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Consistent effects of wind turbines on habitat selection of capercaillie across Europe

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ABSTRACT

There are growing concerns about the effects of wind turbines on wildlife. Additional mortality due to collisions with wind turbines has long been recognized as a direct negative effect, but less obvious effects such as changes in behaviour or displacement of disturbance sensitive wildlife are increasingly moving into focus. We combined systematic mapping of habitat structure and species presence before and after turbine-construction at 6 study areas in Germany, Austria and Sweden to study the effects of wind turbine presence on a large forest grouse species: the capercaillie (*Tetrao urogallus*). We studied effects of wind turbines on the observation density (percent of sampling plots with capercaillie presence per year and study area) and habitat selection. We did not find a significant difference in overall observation densities between turbine and control areas after turbine construction. At the sampling-plot scale, however, selection of habitats affected by wind turbines was reduced, indicating a form of habitat deterioration. This was detectable up to 650 m distance to the turbines, present across all study areas and independent of the structural habitat suitability at the respective site. Our results show that a disturbance-sensitive forest bird species is affected by wind energy development, and that critical-distances should be taken into account when planning wind energy development in grouse habitats.

1. Introduction

During the last decades, an increasing number of wind turbines have been constructed across the globe to reduce greenhouse gas emissions (Renewable Energy Network, 2018). Compared to other methods of generating electricity, wind turbines are considered to be more beneficial for the environment (Bolea et al., 2016). There are however increasing concerns about their effects on wildlife (Kuvlesky et al., 2007; Drewitt and Langston, 2008). For instance, negative effects of wind turbines have been found across taxa for mammals (Barclay et al., 2017; Helldin et al., 2017), reptiles (Lovich and Ennen, 2017), insects (Elzay et al., 2017) and birds (De Lucas and Perrow, 2017; Hötker, 2017). The most obvious effect of wind turbines on wildlife is increased mortality due to collisions with the turbine (Drewitt and Langston, 2008; De Lucas and Perrow, 2017), but other less direct impacts have also been documented. These include changes in birds´ vocalisation (Zwart et al., 2016; Szymański et al., 2017; Whalen et al., 2018; Whalen et al., 2019) or in predator avoidance behaviour (Rabin et al., 2006), avoidance of areas close to the turbines (Hötker, 2017) as well as reduced populations densities after turbine construction (Pearce-Higgins et al., 2009; Samson et al., 2016; Hötker, 2017). Although the amount of habitat loss caused by turbine construction appears to be relatively small in most cases, displacement of animals might be detectable over large distances around the wind turbine site (Samson et al., 2016; Hötker, 2017; Coppes et al., 2020).

The ultimate causes of animal displacement remain, however, often unclear. Possible causes of displacement may include noise, shadow flickering, the movement and sound of the turbine blades or increased

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human presence at the turbines due to maintenance or follow up use of the roads by recreationists (c.f. Langston and Pullan, 2004, Perrow, 2017). The construction of access roads might additionally affect wildlife habitat selection, including changes in habitat use by predator species (Agha et al., 2017; Helldin et al., 2017; Keehn and Feldman, 2018). Most studies showing negative effects of wind turbines on wildlife are, however, case studies, thus precluding general conclusions on the effects of wind turbines for a given species (Drewitt and Langston, 2006; Wang and Wang, 2015; Coppes et al., 2020). In addition, the specific effects of turbine construction and presence may be modulated by habitat type (e.g. grassland or forests), the habitat suitability at the site, the wind turbine type (e.g. height, size, configuration of a wind park) and species-related behavioural traits (e.g. disturbance sensitivity, antipredator behaviour). This makes displacement effects due to wind turbine development also highly species specific (Drewitt and Langston, 2006; Pearce-Higgins et al., 2012; Shaffer and Buhl, 2016). In addition, most studies focussing on displacement effects on birds have been performed in open landscape types such as grasslands (Hötker, 2017), while turbine effects on forest-dwelling species remain mostly unknown.

We studied the effects of wind turbines on capercaillie (*Tetrao urogallus*), a locally threatened forest grouse species, which is considered to be an umbrella species for boreal and mountain forest communities (Suter et al., 2002; Pakkala et al., 2003). By combining detailed records of habitat conditions with systematic records of target species presence in six study areas across a large geographical range in Europe, we explored effects of wind turbines on the target species while accounting for habitat suitability. We considered two levels of habitat selection (Johnson, 1980; Hutto, 1985), studying whether wind turbines affected 1) the percentage of plots with capercaillie presence (henceforth "sign density") and 2) local scale habitat selection.

