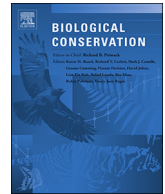




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Wind turbines in high quality habitat cause disproportionate increases in collision mortality of the white-tailed eagle

Christian Heuck^{a,b,*}, Christof Herrmann^c, Christian Levers^d, Pedro J. Leitão^{d,e}, Oliver Krone^f, Roland Brandl^a, Jörg Albrecht^g

^a Faculty of Biology, Department of Ecology, Animal Ecology, Philipps-Universität, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany

^b Bioplan Marburg GbR, Deutschhausstraße 36, 35037 Marburg, Germany

^c Agency for Environment, Nature Conservation, Geology Mecklenburg-Western Pomerania, Goldberger Str. 12, 18273 Güstrow, Germany

^d Geography Department, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany

^e Department Landscape Ecology and Environmental System Analysis, Technische Universität Braunschweig, Langer Kamp 19c, 38106 Braunschweig, Germany

^f Department of Wildlife Diseases, Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

^g Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

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ABSTRACT

The increasing number of wind farms for energy production raises concerns about their effects on wildlife and particularly on birds. To date it is unclear whether models that combine data on wind turbine densities and habitat suitability can explain the actual spatial occurrence of collision fatalities and how well these models perform in comparison to models including measures of bird population densities (e.g., the distribution and density of nest sites). Here we analysed whether collision mortality increases with wind turbine density and whether a high population density or habitat suitability in the vicinity of wind turbines amplifies the effect of wind turbine density on collision mortality. We combined opportunistic records of dead White-tailed Eagles by the public in Northeast Germany during the period 2003 to 2014 with data on the distribution of wind turbines, nest sites and habitat suitability. As expected, wind turbine density was a strong predictor of collision mortality. In addition, we found that wind turbine density and habitat suitability had synergistic effects on collision mortality, so that the effect of wind turbine density was amplified in areas of high habitat suitability. Moreover, combining wind turbine density and habitat suitability allowed for better predictions of collision mortality than combining wind turbine density and nest site density. These results suggest that assessments of the spatial occurrence of collision fatalities based on models that combine data on wind turbine densities and habitat suitability can be useful for the strategic planning of wind farm development on regional scales. In particular, our study highlights that wind turbines should not be placed in core population areas of vulnerable bird species because synergies between wind turbine densities and habitat suitability may cause disproportionate increases in mortality. This might undermine the positive effects of parallel conservation efforts.

1. Introduction

Wind is a renewable and clean source of energy. Therefore, energy production with wind turbines has received strong public and governmental support within the last decades. As a consequence, the number of installed wind turbines is increasing worldwide (GWEC, 2015). Despite the benefits of wind energy, the rapid increase in the number of wind farms raises concerns about their effects on wildlife, particularly on birds and bats (e.g. Drewitt and Langston, 2006; Arnett et al., 2016).

Wind turbines affect birds mainly by displacement as a result of disturbance and/or habitat loss, as well as by collision with rotor blades

(Drewitt and Langston, 2006; Hötker et al., 2006; Pearce-Higgins et al., 2012; Stevens et al., 2013; Watson et al., 2018). In particular, the mortality due to collisions has been identified as a major threat for bird species with large, soaring raptors and vultures being most prone and vulnerable to collision (Krone and Scharnweber, 2003; Langston and Pullan, 2003; de Lucas et al., 2004, 2008; Beston et al., 2016). In addition, these species are characterized by low reproductive rates and long generation times making them sensitive to an increase in mortality (Sæther and Bakke, 2000). Several studies on the demographic effects of wind turbine fatalities revealed that mortality due to wind turbines may reach levels that can threaten local populations. Examples include

* Corresponding author at: Faculty of Biology, Department of Ecology, Philipps-Universität, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany
E-mail address: c.heuck@bioplan-marburg.de (C. Heuck).

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the Egyptian Vulture *Neophron percnopterus* in southern Spain (Carrete et al., 2009), the Golden Eagle *Aquila chrysaetos* in the USA (Hunt, 2002), and the Red Kite *Milvus milvus* in Germany (Bellebaum et al., 2013).

