higher close to WEF. However, there is still a research deficit on the indirect effects of WEF in wildlife, especially for forest-dwelling species (Hötker et al. 2005, Hovick et al. 2014). Despite this knowledge gap, increasing numbers of wind turbines are being constructed in forests (Richarz 2014).

Grouse (*Tetraoninae*) are known for their sensitivity to human disturbance (Storch 2013, Hovick et al. 2014, Bartuszevige and Daniels 2016, Coppes et al. 2017). Many grouse species exhibit high site fidelity and are thus considered particularly vulnerable when their habitat overlaps with high-wind speed areas attractive for turbine construction, especially when alternative habitat is not available (Tabassum-Abbasi et al. 2014, Braunisch et al. 2015). A recent review has identified negative effects of WEF on the behaviour of seven grouse species, such as avoidance, displacement of lekking or nesting sites, or time investment in breeding and non-breeding behaviour, raising concerns about the long-term effects of WEF, particularly for small and threatened populations (Coppes et al. 2020a). We used capercaillie *Tetrao urogallus*, a large forest grouse species, as our model species as it occurs over a large geographical range, and is considered an indicator species of structurally diverse forests with high species diversity (Suter et al. 2002, Pakkala et al. 2003). Furthermore, the species is red-listed at national and European levels. Especially where populations are limited to mountain ranges, there is a large overlap between areas with high-wind speed and habitats of capercaillie (Braunisch et al. 2015), causing growing concerns on the effects of WEF on capercaillie throughout the northern hemisphere. Although indirect presence counts suggest that WEF affect capercaillie habitat use, (González and Ena 2011, González et al. 2016, Coppes et al. 2020b) the effects of WEF in forests on capercaillie are not well understood.

To address this knowledge gap, we used high-resolution GPS-tracking to study capercaillie resource selection in an existing wind farm in central Sweden during two seasons important for the species' reproduction: the lekking season, important for mating and the summer season, important for raising the young. Specifically, we analysed whether capercaillie resource selection was related to WEF presence, density, visibility, noise emissions, shadow and turbine access roads while controlling for habitat characteristics in order to derive management recommendations for the evaluation of WEF development in forest grouse habitat.

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 Jädraås wind farm with 68 Vestas V112 turbines, operational since 2013, and the Mombyåsen 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
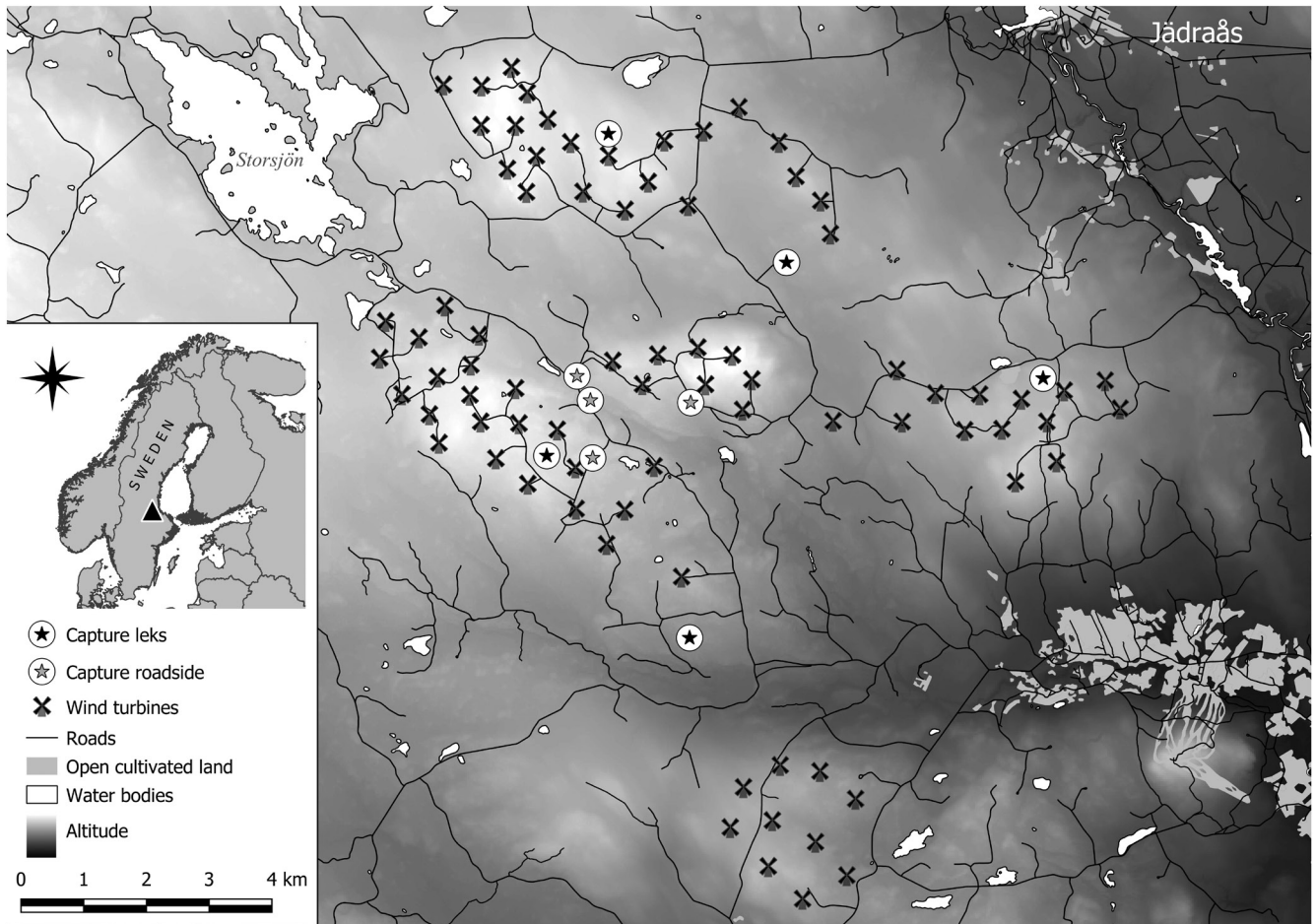
Figure 1. Location of the study area in central Sweden in Dalarna and Gävleborg County is given as a black triangle in the inlay map. Grey shading indicates elevation range between 65 and 465 m. Forest roads have partially been constructed and enlarged as access roads to wind turbines. Open cultivated land includes pastures, buildings and recreational areas. The sites where capercaillie captured are marked with stars, black indicating the lekking sites and grey stars the sand bath capture sites.