2. Material and methods

2.1. Model species

The capercaillie is a large ground-nesting forest grouse (*Tetraoninae*), dependent on well-structured, mature forests with gaps in the canopy and abundant ground vegetation, ideally with a rich cover of bilberry (*Vaccinium myrtillus*) (Storch, 2007; Potapov and Sale, 2013; Zohmann et al., 2014). Owing to its specific habitat requirements and comparatively large spatial demands, capercaillie is considered as indicator species of boreal or mountain forests with high biodiversity (Suter et al., 2002; Pakkala et al., 2003). Due to its wide distribution across Eurasia (Klaus et al., 1989; Coppes et al., 2015), the species is categorized as globally not threatened (BirdLife International, 2016). However, many local or regional populations across Europe are highly fragmented, are declining or already threatened (Storch, 2007) and suffer from decreasing reproductive success (Jahren et al., 2016). Outside of the boreal forests of Fennoscandia, central and southern European populations are typically restricted to mountain forests at higher elevations (Klaus et al., 1989; Storch, 2007) and their distribution therefore largely overlaps with sites suitable for wind energy development (Braunisch et al., 2015; Coppes et al., 2020).

2.2. Study areas

We selected a total of six study areas in three different biogeographical regions across Europe: Fennoscandia (Sweden), the Alps (Austria) and central European low altitude mountain ranges (Germany; Fig. 1), where wind turbines are present, planned or under development within areas of capercaillie occurrence. We strived to select and survey study sites in pairs, one site with turbines present or under development ('impact site') and a control site of comparable topography and habitat composition without turbines ('control site'), whenever possible. An overview of the study site characteristics, sample sizes and survey periods is given in Table 1.

The Austrian study areas were located in the Styrian Alps at elevations between 990 and 1695 m (Fig. 1). There, capercaillie occur in coniferous montane to subalpine forests with the dominant tree species Norway spruce (*Picea abies*), silver fir (*Abies alba*) and European larch (*Larix decidua*). The capercaillie population in this area represents the south-eastern part of the larger Alpine population. Its meta-population status is considered to be stable, although some local populations exhibit decreasing trends (Zeiler, 2001; Storch, 2007). The three impact sites contained 9 wind turbines of type Repower MM92 (total height 146 m), 6 turbines of type Vestas V112 (total height 150 m) and 19 turbines of type ENERCON E82-E4 (total height 119 m) and E70E4 (total height 121 m), respectively. The German study sites were located in the Black Forest mountain range in the state of Baden-Württemberg at elevations between 675 and 1145 m (Fig. 1). At this elevation level, capercaillie occurs in mixed montane forests characterized by Norway spruce, silver fir, Scots pine (*Pinus sylvestris*) and European beech (*Fagus sylvatica*). As many other central and southern European populations, the population in the Black Forest is an isolated population, which has experienced a large reduction in size and range extent over the past decades (Kämmerle et al., 2017; Coppes et al., 2019) and is therefore considered to be threatened with extinction (Bauer et al., 2016). The two impact sites contain one wind turbine of type ENERCON E-70 (total height 120 m) and one of type Südwind S70 (total height 124 m), respectively. The Fennoscandian study site was located in central Sweden in the provinces Gävleborgs län und Dalarnas län at elevations between 245 and 365 m. Sweden contains a large stable capercaillie population (Ottvall et al., 2009) (Fig. 1). At the Swedish sites, capercaillie occurs in hilly landscapes covered by boreal coniferous forest characterized predominantly by Scots pine and Norway spruce and the capercaillie population status is considered to be stable (Zeiler, 2019). The impact site contains 66 wind turbines of type Vestas V112 (total height 175 m).

2.3. Field data collection

We surveyed the occurrence of capercaillie at each study site using a systematic grid of sampling plots with a regular grid cell length of 100 to 200 m, depending on the size of the study area (135–2295 ha). Sites differed in the number of sample plots, but plot locations remained constant at each site throughout the survey period (Table 1). At each site, plots were placed within areas of target species occurrence, based on local experience, and the grid layout was oriented by site topography. Plot locations were located using handheld GPS devices (Garmin Etrex 30× and Etrex 20×). At each sample plot, observers searched for capercaillie signs in a 5 m radius around the plot centre for a duration of 10 min. Mapping of indirect capercaillie signs (i.e. feathers, droppings) is a standard method to study capercaillie occurrence and habitat selection (Storch, 2002; Summers et al., 2007; Moss et al., 2014; Zohmann et al., 2014; Coppes et al., 2018), since capercaillie signs, especially droppings, are detectable over long periods after defecation (Poggenburg et al., 2018). In addition, a set of environmental (biotic and abiotic) characteristics known to be related to capercaillie habitat suitability was recorded in a 20 m radius around the plot centre. Environmental characteristics (Table A1 in Appendix A1) included ground vegetation and canopy cover, the composition of the tree and shrub layer as well as information on topography (Storch, 2002; Bollmann et al., 2005; Bollmann et al., 2008; Coppes et al., 2018). All field personnel were trained before the surveys to achieve consistent data quality. Surveys commenced in different years, most of them between 2012 and 2014 (Table 1). At each site, capercaillie signs were mapped annually between July and August. Signs included droppings, feathers, eggshells and sand baths (which contained feathers). Given the relatively slow rate of environmental change in forest ecosystems, and to save limited resources, environmental characteristics were recorded in the first and every third of the following years, as well as in the last year of the survey period per study site (Table 1).