Existing studies either aimed at predicting spatial patterns of wind turbine collision risk or aimed at assessing relationships between the actual spatial occurrence of collision fatalities and bird behaviour or habitat features. Risk assessment studies implicitly assume that collision mortality increases in areas that are more frequently used or more densely populated and typically combine models of habitat use based on bird movement or nest site locations with data on existing or planned wind farms to make spatial predictions of collision risk (Fielding et al., 2006; Tapia et al., 2009; de Lucas et al., 2012; Reid et al., 2015; Vasilakis et al., 2016, 2017). The assumption that collision mortality increases in densely populated habitats is supported by studies that assessed collision fatalities at the regional scale (e.g. in the Griffon Vulture *Gyps fulvus*, Carrete et al., 2012). In contrast, those studies that assessed determinants of collision mortality at the local scale found no effect of bird activity or abundance in the vicinity of wind farms on the occurrence of collision fatalities in soaring raptors (de Lucas et al., 2008, 2012; Ferrer et al., 2012). At the local scale, species behaviour, topography and wind flows seem to be more important determinants of collision mortality.

Previous work has also shown that collision mortality of birds increases with wind turbine density and depends on the spatial distribution of wind turbines (Schaub, 2012). However, it is unclear whether a high population density or habitat suitability in the vicinity of wind turbines amplifies the effect of wind turbine density on collision mortality. In this case the effects of wind turbine density and, for example, habitat suitability would not be additive but interactive (i.e., synergistic; Fig. 1). We hypothesized that models only including additive effects make unrealistic predictions of collision mortality, because in the extreme case these models would predict elevated collision mortality in areas without wind turbines and high habitat suitability (Fig. 1a). In contrast, models including interactive effects between wind turbine density and habitat suitability should correctly predict no collision mortality for these areas (Fig. 1b) We furthermore hypothesized that models combining data on wind turbine densities and habitat suitability may be better suited to predict collision fatalities than comparable models including data on nest site densities, because habitat suitability might better reflect actual habitat use in species with large home ranges (Krone and Treu, 2018). Therefore, combining data on wind turbine densities with habitat suitability maps that identify habitat preferences and core population areas may be useful to assess large-scale patterns of collision mortality and could thus support

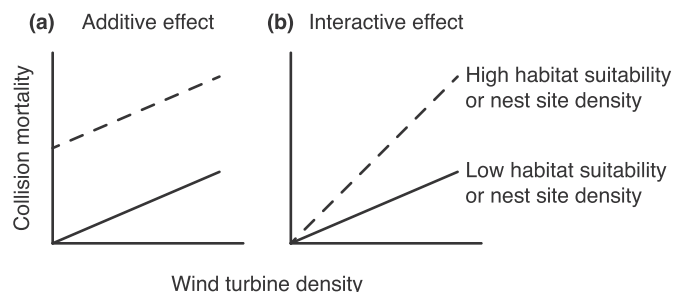


Fig. 1. Illustration of expected patterns of collision mortality if the effects of wind turbine density and habitat suitability or nest site density were additive or interactive. (a) Models only including additive effects of wind turbine density and habitat suitability (or population density) make unrealistic predictions of collision mortality, because in the extreme case these models would predict elevated collision mortality in areas without wind turbines and high habitat suitability (or population density). (b) In contrast, models including interactive effects between wind turbine density and habitat suitability (or population density) should correctly predict no collision mortality for these areas.

regional planning processes.

In the present study, we focussed on the effects of wind turbine density, nest site density, and habitat suitability on the occurrence of wind turbine collision fatalities of the White-tailed Eagle (WTE). This species is one of the most affected species by onshore wind farms within Central Europe (Hötter et al., 2006; Dahl et al., 2013; Grünkorn et al., 2016). In particular, we focussed on a breeding population of the WTE in Northeast Germany, as it has been intensively monitored within the last decades (Langgemach, 2002; Struwe-Juhl and Grünkorn, 2007; Hauff, 2009; HELCOM, 2015) and therefore represents an excellent model population. We tested whether the occurrence of collision fatalities was related to wind turbine density and whether a high density of nest sites or habitat suitability in the vicinity of wind turbines amplifies the effect of wind turbine density on collision mortality. We expected (1) synergistic effects between wind turbine density and population density or habitat suitability, so that the effect of wind turbine density on the occurrence of collision fatalities is larger in areas of high population density or habitat suitability compared with more sparsely populated and less suitable areas. To assess the potential for such synergies we explicitly tested for interactive effects between wind turbine density and nest site density or habitat suitability in our analysis. We furthermore compared the performance of models containing either nest site density or habitat suitability at predicting the occurrence of collision fatalities. We hypothesized that (2) models containing habitat suitability perform better at predicting the occurrence of collision fatalities than models containing nest site density, because habitat suitability is a more integrated measure of potential habitat use than the mere distribution of nest sites.