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 Skogskarta 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, Mikoláš 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

Table 1. Predictors considered for modelling resource selection of capercaillie during the lekking (model lek) or the summer (model summer) season. Notes: variables correlated > |0.5| and/or with no explanatory power were rejected from the multivariate full-models. The check marks indicate which predictors were included in the RSF models for the lekking and summer season, respectively. Data is described as categorical (cat.) or continuous (cont.).

Category	Description	Unit	Type	Model lek	Model summer
Land cover	Land cover types	Pine *Pinus sylvestris* forest	cat.		✓
		Spruce *Pica abies* forest			✓
		Mixed forest			✓
		Other forest			✓
		Open bog			✓
		Forest bog			✓
		Clear-cut < 5 years			✓
		Clear-cut > 5 years			✓
	Distance to open bog	m	cont.	✓	✓
	Distance to forest bog	m	cont.	✓	✓
Forestry	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		cont.	✓	✓
	Distance to turbine	m	cont.		✓
	No. of visible turbines		cont.	✓	✓
	Distance to access road	m	cont.	✓	✓

4

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 Urbano and Cagnacci 2014) separately for the two seasons considered (i.e. lekking and summer) and per individual within each individual's 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 for all covariates.

To estimate selection coefficients, we fitted GLMMs for each season with presence locations (1) and random locations (0) as a binary response variable and animal-ID as a random intercept. We included a total of six wind turbine predictors and seven environmental covariates in the models (Table 1). We dropped land cover and mean stand density from the models for the lekking season due to convergence issues on the comparatively small dataset for this season. Prior to analysis we calculated pairwise correlations of environmental predictors and only retained covariates with a Pearson correlation coefficient of $|r| \leq 0.5$. Due to high collinearity among wind turbine predictors (Supplementary information) we built four different competing models, each including the distance to turbine access roads and number of visible turbines at a given location with one of the following four predictors respectively: the meteorologically plausible amount of shadow, the distance to the turbine, the noise emission of the turbine and the number of wind turbines within a radius of 800 m around each location. We refrained from using the distance to the turbines in the models for the lekking season, because the position of animal home ranges relative to the turbines was considered biased by the position of the lekking site during this season (as animals were caught at lekking sites close to turbines), whereas noise and shadow could potentially affect small-scale resource selection within home ranges. We included higher-order polynomials when a non-linear response was expected and retained them if there was support. We otherwise compared and interpreted full models for each season and predictor combination. All final models were also fitted on the reduced dataset to evaluate potential effects of location error on the estimated selection coefficients. We found no evidence for such an influence and thus proceeded with the complete dataset. Before proceeding with building the RSF, we evaluated the stability of beta coefficient estimates in the final models (and particularly the higher-order terms) by means of blocked cross-validation (CV; 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 β_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 meter 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. Data

5

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			–	✓	✓
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	–	–	–	153	430	832		✓
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	✓	✓
m	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 R^2 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 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 R^2 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).

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 R^2 and Conditional R^2 are provided for the models. Model coefficients (β), standard errors (SE) default p-values are provided for the predictors.