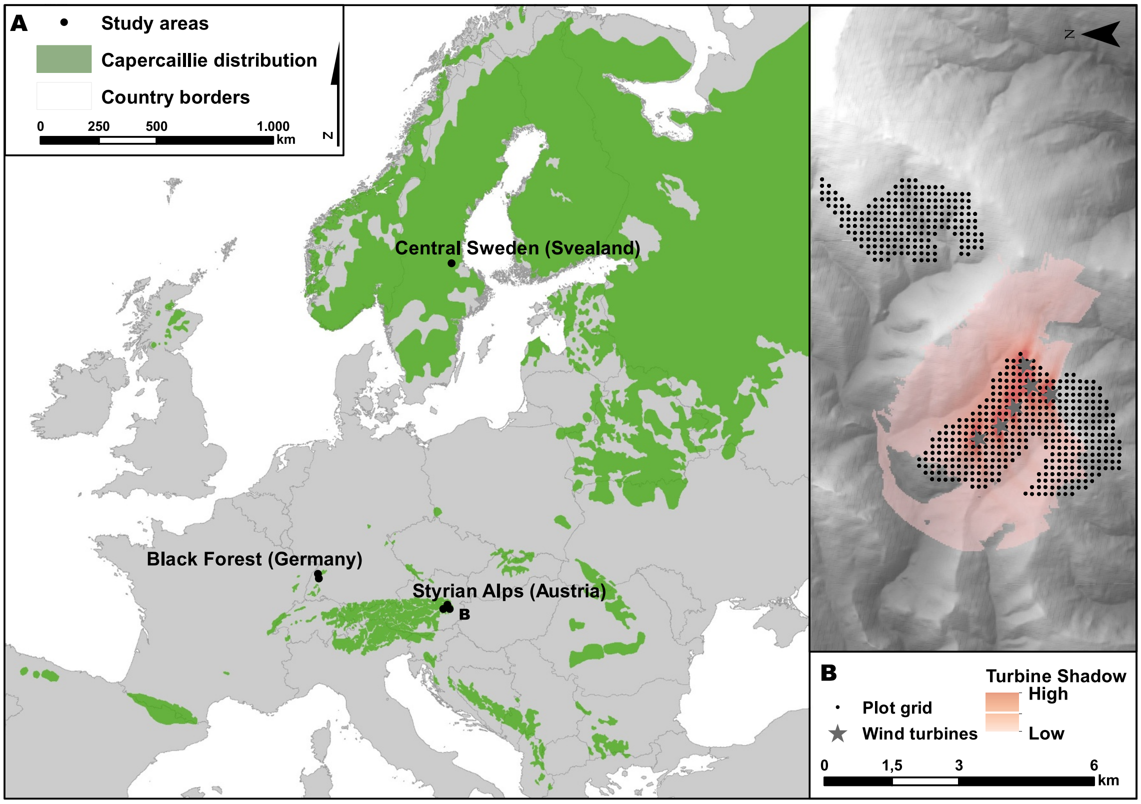

Fig. 1. Locations of the six study areas in three biogeographical regions of Europe. The capercaillie distribution is shaded green (Coppes et al., 2015). The insert map depicts an example of the survey design using a systematic grid of sample plots at an impact site with wind turbines present and a comparable control site without turbines in Austria (B). The modelled shadow of the wind turbines is visualized as an example of the potential turbine effects tested in this study, ranging from high (236 h/year) to low (1 h/year). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Study sites in three biogeographical regions in Europe: the survey period, the year of turbine construction, the number of years with data before and after construction (B/A), the number of sampling plots per site, the number of years in which environmental characteristics were recorded at the plots and the size (ha) are provided for each study site.

Biogeographical region	Study sites	Survey period	Turbine construction	Before/after	Number of plots	Years env. data	Study site size (ha)
Central Austria (Styrian Alps)	1-AUS-Impact	2012–2018	2012	1/6	350	3	655
	1-AUS-Control	2012–2018	–	–	200	3	325
	2-AUS-Impact	2013–2018	2017	4/2	404	3	360
	2-AUS-Control	2013–2018	–		203	3	170
	3-AUS-Impact	2013–2018	2016	3/3	427	4	360
	3-AUS-Control	2013–2018	–		264	4	225
Southern Germany (Black Forest)	1-GER-Impact	2014–2018	2015	2/3	318	3	300
	1-GER-Control	2014–2018	–		171	3	135
	2-GER-Impact	2012; 2016	2002	0/2	174	2	160
Central Sweden (Svealand)	1-SWE-Impact	2017	2011	0/1	659	1	2295
	1-SWE-Control	2017	–		374	1	1335

2.4. Data preparation

We analysed potential effects of wind turbines on capercaillie at two spatial scales, reflecting two levels of habitat selection: (1) at the level of the study sites (henceforth: 'large-scale') we used sign density, i.e. the percentage of samples plots with signs of capercaillie presence per study site in a given year; (2) at the scale of individual plots within each study site (henceforth: 'small-scale') we used the presence or absence of capercaillie at a plot in a given year to analyse small-scale habitat selection.