2. Methods

2.1. Study species

The WTE is the largest eagle in Europe and occurs across large parts of the Palaearctic (Glutz von Blotzheim et al., 1971). The global population has been estimated at ca. 7000 breeding pairs, with the majority being located in Europe (Hailer, 2006). After severe population declines all over Europe within the last century due to persecution and environmental pollutants, the Baltic population has successfully recovered (Helander et al., 2008; Bignert et al., 2015; HELCOM, 2015; Treinys et al., 2016; Heuck et al., 2017).

WTEs are monogamous and pairs continue to breed in the same area year after year (Glutz von Blotzheim et al., 1971). Being central place foragers, mated pairs use the same home range throughout the year unless forced to temporarily leave the home range due to harsh weather conditions (Helander, 1990; Krone et al., 2013). The species is a habitat generalist, but usually prefers coastal and freshwater areas (Treinys et al., 2016). Accordingly fish, waterfowl and carrion are the primary food resources of the species (Wilman et al., 2014; Nadjafzadeh et al., 2016).

2.2. Data on nesting sites, collision fatalities and wind turbines

For our analysis, we combined spatial data on the occurrence of wind turbine collision fatalities, the distribution of nesting sites of the species, and wind turbines for the federal German states Schleswig-Holstein, Mecklenburg-Western Pomerania, and Brandenburg. The annual monitoring of breeding sites of the WTE within our study area is coordinated on federal state level by the Project Group for WTE Conservation Schleswig-Holstein, the State Bird Conservancy of Brandenburg and the Agency for Environment, Nature Conservation, and Geology Mecklenburg-Western Pomerania. Data for all three federal states is available since 1995. This monitoring is based on a network of volunteers (mainly ornithologists and foresters). These volunteers check all known breeding places to get information about nest occupancy. If known nests are not occupied, but Eagles are observed

within their territory, the new nesting site is searched for. The same is done if new territorial pairs are observed. Furthermore, incidental records of new nesting sites by foresters, hunters or other people are usually reported to the monitoring coordinators.

Data on wind turbine collision fatalities of WTEs in Germany were compiled by the State Bird Conservancy of Brandenburg and later georeferenced by the Agency for Environment, Nature Conservation, and Geology Mecklenburg-Western Pomerania. This dataset is almost exclusively based on opportunistic records of dead WTEs by the general public (e.g. farmers, hunters, and conservationists) and covers the period 2002 to 2017. The findings are usually reported to the regional authorities so that the birds can be collected for further examination in laboratories. During this period a total of 1054 dead WTEs have been documented. Depending on the state of decay, the necropsy protocols provide information about the cause of death (including for instance lead poisoning, collision with trains, intraspecific conflicts). Out of the total of 1054 collected birds, 137 birds have been determined as fatalities due to wind turbine collisions. Most collision fatalities were recovered within our study area (Schleswig Holstein: 37, Mecklenburg-Western Pomerania: 38, Brandenburg: 44, outside study area: 18), which harbours most of the breeding population in Germany. Since the public reports all dead eagles (not just wind turbine collision fatalities) to the regional authorities, we assume that the data are not spatially biased towards wind turbines. However, it must be emphasized that our study does not rely on systematically collected data but on opportunistic data collected by the public. Given the large spatial and temporal extent of the study, conducting systematic surveys in the vicinity of wind turbines across the entire study area was not feasible. Therefore, although our records cover a wide area, we do not know if the search regime was comparable across the study area. Two dead eagles were found during two local standardized monitoring schemes of collision fatalities, but these birds were excluded from the analysis to avoid spatial bias towards wind turbines. Furthermore, we have no data about removal rates of carcasses by scavengers or about vegetation density, so that we were not able to apply any correction factors with respect to detection probability. Thus, the dataset only allows for the estimation of spatial occurrence of collision fatalities, but not for more detailed estimation of collision rates for each wind turbine.