(a) Turbine shadow	Marginal R^2: 0.221			(b) Turbine noise	Marginal R^2: 0.250		
AIC: 5888.6 (Δ2.6)	Conditional R^2: 0.310			AIC: 5894.3 (Δ8.3)	Conditional R^2: 0.411		
Predictor	β	SE	p-value	Predictor	β	SE	p-value
Intercept	−2.888	0.258		Intercept	−3.191	0.358	
Turbine shadow	−0.271	0.112	0.015	Turbine noise	−0.443	0.140	0.002
Turbine shadow^2	−0.186	0.070	0.008	Turbine noise^2	0.309	0.082	< 0.001
No. visible turbines	−0.010	0.068	0.879	No. visible turbines	−0.052	0.068	0.442
No. visible turbines^2	−0.160	0.045	< 0.001	No. visible turbines^2	−0.181	0.046	< 0.001
Distance access road	0.617	0.103	< 0.001	Distance access road	0.710	0.109	< 0.001
Mean tree diameter	−0.119	0.065	0.070	Mean tree diameter	−0.100	0.066	0.129
Mean tree diameter^2	−0.064	0.034	0.060	Mean tree diameter^2	−0.052	0.034	0.120
Distance clear-cut < 5 y	−0.403	0.119	< 0.001	Distance clear-cut < 5 y	−0.221	0.126	0.080
Distance clear-cut > 5 y	0.302	0.087	< 0.001	Distance clear-cut > 5 y	0.382	0.090	< 0.001
Distance forest bog	0.079	0.110	0.472	Distance forest bog	0.233	0.113	0.039
Distance forest bog^2	0.269	0.054	< 0.001	Distance forest bog^2	0.210	0.056	< 0.001
Distance open bog	0.467	0.091	< 0.001	Distance open bog	0.469	0.090	< 0.001
Distance open bog^2	0.156	0.042	< 0.001	Distance open bog^2	0.101	0.045	0.023

(c) No. of turbines < 800 m	Marginal R^2: 0.249		
AIC: 5886.0 (Δ0.0)	Conditional R^2: 0.366		
Predictor	β	SE	p-value
Intercept	−3.181	0.304	
No. turbines < 800 m	−0.577	0.109	< 0.001
No. turbines < 800 m^2	0.275	0.076	< 0.001
No. visible turbines	−0.056	0.068	0.407
No. visible turbines^2	−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 diameter^2	−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 bog^2	0.212	0.056	< 0.001
Distance open bog	0.479	0.091	< 0.001
Distance open bog^2	0.091	0.044	0.040

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-
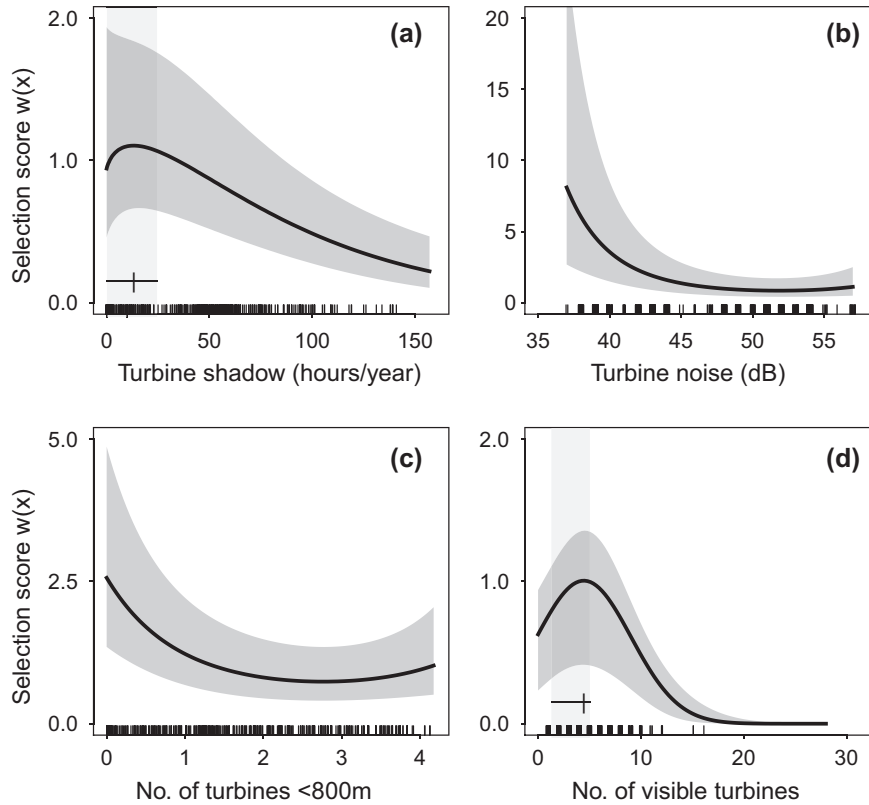
Figure 2. Conditional effect plots for capercaillie resource selection during the lekking season (expressed by the RSF selection score $w(x)$) in dependence of wind turbine predictors. All other covariates were held at their mean. Predictions for the number of visible turbines were obtained using the model containing the number of turbines < 800 m (i.e. model (c) in Table 3). Crossbars and shaded areas in the background denote estimated effect thresholds and associated uncertainty estimates (95% quantile range in cross-validation).