2.4.1. Sign density per site

To test for differences in capercaillie sign densities before and after turbine construction, we calculated the percentage of sampling plots that had capercaillie signs at each study site and in each study year, including only the study sites that met the criteria of a BACI-design (i.e. for which data from before and after turbine construction at both an impact and control site were available). This yielded N = 48 data points (study sites ∗ years) from eight study sites (four pairs of sites), excluding the data from the Swedish sites and one German site, since they only yielded data from after turbine construction. We then classified the data in a given year according to the BACI design (as a binary variable: 'B'-'A': 'before'-'after' turbine construction; 'C'-'I': 'control'-'impact' site) and calculated the sampling year relative to the year of turbine construction (negative values indicating years before construction).

2.4.2. Predictors of wind turbine effects at the plot locations

We created four different predictors of turbine effects to model a potential influence of wind turbines on capercaillie habitat selection: 1) We calculated the distance of each plot location to the closest wind turbine in meters. 2) The expected yearly amount (hours) of turbine shadow at each plot was calculated using the software WindPRO 3.1 (EMD International A/S), accounting for the location of turbines within study sites, site topography and latitude, turbine height and rotor diameter (Fig. 1). We obtained two metrics, i.e. the annual maximum of shadow received by each plot and the meteorologically plausible amount, which accounts for average weather patterns and sunshine hours at each site. 3) The expected amount (decibel) of turbine noise emission at each plot was quantified using the maximum noise volume 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 and calculations were based on the ISO 9613-2 method (DIN, 2015). Finally, we 4) determined in the field whether a wind turbine was visible or not at each plot (1/0) at 50 cm above the forest floor (i.e. approx. head height of adult capercaillie).

2.5. Statistical analysis

2.5.1. Correcting for responses of capercaillie to habitat suitability

In order to adequately depict wind turbine effects in our analysis, we strived to correct for the differences in the probability of capercaillie presence at a plot, which are related to differences in habitat suitability. For this, we chose a two-step modelling process.

We (1) first predicted the probability of finding capercaillie signs at a plot location purely based on environmental covariates *without* wind turbine effects based on the data from the control sites and from impact sites *before* construction of wind turbines (i.e. including data from all biogeographical regions in order to adequately model habitat suitability). Since environmental data were not collected every year (Table 1), we only used data of those years, in which environmental covariates had been recorded at the plots in the respective years ($N = 4929$ plots $*$ years). We trained three different model types with a binary response variable (i.e. 0/1 = capercaillie not detected/detected on a plot) and compared their performance in order to obtain the most robust approach to extrapolate the probability of capercaillie presence at turbine sites. We trained: a) a random forest using R package randomForest (Liaw and Wiener, 2002); b) boosted regression trees using R packages dismo (Hijmans et al., 2017) and gbm (Greenwell et al., 2019); c) a generalized linear mixed effect model (GLMM) with logit link and a nested random intercept for study years within study sites, as implemented in the R package lme4 (Bates et al., 2015). For the GLMM, higher order polynomials were included when considered to be ecologically meaningful. We used a large number of plot level covariates in each model with already known importance for capercaillie habitat suitability (Storch, 2002; Suchant et al., 2003; Bollmann et al., 2008; Miettinen et al., 2010), including ground vegetation structure, forest stand characteristics, topography and human recreational use (initially up to 18 predictors; see Appendix A1 and Table 1). For further details on the modelling process and the final models see Appendix A1. We evaluated model performance using a range of metrics to select the best model for predicting on the turbine sites. Performance metrics can be found in Appendix A1 in the supplementary information. We deemed the GLMM to exhibit the best overall performance, because a) the drop in the area under the receiver operating curve (ROC AUC; (Fawcet, 2006)) indicated the least overfit when predicting on the turbine data as well as in cross-validation (5-fold random holdout and spatially-blocked cross-validation) and b) it had the lowest AIC value.

(2) In order to be able to account for differences in habitat suitability in our large-scale small-scale analysis (i.e. plot level), we used the GLMM to predict the baseline probability of capercaillie presence for all sample plots *at* wind turbine sites and *after* turbine construction ($N = 5127$ plots $*$ years; holding random effects constant). For those years in which we had not recorded habitat covariates at the plots, we assigned the corresponding values of the proximate year with records to each plot location.

We chose this two-step process over a modelling approach that comprised environmental covariates of capercaillie presence concurrently with predictors of wind turbine effects, to account for the effects of habitat conditions on habitat selection using an unbiased estimate (i.e. not affected by the presence of turbines), so as to clearly disentangle habitat effects from that of the turbine predictors.