Data on the locations of wind turbines in our study area were

available for the years 2003 to 2014 (Fig. 2a; data provided by the Agency for Agriculture, Environment, and Rural Areas Schleswig-Holstein; Agency for Environment, Nature Conservation, and Geology Mecklenburg-Western Pomerania; Agency for Environment Brandenburg, LfU Brandenburg, 2017). This period covered a total of 101 wind turbine fatalities from opportunistic sightings. As the wind turbine data did not include information about the tower height or rotor blade length, we could not include these variables into our analysis.

2.3. Habitat suitability

We modelled habitat suitability of the WTE using nest site locations from the period 2003 to 2012 as the response variable. We pooled all reported nest site locations ($N = 5744$) and removed redundant observations using a radius of 5 m (approximate spatial accuracy of GPS), resulting in a sample size of 1203 nest site locations. We did not weight nest site locations by the number of years in which they were occupied, to avoid bias due to the circumstance that more peripheral population areas have only recently been recolonized (HELCOM, 2015). If only information about species presence is available, most species distribution models utilize environmental conditions at observed species presence locations (in our case: nest sites) in contrast to environmental conditions at randomly distributed pseudo-absence locations (Barbet-Massin et al., 2012). As we had only data on the location of nest sites (i.e., species presence), we consequently generated pseudo-absence points. To assess the sensitivity of the habitat suitability model to the ratio of presences to pseudo-absences of nest sites (Barbet-Massin et al., 2012), we created sets of pseudo-absences for our response variable, in which we varied the ratio of presences to pseudo-absences from 1:1 to 1: 25. We created the pseudo-absences of nest sites using a random sampling scheme outside buffers of 2500 m around observed nest sites (Barbet-Massin et al., 2012), approximating the home range size of the WTE (Fischer, 1984; Struwe-Juhl, 2000; Krone et al., 2009, 2013; Nadjafzadeh et al., 2016; Krone and Treu, 2018). Moreover, we created training and testing subsets using an 80/20 ratio and controlled for spatial sorting bias, which is the difference between the distance from testing-presence to training-presence sites and from testing-absence (or testing-background) to training-absence sites (Hijmans, 2012). Values near one indicate no bias; values near zero indicate strong bias. Our