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 *Centrocercus 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
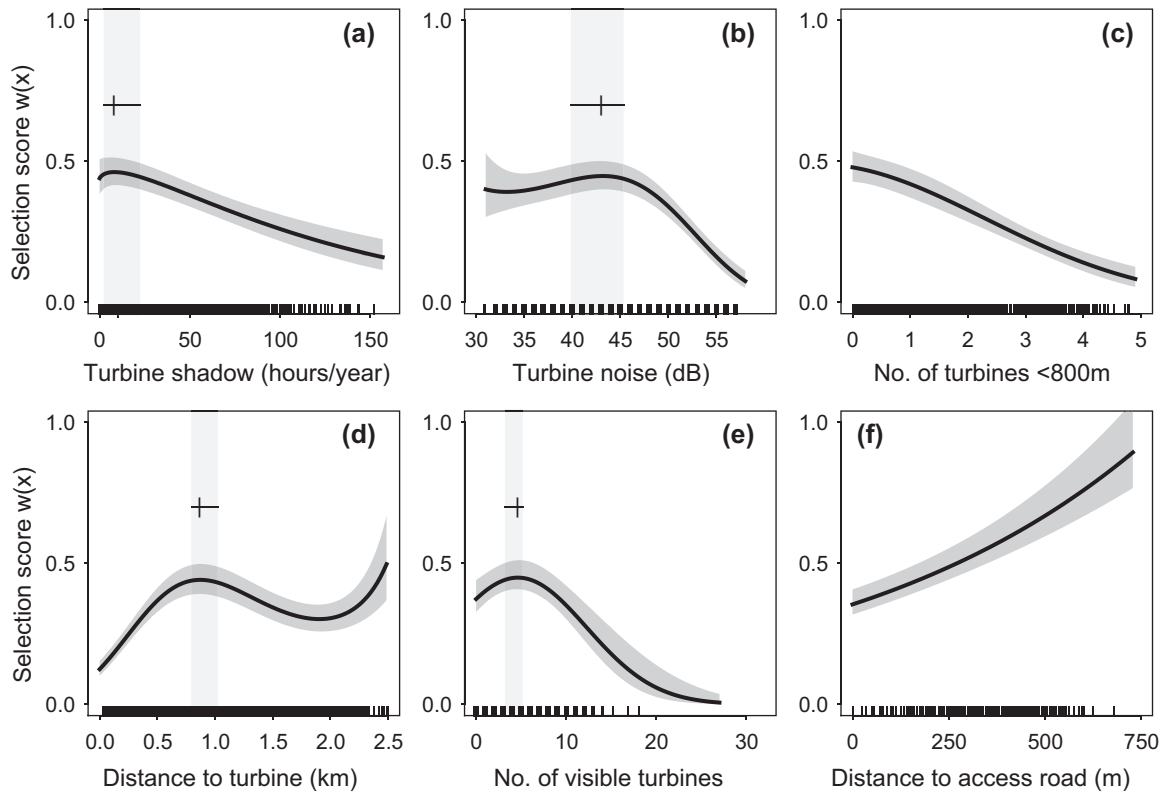
Figure 3. Conditional effect plots for capercaillie resource selection during the summer season (expressed by the RSF selection score $w(x)$) in dependence of wind turbine predictors. All other covariates were held at their mean. Predictions for the number of visible turbines and the distance to access 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).

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 (Helldin 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-

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 (β), 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	Marginal R^2: 0.195			(b) Turbine noise	Marginal R^2: 0.201		
AIC: 32341.5 (Δ118.4)	Conditional R^2: 0.199			AIC: 32261.9 (Δ38.8)	Conditional R^2: 0.207		
Predictor	β	SE	p-value	Predictor	β	SE	p-value
Intercept	−1.954	0.087		Intercept	−1.841	0.089	
Shadow	−0.062	0.027	0.021	Turbine noise	−0.012	0.044	0.786
Shadow^2	−0.066	0.016	< 0.001	Turbine noise^2	−0.160	0.021	< 0.001
				Turbine noise^3	−0.062	0.019	< 0.001
No. visible turbines	−0.004	0.027	0.879	No. visible turbines	0.010	0.027	0.700
No. visible turbines^2	−0.073	0.015	< 0.001	No. visible turbines^2	−0.070	0.016	< 0.001
Distance access road	0.163	0.016	< 0.001	Distance access road	0.166	0.016	< 0.001
Mean tree diameter	0.417	0.027	< 0.001	Mean tree diameter	0.404	0.027	< 0.001
Mean tree diameter^2	−0.164	0.023	< 0.001	Mean tree diameter^2	−0.165	0.024	< 0.001
Distance clear-cut < 5 years	−0.044	0.020	0.029	Distance clear-cut < 5 years	−0.042	0.020	0.037
Distance clear-cut > 5 years	0.138	0.019	< 0.001	Distance clear-cut > 5 years	0.140	0.020	< 0.001
Distance forest bog	−0.219	0.028	< 0.001	Distance forest bog	−0.193	0.028	< 0.001
Distance forest bog^2	0.024	0.012	0.037	Distance forest bog^2	0.029	0.012	0.014
Distance open bog	0.052	0.023	0.022	Distance open bog	0.071	0.023	0.002
Distance open bog^2	0.034	0.013	0.006	Distance open bog^2	0.029	0.013	0.020
Mean stand density	0.077	0.028	0.006	Mean stand density	0.075	0.028	0.007
Mean stand density^2	−0.050	0.017	0.004	Mean stand density^2	−0.047	0.017	0.007
LU: clear-cut > 5 years	−0.760	0.120	< 0.001	LU: clear-cut > 5 years	−0.821	0.120	< 0.001
LU: forest bog	−0.459	0.091	< 0.001	LU: forest bog	−0.474	0.091	< 0.001
LU: open bog	−1.789	0.228	< 0.001	LU: open bog	−1.834	0.229	< 0.001
LU: mixed forest	−0.789	0.073	< 0.001	LU: mixed forest	−0.805	0.073	< 0.001
LU: other forest	−0.568	0.106	< 0.001	LU: other forest	−0.595	0.106	< 0.001
LU: pine forest	−0.534	0.074	< 0.001	LU: pine forest	−0.557	0.075	< 0.001
LU: spruce forest	−1.203	0.123	< 0.001	LU: spruce forest	−1.210	0.123	< 0.001