2.5.2. Large scale effects of turbine presence

We tested for effects of turbine presence on capercaillie sign density by fitting linear mixed-effect models in R package lme4 (Bates et al., 2015) with a random intercept for study site ID to correct for differences in baseline sign density between study sites. We fitted two models, one depicting the BACI design, thus using 'Before-After' and 'Control-Impact' as predictors as well as their interaction; for the other model we used the years since turbine construction interacting with 'Control-Impact'. We included a quadratic term for the years since construction to explore a potential gradual effect of turbine presence on capercaillie sign density. We obtained p-values using the Satterthwaite approximation in package lmerTest (Kuznetsova et al., 2019) and set the level of significance at $p \le 0.05$. Assumptions for the use of linear models were met. Prior to analysis we verified that trends in capercaillie sign density at the study sites were not biased by developments in habitat suitability at the sites by comparing the mean values of the predicted habitat suitability index across years and sites. We found no indication for such a bias.

2.5.3. Small scale effects of turbine presence

We analysed the probability of capercaillie presence at each plot (i.e. small scale habitat selection) at wind turbine sites after the construction of the turbines using generalized additive mixed models from package gamm4 (Wood and Scheipl, 2017) with a binary response (0/1 = capercaillie not present/present) and logit link. We used data from all sample plots *at* wind turbine sites and *after* turbine construction for this analysis ($N = 5127$ plots $*$ years; i.e. all the plots at which we predicted habitat suitability). The different turbine predictors (i.e. distance, noise, shadow) were highly correlated ($r \ge |0.7|$) and we therefore considered them in separate models. We fitted a cubic regression spline with shrinkage for the distance to the wind turbine (in meters), the meteorologically plausible amount of shadow of the turbine (in hours per year) and the turbine noise (in decibel), respectively. We limited the flexibility of the splines to three degrees of freedom to avoid ecologically unreasonable patterns. The amount of turbine shadow was log-transformed to adjust the distribution of the data. We included the previously described index of habitat suitability as a regular linear term and the visibility of the turbine from each plot as a factor covariate (with the two levels visible/not visible) in all models. To account for the grouped nature of the data and the differences in detection probability among sites and years we included a nested random intercept for study year within study site into the model. All variables were standardized by subtraction of the mean and dividing by the standard deviation. We tested whether an inclusion of interaction terms improved model fit by means of AIC. We tested for interactions of a) turbine visibility with the other turbine predictors (distance, noise, shadow) to address a mechanistic explanation of turbine effects (i.e. that turbine effects are present or larger were turbines are also visible) and b) the index of habitat suitability with the turbine predictors to explore the potential for compensatory effects of high habitat suitability (i.e. expecting turbine-effects to be reduced at high suitability). Since there was no support for any interaction we fitted final models without interaction terms. We approximated the effect threshold (up to which effects were detectable) as the point at which the response curve reached an asymptote, or diverged from it.

We finally assessed the stability of the effect patterns related to the wind turbine predictors by refitting models on a number of subsets of the data: a) recursively dropping individual study sites, b) considering either only male or female droppings at the plots and c) considering only droppings classified as either originating from the field season (summer) or the previous winter. Furthermore we fitted our models on the data at impact sites before construction of the wind turbines to verify that selection patterns were actually different once turbines had been constructed.

Table 2
Model summary of the GLMM predicting the probability of detecting capercaillie signs at a plot location (i.e. index of habitat suitability). Coefficient estimates, associated standard errors and approximate p-values are provided. Full details on the predictors are provided in Appendix A1.

Predictor	Estimate	SE	p-Value
Intercept	−0.958	0.215	< 0.001
Percentage canopy cover	−0.190	0.056	< 0.001
Percentage canopy cover^2	−0.322	0.041	< 0.001
Tree composition: Percentage Fir	−0.059	0.048	0.219
Tree composition: Percentage Pine	0.236	0.061	< 0.001
Tree composition: Percentage Larch	−0.076	0.038	0.046
Percentage ground vegetation cover	0.063	0.046	0.174
Height ground vegetation	−0.115	0.051	0.026
Percentage bilberry cover	0.167	0.049	< 0.001
Percentage bilberry cover ^{2}	−0.171	0.049	< 0.001
Percentage other berry cover	0.020	0.049	0.681
Slope	−0.121	0.050	0.015
Distance recreational infrastructure	0.333	0.099	< 0.001
Distance recreational infrastructure^2	−0.121	0.066	0.067
Presence of canopy gaps	0.216	0.082	0.008

Table 3
Model summaries of the large-scale GLMMs on the effects of turbine development on capercaillie sign density (i.e. proportion of plots with signs) at the study sites.

a) Model: BACI-Design

Predictor	Estimate	SE	p-Value
Intercept	0.254	0.054	< 0.001
Before-after: before	−0.079	0.041	0.061
Impact-control: impact	−0.056	0.076	0.481
Before ∗ impact	0.056	0.058	0.341

b) Model: years since turbine construction

Predictor	β	SE	p-Value
Intercept	0.204	0.056	0.005
Years since construction	0.021	0.012	0.083
Years since construction^2	−0.030	0.079	0.711
Impact-control: impact	−0.002	0.002	0.556
Years since construction ∗ impact	−0.001	0.017	0.950
Years since construction^2 ∗ Impact	< 0.001	0.004	0.967

3. Results

3.1. Index of capercaillie habitat suitability

The probability of capercaillie presence without the influence of wind turbines, used as an index of habitat suitability, was positively associated with open, pine-dominated forests characterized by an intermediate canopy cover and an abundant, but low ground vegetation with intermediate amounts of bilberry (Table 2).