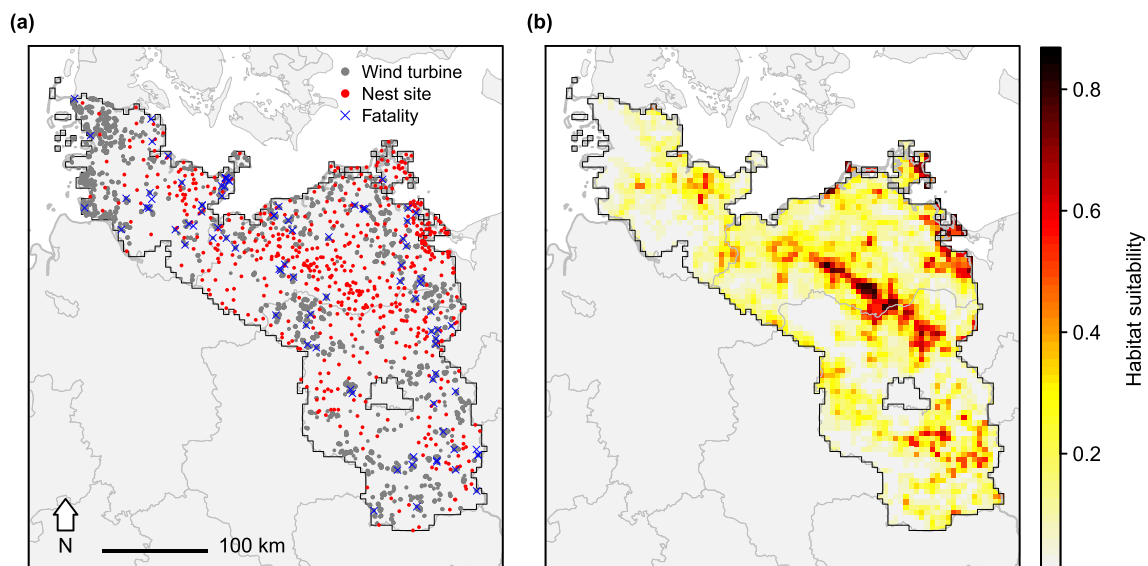


Fig. 2. Occurrence of wind turbine collision fatalities in a population of the White-tailed Eagle in Northeast Germany during the period 2003 to 2014. The map in (a) shows the geographic locations of wind turbines (grey dots), nest sites of White-tailed Eagles (red dots) and recoveries of wind turbine fatalities (blue crosses) during the study period. The map in (b) depicts the habitat suitability as predicted from boosted regression trees (see [Methods](#) section). Dark colours correspond to high habitat suitability and light colours to low habitat suitability. A colour-version of the figure is included in the online-version of the article. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

data showed very weak spatial sorting bias ($p = 0.98$).

As predictors, we selected habitat variables for WTE nest site occurrence based on literature about habitat preferences (see Table S1 in Supplementary materials). We extracted CORINE land cover information from 2000 (EEA, 2016) for the presence-absence points and implemented land cover categories as a factor variable into our model. We further calculated the distance between nest sites and the different land cover types. Furthermore, we considered distance to and density of roads from the year 2000 to include human disturbance effects (hence we assumed temporal consistency of land cover and road networks), and included elevation as a measure for topography. We harmonized predictor data to match CORINE's native spatial resolution of 100×100 m, either by defining this resolution for newly calculated layers (distance to and density of roads) or by calculating the grid cell average for data of higher resolution (elevation). We used the same grid size for the prediction of habitat suitability across the study area.

We used Boosted Regression Trees (BRTs) to model the occurrence of WTE nest sites and to predict their habitat suitability in the study area. BRTs are a machine-learning technique and build on the concepts of decision trees and gradient boosting (Friedman, 2001; Elith et al., 2008; Hastie et al., 2011). BRTs gained recent popularity due to several advantages over traditional, frequentist statistical methods. They offer a high predictive accuracy and good interpretability of results, do not tend to overfit (Dormann et al., 2013), are robust against missing data and collinearity of predictors, and are able to handle non-linearity and interaction effects (Friedman, 2001; Elith et al., 2008; Hastie et al., 2011).

Four parameters are important for calibrating BRTs: (1) bag fraction, (2) tree complexity, (3) learning rate, and (4) number of trees. The bag fraction specifies the share of data that is randomly withheld while fitting the model (i.e., each single tree), thereby introducing stochasticity and avoiding overfitting. The tree complexity defines the maximum order of interactions between predictors in each single tree. The learning rate reduces the contribution of each single tree to the entire model and can be interpreted as a penalizing parameter. The number of trees determines the number of single decision trees included in the model and represents the model complexity.

We used the *dismo* package (Hijmans et al., 2013) in R (R Core Team, 2017) to implement our model and the function *gbm.step* to automatically derive the optimal number of trees (in our case 2530) using a tree complexity of 4, a learning rate of 0.0075, and a default bag fraction value of 0.5 following Friedman (2001). In this function, the best values for tree complexity and learning rate were selected based on a grid search (tree complexity: 1 to 10; learning rate: 0.1 to 0.001), optimizing for explained deviance in a cross-validation procedure. We compared the goodness of fit among the models and selected the model with a ratio of presences to pseudo-absences of 1:5 ($N_{\text{pseudo-absence}} = 1203 \times 5$), as it maximized the product of true positive and true negative rate of the predicted habitat suitability (Table S2). We evaluated the goodness of fit of our final model (1:5 ratio of presences to pseudo-absences) using 10-fold cross-validated ROC AUC values (Receiver Operating Characteristic Area Under the Curve). We further assessed the influence of each predictor in explaining WTE nest site occurrences by calculating their relative importance in the model (number of times a variable is selected in a tree, weighted by the squared improvements, and averaged over all trees; Friedman, 2001). Finally, we predicted WTE breeding habitat suitability for the entire study area using the final model.