(c) No. of turbines < 800 m	Marginal R^2: 0.205			(d) Distance to the closest turbine	Marginal R^2: 0.201		
AIC: 32223.0 (Δ0.0)	Conditional R^2: 0.211			AIC: 32246.6 (Δ23.6)	Conditional R^2: 0.208		
Predictor	β	SE	p-value	Predictor	β	SE	p-value
Intercept	−1.938	0.088		Intercept	−1.724	0.093	
No. turbines < 800 m	−0.156	0.046	< 0.001	Distance turbine	0.031	0.036	0.385
No. turbines < 800 m^2	−0.068	0.023	0.003	Distance turbine^2	−0.345	0.031	< 0.001
				Distance turbine^3	0.118	0.014	< 0.001
No. visible turbines	0.024	0.026	0.356	No. visible turbines	0.006	0.027	0.820
No. visible turbines^2	−0.072	0.016	< 0.001	No. visible turbines^2	−0.069	0.016	< 0.001
Distance access road	0.166	0.016	< 0.001	Distance access road	0.163	0.016	< 0.001
Mean tree diameter	0.404	0.027	< 0.001	Mean tree diameter	0.402	0.027	< 0.001
Mean tree diameter^2	−0.166	0.023	< 0.001	Mean tree diameter^2	−0.168	0.024	< 0.001
Distance clear-cut < 5 years	−0.035	0.020	0.089	Distance clear-cut < 5 years	−0.039	0.021	0.060
Distance clear-cut > 5 years	0.133	0.019	< 0.001	Distance clear-cut > 5 years	0.133	0.020	< 0.001
Distance forest bog	−0.190	0.028	< 0.001	Distance forest bog	−0.185	0.028	< 0.001
Distance forest bog^2	0.031	0.012	0.008	Distance forest bog^2	0.027	0.012	0.022
Distance open bog	0.078	0.023	< 0.001	Distance open bog	0.065	0.023	0.005
Distance open bog^2	0.026	0.013	0.040	Distance open bog^2	0.026	0.013	0.043
Mean stand density	0.073	0.028	0.008	Mean stand density	0.073	0.028	0.008
Mean stand density^2	−0.050	0.017	0.040	Mean stand density^2	−0.042	0.017	0.016
LU: clear-cut > 5 years	−0.829	0.120	< 0.001	LU: clear-cut > 5 years	−0.866	0.121	< 0.001
LU: forest bog	−0.468	0.091	< 0.001	LU: forest bog	−0.506	0.091	< 0.001
LU: open bog	−1.826	0.228	< 0.001	LU: open bog	−1.887	0.229	< 0.001
LU: mixed forest	−0.805	0.073	< 0.001	LU: mixed forest	−0.821	0.074	< 0.001
LU: other forest	−0.597	0.106	< 0.001	LU: other forest	−0.605	0.106	< 0.001
LU: pine forest	−0.557	0.074	< 0.001	LU: pine forest	−0.587	0.075	< 0.001
LU: spruce forest	−1.209	0.123	< 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 from Rolstad (1988) in Norway (170 ha) and Storch (1993) from the Bavarian Alps (248 ha), possibly explained by a longer time period included in our study, but were of similar size to those found in the Black Forest (581 and 207 ha, respectively, Coppes et al 2017). Because we only had data on capercaillie resource selection after the construction of the wind farm, we could not determine whether capercaillie home range size or selection was affected by the presence of the wind turbines or associated infrastructure, as has been reported for greater prairie-chicken (Winder et al. 2014a).

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 additional causes of habitat deterioration should be minimised. We therefore advise to apply the precautionary principle and, in areas with threatened and/or small 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.

References

Aldridge, C. L. and Boyce, M. S. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. – Ecol. Appl. 17: 508–526.

Arnett, E. B. et al. 2008. Patterns of bat fatalities at wind energy facilities in North America. – J. Wildl. Manage. 72: 61–78.