3.2. Large scale effects of turbine presence

There were neither significant differences in mean capercaillie sign density between impact and control sites, nor between years before and after construction of the turbines (Table 3). We found a trend towards increasing sign densities at the study sites over time that was also reflected by the slopes of the model with the 'years since construction' as predictor (Table 3). The trend was stronger on control than impact sites across all study areas and study years and the p-value for this difference was small ($p = 0.061$), but confidence intervals clearly overlapped (Fig. 2).

3.3. Small scale effects of turbine presence

There was a strong significant positive effect of the predicted index of habitat suitability on the probability of capercaillie presence at plot level (Table 4, Fig. 3). Moreover, we found a significant negative effect of three out of four turbine predictors: The probability of capercaillie presence increased with increasing distance to the turbine for distances up to approximately 650 m (Fig. 3); it decreased with increasing shadow for plots receiving more than approximately 2 h of meteorologically plausible turbine shadow a year (Fig. 3); and it decreased with increasing turbine noise emissions for values exceeding approximately 30–35 dB (Fig. 3). We did not find a significant effect of turbine visibility on the probability of capercaillie presence (Table 4).

The effect patterns estimated by the models were, minor variation in the exact shape of the estimated slope notwithstanding, overall highly stable for all tested subsets of data and the three different wind turbine predictors. In addition, the shape of the effect pattern was highly different before and after construction for all the turbine predictors (Appendix A2).

4. Discussion

We are the first to systematically study the effects of wind turbines on a forest-dwelling bird species across three different biogeographical regions, representing different forest ecosystems of capercaillie distribution. After accounting for variation in habitat suitability, we found that the probability of habitat selection by capercaillie decreased with increasing turbine impacts (i.e. proximity, shadow, noise), with effects being detectable up to a distance of approximately 650 m to the wind turbine (Fig. 3). Affected areas were, however, not entirely avoided, which might explain why capercaillie are also prone to collisions with wind turbines (González, 2018; Coppes et al., 2020). However, this reduction in the probability of selecting habitat patches that were more strongly affected by wind turbines, as compared to patches with lower turbine impact under similar habitat conditions, implies that the de facto habitat suitability of areas close to the wind turbines was reduced. Net usability of these patches is thus "deteriorated" by the construction or presence of the wind turbines.

Nonetheless, habitat suitability (i.e. vegetation structure and composition) was still the most important predictor of capercaillie presence at the study sites. A previous study on the impact of recreation infrastructure on capercaillie habitat selection clearly demonstrated that negative effects can, under some circumstances, be mitigated by improving habitat suitability (Coppes et al., 2018). However, the lack of support for an interaction between the index of habitat suitability and the wind energy predictors in our analysis indicates that the negative impact of wind turbines on habitat selection cannot be mitigated by increasing the suitability of the affected habitat patches.

Due to high degree of collinearity of the wind turbine predictors (i.e. proximity, shadow, noise), we were unable to disentangle individual turbine effects, so as to determine which of them caused the observed reductions in the probability of presence. The movement of the turbines blades as well as shadow flickering, both unpredictable for capercaillie, might trigger an anti-predator response in the birds, similar to other overhead movement. Noise generated by wind turbines has been shown to affect the acoustic signals generated by lekking male greater prairie-chickens (*Tympanuchus cupido pinnatus*) (Whalen et al., 2018; Whalen et al., 2019), and this might explain the relocation of lekking sites following wind turbine construction found in other grouse species (Coppes et al., 2020).

Since capercaillie are known to avoid areas with regular human presence, e.g. recreation infrastructure (Summers et al., 2007; Thiel et al., 2008; Coppes et al., 2017; Coppes et al., 2018), an avoidance of areas close to wind turbines might also be related to the higher frequency of human presence (e.g. maintenance work or follow-up use of the construction roads for recreational purposes (Helldin et al., 2017)). Moreover, access roads to the wind turbines can alter the habitat selection of mammalian predators (Helldin et al., 2017; Sirén et al.,