2.4. Occurrence of wind turbine collision fatalities

We analysed the occurrence of wind turbine fatalities in response to the number of wind turbines, number of nest sites and habitat suitability across several spatial resolutions using generalized linear models. We first created a grid with a cell size of $5 \text{ km} \times 5 \text{ km}$ that covered the study area. We only considered raster cells, which had their

centre within the boundaries of the study area. We counted the number of wind turbines as well as the number of nest sites in each grid cell and in each year of the study period. Moreover, we calculated the mean habitat suitability for each grid cell based on the predicted probability of occurrence from the habitat suitability model. Following Barbet-Massin et al. (2012), we randomly sampled 100 pseudo-absence points from within the study area for each observed wind turbine fatality corresponding to a presence:pseudo-absence ratio of 1:100. We had to exclude 13 wind turbine fatalities that were located outside of the grid resulting in a final sample size of 88 collision fatalities. As for the habitat suitability model, we created the pseudo-absences using a random sampling scheme outside buffers of 2500 m around observed fatalities (Barbet-Massin et al., 2012). Finally, we extracted the number of wind turbines, the number of nest sites and the mean habitat suitability for the presence-absence points from the grid cell in which a given point was located. For the extraction of the number of wind turbines and nest sites we also considered the respective year, in which the fatality occurred (e.g., if a wind turbine fatality occurred in 2003, we extracted the number of wind turbines and nest sites in a cell in that particular year).

Based on this dataset we fitted generalized linear models with a *logit*-link function, in which the presence:pseudo-absence records of wind turbine fatalities were treated as a binomial response variable. In the models we weighted pseudo-absences equally to the presences (i.e. the weighted sum of presences equalled the weighted sum of pseudo-absences; Barbet-Massin et al., 2012). To investigate whether nest site density or habitat suitability and their interaction with wind turbine density were better predictors of the occurrence of collision fatalities, we examined a set of a priori specified models. This model set included a series of models that either contained wind turbine density, nest site density and their interaction or wind turbine density, habitat suitability (range: 0–1) and their interaction as well as all possible combinations of these variables. We did not allow models to contain both nest site density and habitat suitability, to limit the number of models, to avoid over-fitting, and to reduce the risk of finding spurious effects. Therefore, the model set included 8 models (including the null model with only the intercept term; Table 1). We ranked the models based on an information theoretic approach according to AIC_c -values (lowest = best), and used results from all models to calculate model-averaged parameter estimates (Burnham and Anderson, 2010). We considered effects to be significant, if 95% confidence intervals of the model-averaged parameter estimates did not overlap zero. We also assessed model fit based on explained deviance using Nagelkerke's R^2 -values (Nagelkerke, 1991). To assess the sensitivity of our results to the resolution of the grid for the explanatory variables, we repeated the analysis using alternative grid sizes (7.5 km, 10 km, 15 km, and 25 km edge length). The results were highly consistent, but Nagelkerke's R^2 -values were highest for the $5 \text{ km} \times 5 \text{ km}$ grid (Table 1; Table S3). Therefore, we report results based on the $5 \text{ km} \times 5 \text{ km}$ grid size in the main text.

2.5. Limitations

Even though the WTE is still recolonizing its former range in Central Europe, our habitat suitability model predicted the occurrence of nest sites and habitat suitability of the species with high accuracy. As we contrasted actual nest sites with randomly selected pseudo-absences, it is of minor importance, whether the current range of a species is in equilibrium with its environment (i.e., all suitable habitat is occupied; Zimmermann et al., 2010). Therefore, our habitat suitability model is not biased by the circumstance that the WTE might not yet have entirely recolonized its former breeding distribution in Central Europe.

However, some sources of uncertainty still exist. First, we were not able to consider other factors influencing the occurrence of collision fatalities, such as the size or type of the wind turbines (Marques et al., 2014). If available, these data should be used to assess the effect of