Bartuszevige, A. M. and Daniels, A. 2016. Impacts of energy development, anthropogenic structures, and land use change on lesser prairie chickens. – In: Haukos, D. A. and Boal, C. (eds), Ecology and conservation of lesser prairie chickens. Taylor & Francis.

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bauer, H. G. et al. 2005. Das Kompendium der Vögel Mitteleuropas: Band 1: Nonpasseriformes. 2. – Aula-Verlag Wiebelsheim, Auflage, pp. 175–178.

Blickley, J. L. et al. 2012. Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. – Conserv. Biol. 26: 461–471.

Bollmann, K. et al. 2008. Small-scale habitat use of western capercaillie in the Alps. – Der Ornithol. Beobachter 105: 53–61.

Braunisch, V. et al. 2015. Underpinning the precautionary principle with evidence: a spatial concept for guiding wind power development in endangered species' habitats. – J. Nat. Conserv. 24: 31–40.

Breuer, W. 2001. Windenergie und Vögel – Planerische Konsequenzen, Anforderungen und Probleme. – In: Tagungsband der Fachtagung 'Windenergie und Vögel – Ausmaß und Bewältigung eines Konfliktes'. 29. Technische Universität Berlin.

Casper, R. M. 2009. Guidelines for the instrumentation of wild birds and mammals. – Anim. Behav. 78: 1477–1483.

Ciuti, S. et al. 2018. An efficient method to exploit Li DAR data in animal ecology. – Methods Ecol. Evol. 9: 893–904.

Cochran, W. W. 1980. Wildlife telemetry. – In: Schemnitz, S. D. et al. (eds), Wildlife management techniques manual. The Wildlife Society, Washington DC, pp. 507–520.

Coppes, J. et al. 2015. The challenge of creating a large-scale capercaillie distribution map. – Grouse News 50: 21–23.

Coppes, J. et al. 2017. Outdoor recreation causes effective habitat reduction in capercaillie *Tetrao urogallus*: a major threat for geographically restricted populations. – J. Avian Biol. 48: 1583–1594.

Coppes, J. et al. 2018a. The importance of individual heterogeneity for interpreting faecal glucocorticoid metabolite levels in wildlife studies. – J. Appl. Ecol. 55: 2043–2054.

Coppes, J. et al. 2018b. Habitat suitability modulates the response of wildlife to human recreation. – Biol. Conserv. 227: 56–64.

Coppes, J. et al. 2020a. The impact of wind energy facilities on grouse: a systematic review. – J. Ornithol. 161: 1–15.

Coppes, J. et al. 2020b. Consistent effects of wind turbines on habitat selection of capercaillie across Europe. – Biol. Conserv. 244: 108529.

De Lucas, M. and Perrow, M. 2017. Birds: collisions. – In: Perrow, M. (ed.), Wildlife and wind farms: conflicts and solutions, Vol. 1. Onshore: potential effects. Pelagic, Exeter, pp. 155–190.

De Lucas, M. et al. 2007. Birds and wind farms: risk assessment and mitigation. – Quercus, Madrid, Spain.

EMD International A/S 2018. WindPRO 3.1. – <www.emd.dk>.

Gjerde, I. and Wegge, P. 1989. Spacing pattern, habitat use and survival of capercaillie in a fragmented winter habitat. – Ornis Scand. 20: 219–225.

Gómez-Catasús, J. et al. 2018. Landscape changes associated to wind farm implementation increase predation on artificial ground-nests. – In: Proc. 5th European Congr. of conservation biology.

González, M. A. and Ena, V. 2011. Cantabrian capercaillie signs disappeared after a wind farm construction. – Chioglossa 3: 65–74.

González, M. A. et al. 2016. Severe decline in Cantabrian capercaillie *Tetrao urogallus cantabricus* habitat use after construction of a wind farm. – Bird Conserv. Int. 26: 256–261.

Graf, R. F. et al. 2009. Habitat assessment for forest dwelling species using LiDAR remote sensing: capercaillie in the Alps. – For. Ecol. Manage. 257: 160–167.

Harju, S. M. et al. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. – J. Wildl. Manage. 74: 437–448.

Helldin, J. O. et al. 2017. Terrestrial mammals. – In: Perrow, M. (ed.), Wildlife and wind farms: conflicts and solutions, Vol. 1. Pelagic, Exeter, UK, pp. 222–240.

Hoover, S. L. and Morrison, M. L. 2005. Behavior of red-tailed hawks in a wind turbine development. – J. Wildl. Manage. 69: 150–159.

Hötker, H. 2017. Birds: displacement. – In: Perrow, M. (ed.), Wildlife and wind farms: conflicts and solutions, Vol. 1. Pelagic, Exeter, UK, pp. 119–154.

Hötker, H. et al. 2005. Auswirkungen regenerativer Energiegewinnung auf die biologische Vielfalt am Beispiel der Vögel und der Fledermäuse. –BfN Skripten 142: 1–83.

Hovick, T. J. et al. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. – J. Appl. Ecol. 51: 1680–1689.

Hradsky, B. A. et al. 2017. Human-modified habitats facilitate forest-dwelling populations of an invasive predator, *Vulpes vulpes*. – Sci. Rep. 7: 1–12.