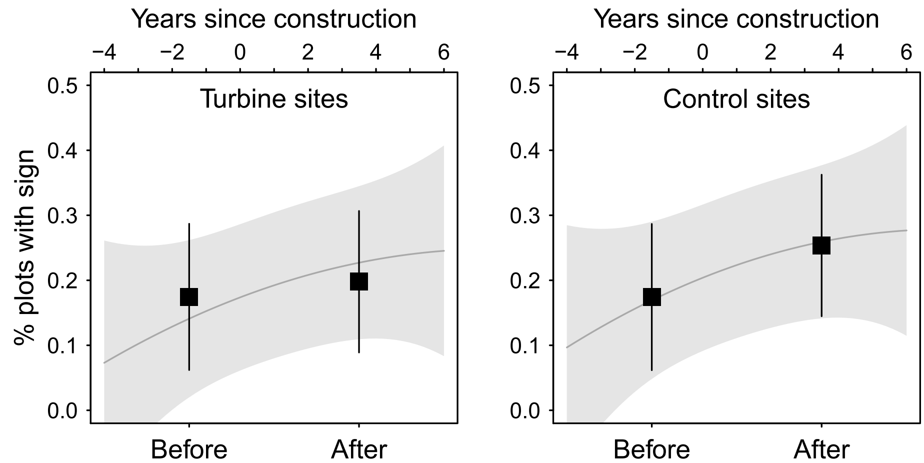

Fig. 2. Effects of wind turbine presence on capercaillie sign density (i.e. % of plots with capercaillie signs) at the study sites with a complete BACI design (N = 48) as predicted by the large-scale GLMMs. Negative numbers on the "years since construction" axis indicate years before the construction of wind turbines.

Table 4
Model summaries of the small-scale GAMMs on the effects of wind turbines (a: distance; b: shadow; c: noise) on capercaillie habitat selection at the study sites.

a) Model: distance turbine

Predictor	**Estimate**	**SE**	**p-Value**
Intercept	−2.033	0.204	< 0.001
Turbine visibility – yes	−0.178	0.102	0.081
Index of habitat suitability	0.542	0.056	< 0.001
Predictor	**Edf**		**p-Value**
Distance to turbine (m)	2.787		< 0.001

b) Model: turbine shadow

Predictor	**Estimate**	**SE**	**p-Value**
Intercept	−2.120	0.215	< 0.001
Turbine visibility – yes	−0.092	0.103	0.370
Index of habitat suitability	0.548	0.057	< 0.001
Predictor	**Edf**		**p-Value**
Turbine shadow (hours)	2.762		< 0.001

c) Model: turbine noise

Predictor	**Estimate**	**SE**	**p-Value**
Intercept	−2.029	0.206	< 0.001
Turbine visibility – yes	−0.197	0.102	0.054
Index of habitat suitability	0.544	0.056	< 0.001
Predictor	**Edf**		**p-Value**
Turbine noise (dB)	2.335		< 0.001

2017), possibly increasing the predation pressure close to these roads. It thus appears plausible that the avoidance of areas close to turbines might be related to the combined effect of different factors. Although capercaillie signs were also found closer to wind turbines, our analysis demonstrated reductions in usability at a spatial extent that may remain undetected if only the minimum distance of species observations from wind turbines are reported (Hötker, 2017), which generally yields smaller values than the effect distances in our study.

Our results are in line with previous studies indicating that grouse (*Tetraoninae*) react sensitive to wind energy developments (for a review see (Coppes et al., 2020)). However for some species different effect were found between different studies: whereas (Falkdalen et al., 2013) found reduced numbers of willow ptarmigan (*Lagopus lagopus*) after construction of a wind park, two other studies did not find significant effects of wind energy developments (Bevanger et al., 2010a; Bevanger et al., 2010b). Black grouse (*Tetrao tetrix*) have also been found to be affected over distances up to approx. 500 m (Grünschachner-Berger and Kainer, 2011; Zwart et al., 2015). A reduced probability of presence close to wind turbines might explain the reduced number of indirect capercaillie signs found after the construction of a wind park in Spain (González and Ena, 2011; González et al., 2016) and the reduced number of lekking capercaillie males at a lekking site after construction of a wind park reported in Sweden (Rönning, 2017). The Working Group of German State Bird Conservancies (LAG VWS) recommends not to construct wind turbines within 1000 m of capercaillie occurrence (LAG VSW, 2015). This distance slightly exceeds the effect distance we found in our study, and thus takes the precautionary principle (Myers, 1993) into account, since - based on our findings - it is unlikely that capercaillie are affected by wind turbines constructed more than 1000 m from their occurrence.

The effects of wind turbines might be stronger during or shortly after construction (Pearce-Higgins et al., 2012; Farfán et al., 2017). In our study areas, the wind turbines had been in place for different time periods (1–8 years) and turbine effects were detectable even several years after construction. Accordingly, there were no indications that capercaillie habituate to wind turbines within eight years after construction and turbine effects may thus need to be considered as permanent impacts on the species and its habitat. However, this may be further substantiated by additional surveys five to ten years in the future.

We did not find a significant negative effect of wind energy development on the density of indirect signs at turbine sites, which indicates that birds reduce their habitat use in the vicinity of the turbines but do not leave the wider surrounding. Although the relationship between the density of indirect signs and population density of capercaillie seems likely, the exact shape of this relationship is unknown. Whether the reduced usability of areas close to the wind turbines will affect the local population probably depends on the total area of available habitat: the less suitable and unaffected habitat is available, the larger effects of habitat deterioration on the local population can be expected (Andrén, 1994). Construction of wind turbines in large and highly suitable habitats (e.g. Central Sweden) is therefore unlikely to affect population density, whereas in small and fragmented populations (e.g. Black Forest) additional reduction of habitat usability, caused by wind turbine construction, might have negative effects on population density.