Jahren, T. et al. 2016. Declining reproductive output in capercaillie and black grouse – 16 countries and 80 years. – Anim. Biol. 66: 363–400.

Johnsgard, P. A. 1983. The grouse of the world. – Univ. of Nebraska Press, Lincoln, NE.

Klaus, S. et al. 1989. Die Auerhühner. – Westarp Wissenschaften, Magdeburg.

Kunz, T. H. et al. 2007. Ecological impacts of wind energy development on bats: question, research needs and hypotheses. – Front. Ecol. Environ. 5: 315–324.

Kurki, S. et al. 1998. Abundances of red fox and pine marten in relation to the composition of boreal forest landscapes. – J. Anim. Ecol. 67: 874–86.

Langston, R. H. W. and Pullan, J. D. 2003. Windfarms and birds: an analysis of the effects of wind farms on birds, and guidance on environmental assessment criteria and site selection issues. – RSPB/Birdlife International, Strasbourg.

Lantmäteriet 2017a. Maps. – <www.lantmateriet.se/en/Maps-and-geographic-information/Maps/>, accessed 14 June 2017.

Lantmäteriet 2017b. Elevation data. – <www.lantmateriet.se/en/Maps-and-geographic-information/Elevation-data-/>, accessed 14 June 2017.

Lantmäteriet 2018. LiDAR data. – <ftp://download-opendata.lantmateriet.se/Laserdata_Skog/2018/18D022/>, accessed 1 September 2018.

LeBeau, C. W. et al. 2017. Greater sage-grouse habitat selection, survival, and wind energy infrastructure. – J. Wildl. Manage. 81: 690–711.

Lele, S. R. et al. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. – J. Anim. Ecol. 82: 1183–1191.

Lior, N. 2008. Energy resources and use: the present situation and possible paths to the future. – Energy 33: 842–857.

Loss, S. R. et al. 2013. Estimates of bird collision mortality at wind facilities in the contiguous United States. – Biol. Conserv. 168: 201–209.

Lyon, A. G. and Anderson, S. H. 2003. Potential gas development impacts on sage grouse nests initiation and movement. – Wildl. Soc. Bull. 31: 486–491.

MacDonald, D. W. 1980. Patterns of scent marking with urine and faeces amongst carnivore communities. – In: Symp. Zool. Soc. London, Vol. 45, No. 107, p. e139.

Madsen, J. and Boertmann, D. 2008. Animal behavioral adaptation to changing landscapes: spring-staging geese habituate to wind farms. – Landscape Ecol. 23: 1007–1011.

Manly, B. F. J. et al. 2002. Resource selection by animals: statistical design and analysis for field studies. – Kluwer Academic Publishers.

Mikoláš, M. et al. 2015. Evaluating forest management intensity on an umbrella species: capercaillie persistence in central Europe. – For. Ecol. Manage. 354: 26–34.

Miettinen, J. et al. 2010. Capercaillie (*Tetrao urogallus*) habitat characteristics in north-boreal Finland. – Silva Fenn. 44: 235–254.

12

Miller, T. A. et al. 2014. Assessing risk to bird from industrial wind energy development via paired resource selection models. – Conserv. Biol. 28: 745–755.

Moss, R. et al. 2014. Impacts of human disturbance on capercaillie *Tetrao urogallus* distribution and demography in Scottish woodland. – Wildl. Biol. 20: 1–18.

Pakkala, T. et al. 2003. Capercaillie *Tetrao urogallus* – a good candidate for an umbrella species in taiga forests. – Wildl. Biol. 9: 309–316.

Pasanen-Mortensen, M. and Elmhagen, B. 2015. Land cover effects on mesopredator abundance in the presence and absence of apex predators. – Acta Oecol. 67: 40–48.

Pearce-Higgins, J. W. et al. 2009. The distribution of breeding birds around upland wind farms. – J. Appl. Ecol. 46: 1323–1331.

Pearce-Higgins, J. W. et al. 2012. Greater impacts of wind farms on bird populations during construction than subsequent operation: results of a multi-site and multi-species analysis. – J. Appl. Ecol. 49: 386–394.

Percival, S. 2005. Birds and windfarms: what are the real issues? – Br. Birds 98: 194–204.

Plumb, R. T. et al. 2018. Lesser Prairie chicken space use in relation to anthropogenic structures. – J. Wildl. Manage. 83: 216–230.

Proett, M. C. 2017. The influence of wind energy development on Columbian sharp-tailed grouse (*Tympanuchus phasianellus columbianus*) breeding season ecology in eastern Idaho. – MSc thesis, Utah State Univ.

Proett, M. C. et al. 2019. Columbian sharp-tailed grouse nesting ecology: wind energy and habitat. – J. Wildl. Manage. 83: 1214–1225.

Pruett, C. L. et al. 2009. Avoidance behavior by prairie grouse: implications for development of wind energy. – Conserv. Biol. 23: 1253–1259.

Rabin, L. A. et al. 2006. The effects of wind turbines on antipredator behavior in California ground squirrels (*Spermophilus beecheyi*). – Biol. Conserv. 131: 410–420.

Renewable Energy Network. 2018. Renewables global status report-a comprehensive annual overview of the state of renewable energy. – REN21.

Richarz, K. 2014. Energie und Naturschutz. Windenergie im Lebensraum Wald. Statusreport und Empfehlungen. – Deutsche Wildtier Stiftung, Hamburg, <www.deutschewildtierstiftung.de/content/3-naturschutz/3-windenergie-und-artenschutz/studie-windenergie-im-wald-deutsche-wildtier-stiftung.pdf>, accessed 14 February 2020.

Roberts, D. R. et al. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical or phylogenetic structure. – Ecography 40: 913–929.

Rolstad, J. 1988. Autumn habitat of capercaillie in southeastern Norway. – J. Wildl. Manage. 52: 747–753.

Rolstad, J. 1989. Habitat and range use of capercaillie *Tetrao urogallus* L. in southcentral Scandinavian boreal forests, with special reference to the influence of modern forestry. – AgricD thesis, Dept of Nature Conservation, Agricultural Univ. of Norway, Ås, Norway.

Rolstad, J. and Wegge, P. 1989. Effects of logging on capercaillie (*Tetrao urogallus*) leks. – Scand. J. For. Res. 4: 111–127.

Rönning, G. 2017. Wind power developments kill capercaillie. – Tjäderkommittén <www.tjade robs.se/>, accessed 22 Feb 2018.

Sirén, A. P. et al. 2017. Potential influence of high-elevation wind farms on carnivore mobility. – J. Wildl. Manage. 81: 1505–1512.

Skogsstyrelsen 2018. Skogsdata. – <http://skogsdataportalen.skogsstyrelsen.se/Skogsdataportalen/>, accessed 20 January 2018.

SLU Skogskarta 2017. Skogsmarken data 2010. – <ftp://salix.slu.se/download/skogskarta>, accessed 10 October 2017.

Smith, A. and Willebrand, T. 1999. Mortality causes and survival rates of hunted and unhunted willow grouse. – J. Wildl. Manage. 67: 722–730.

Storch, I. 1993. Habitat selection by capercaillie in summer and autumn: is bilberry important? – Oecologia 95: 257–265.

Storch, I. 1995. The importance of scale in habitat conservation for an endangered species: the capercaillie in central Europe. – In: Bissonette, J. A. (ed.), Wildlife and landscape ecology. Effects of pattern and scale. Springer.

Storch, I. 1997. Male territoriality, female range use and spatial organisation of capercaillie *Tetrao urogallus* leks. – Wildl. Biol. 3: 149–161.

Storch, I. 2007. Grouse: status survey and conservation action plan 2006–2010. – IUCN, Gland, Switzerland and Fordingbridge, UK.

Storch, I. 2013. Human disturbance of grouse-why and when? – Wildl. Biol. 19: 390–403.

Summers, R. W. et al. 2004. Habitat selection and diet of the capercaillie *Tetrao urogallus* in Abernethy Forest, Strathspey, Scotland. – Bird Study 51: 58–68.

Summers, R. W. et al. 2007. Measuring avoidance by capercaillie *Tetrao urogallus* of woodlands close to tracks. – Wildl. Biol. 13: 19–27.

Suter, W. et al. 2002. Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. – Conserv. Biol. 16: 778–788.

Tabassum-Abbasi, P. M. et al. 2014. Wind energy: increasing deployment, rising environmental concerns. – Renew. Sustain. Energy Rev. 31: 270–288.

Thiel, D. et al. 2011. Winter tourism increases stress hormone levels in the capercaillie *Tetrao urogallus*. – Ibis 153: 122–133.

Urbano, F. and Cagnacci, F. 2014. Spatial database for gps wildlife tracking data – a practical guide to creating a data management system with PostgreSQL/PostGIS and R. – Springer International.

Wegge, P. and Larsen, B. B. 1987. Spacing of adult and subadult male common capercaillie during the breeding season. – Auk 104: 481–490.

Wegge, P. et al. 2005. Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. – Can. J. Zool. 83: 1547–1555.

Whalen, C. E. et al. 2018. Male greater prairie-chickens adjust their vocalizations in the presence of wind turbine noise. – Condor 120: 137–148.

Whalen, C. E. et al. 2019. Wind turbine noise limits propagation of greater prairie-chicken boom chorus, but does it matter? – Ethology 125: 863–875.

Winder, V. L. et al. 2014a. Space use by female greater prairie chickens in response to wind energy development. – Ecosphere 5: 1–17.

Winder, V. L. et al. 2014b. Effects of wind energy development on survival of female greater prairie chickens. – J. Appl. Ecol. 51: 395–405.

Zwart, M. C. et al. 2015. Using environmental impact assessment and post-construction monitoring data to inform wind energy developments. – Ecosphere 6: 1–11.

Zwart, M. C. et al. 2016. Wind farm noise suppresses territorial defense behavior in a songbird. – Behav. Ecol. 27: 101–108.

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