5. Conclusions and management implications

Especially in locally threatened capercaillie populations and at sites where topography limits the extent and amount of suitable habitats (e.g. alpine habitats) we advise to apply the precautionary principle (Braunisch et al., 2015), and refrain from the construction of wind turbines in capercaillie habitats. Our study provides distances up to which capercaillie responds to the presence of wind turbines in terms of habitat selection, which is a solid base for evidence-based management

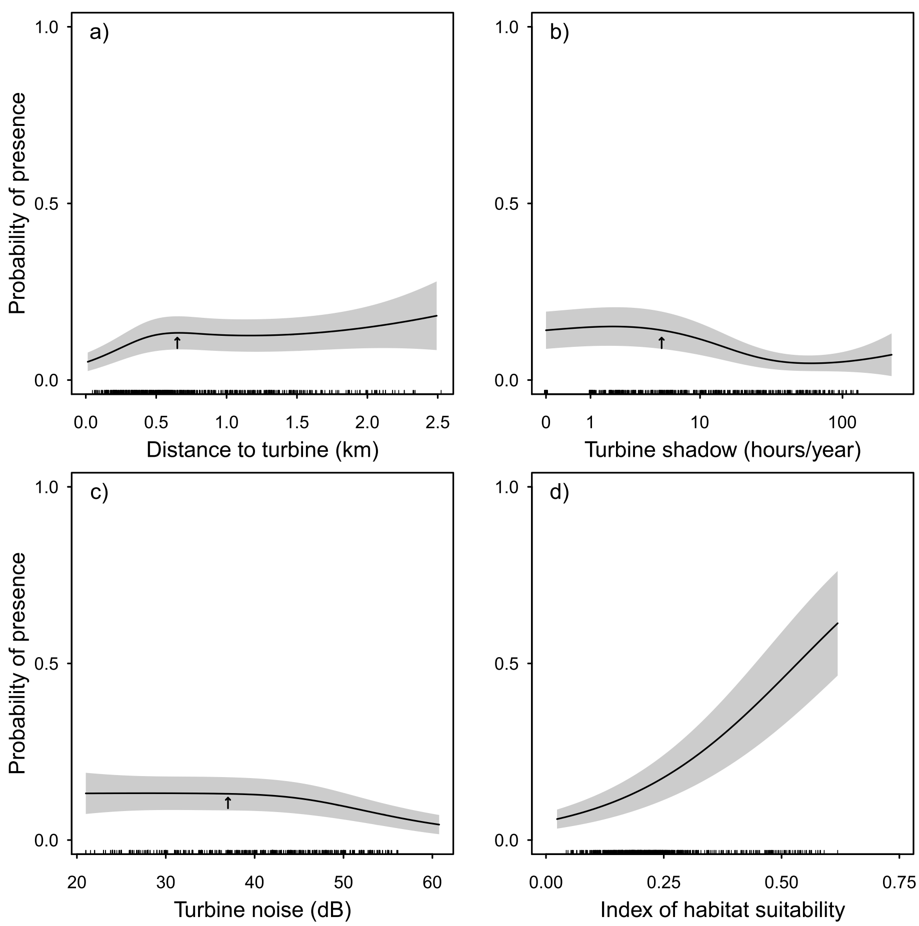

Fig. 3. Conditional effect plots of wind turbine effects (a: distance to turbine, b: turbine shadow, c: turbine noise) on capercaillie habitat selection at six study sites across Europe as predicted by the small-scale GAMMs. Predicted capercaillie occurrence was held at its mean to depict turbine effects independently of habitat suitability. Arrows indicate approximate effect thresholds. The effect plot for the index of habitat suitability (d) was exemplified using the turbine shadow model (b, Table 4), holding all other predictors at their mean.

targeting at an avoidance of any negative effects of wind energy developments on capercaillie.

CRediT authorship contribution statement

Joy Coppes:Conceptualization, Methodology, Investigation, Resources, Data curation, Writing - original draft, Supervision, Project administration, Funding acquisition.**Jim-Lino Kämmerle**: Formal analysis, Data curation, Visualization, Writing - review & editing.**Veronika Grünschachner-Berger**:Conceptualization, Methodology, Investigation, Resources, Writing - review & editing. **Veronika Braunisch**:Conceptualization, Methodology, Writing - review & editing.**Kurt Bollmann**:Conceptualization, Methodology, Writing - review & editing.**Pierre Mollet**:Conceptualization, Methodology, Writing - review & editing.**Rudi Suchant**:Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.**Ursula Nopp-Mayr**:Conceptualization, Methodology, Investigation, Resources, Writing - review & editing.

Declaration of competing interest

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

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Author statement

All authors declare that they have no financial or personal relationships with other people or organizations that could inappropriately influence their work. The funding organizations had no influence on study design, interpretation of the results, content of this manuscript and the choice to publish the results. The authors declare that all the work is original research carried out by the authors and it is not being considered for publication elsewhere while it is being considered for publication in this journal. All authors agree with the contents of the manuscript and its submission to the journal. All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication. All appropriate permits were obtained for the research.

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Appendix A. Supplementary data

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