Table 1

Summary of model selection. The models tested for a relationship of the probability of occurrence of a wind turbine fatality with (a) the number of wind turbines (WT), the number of nest sites (NS) and their interaction (WT × NS), as well as with (b) the number of wind turbines, habitat suitability (HS) and their interaction (WT × HS) within a population of the White-tailed Eagle in Northeast Germany during the period 2003 to 2014. Parameters include Nagelkerke's R^2 -value; the number of free parameters (df); the small sample corrected Akaike information criterion (AIC_c), the difference in AIC_c between the i th model and the best model (Δ_i); and the model weight (w_i). Models are arranged in order from best (lowest Δ_i) to worst (highest Δ_i). The weight of the model (w_i) is the probability that a given model is the best model in a given set of models. Model-averaged parameter estimates (MAP) with upper (97.5%) and lower (2.5%) bounds of the 95% confidence intervals, as well as their importance (sum of w_i of those models that include the respective predictor variable) are given in the bottom rows. The models are based on observed wind turbine fatalities ($n_{\text{presence}} = 88$), as well as on randomly sampled pseudo absences ($n_{\text{pseudo-absence}} = 8800$; presence/pseudo-absence ratio 1:100). We used a grid size of 5 km × 5 km. Alternative grid sizes yielded similar results (Table S3).

	Intercept	Wind turbine density (WT)	(a) Nest site density (NS)		(b) Habitat suitability (HS)		R^2	df	AIC_c	Δ_i	w_i
			NS	WT × NS	HS	WT × HS					
	-1.1	2.8			-0.34	1.8	0.54	4	64.3	0	0.797
	-1.1	1.6					0.42	2	68.4	4.1	0.101
	-1.1	1.5			-0.22		0.42	3	70.3	6.0	0.0403
	-1.1	1.6	0.087				0.42	3	70.4	6.1	0.0385
	-1.1	1.7	0.032	0.65			0.43	4	71.3	7.0	0.0239
	-0.37				-1.1		0.26	2	113	49	0.0000
	0.0						0	1	124	60	0.0000
	-0.0042		-0.10				0.0031	2	126	61	0.0000
MAP	-1.1	2.5	0.066	0.65	-0.33	1.8					
2.5% CI	-1.7	1.1	-0.41	-0.36	-1.1	0.58					
97.5% CI	-0.55	3.9	0.54	1.7	0.47	3.1					
Importance		1.0	0.062	0.024	0.84	0.80					

turbine features on the occurrence of collision fatalities in future studies. Second, we used temporally static predictors for our habitat suitability model, as annual land cover maps for Germany are not available at high spatial resolution, thereby preventing the use of time-varying habitat suitability models (Nogués-Bravo, 2009; Kuemmerle et al., 2011; Sieber et al., 2015). However, as our study region in Northeast Germany did not experience strong land conversions over recent decades (Kuemmerle et al., 2016), the assumption that the land cover variables are representative for our study period (2003 to 2014) should not bias our results. In addition, CORINE land cover maps include uncertainties, especially for land-change processes such as agricultural abandonment or deforestation (Kuemmerle et al., 2016), but also for changes in land-management intensity in agriculture or forestry (Stoate et al., 2009). As we used single-date land cover data for which total reliability is 87.0% ($\pm 0.8\%$; EEA, 2006), we deem CORINE land cover maps as a generally useful data source for our purpose.

3. Results

3.1. Habitat suitability

The habitat model performed well ($AUC = 0.946$). Land cover was the most important determinant of WTE nest site occurrence (relative variable importance of 28.5%; Table S4), followed by the distance to marine water bodies (including coastal lagoons and estuaries; 14.8%), distance to inland water bodies (14.2%), distance to urban fabric (i.e. settled area; 7.12%), distance to coastal wetlands (4.51%), and elevation (4.49%). The model indicated that the species prefers nest sites within forested areas that are close to inland and marine water bodies (Fig. S1). In contrast, the species avoids human settlements. The habitat suitability as predicted by the model is shown in Fig. 2b.

3.2. Occurrence of wind turbine collision fatalities

Of the 8 models we considered for the analysis of collision mortality, only the model containing wind turbine density, habitat suitability and their interaction had substantial support (model weight (w_i) = 0.80; Table 1). The best model was supported 7.9 times more strongly than the second best model including only wind turbine density (evidence ratio = $w_i/w_j = 0.797/0.101 = 7.9$). The model including only wind turbine density explained 42%. Including habitat suitability and its

interaction with wind turbine density into this model increased the explained variance to 54% (Table 1). Considering estimates of parameters averaged across models, increases in the density of wind turbines increased the occurrence probability of collision fatalities. This effect was amplified in areas with a high habitat suitability (as indicated by the positive interaction term in Table 1; Fig. 3). For all other parameter estimates the 95% confidence intervals included zero, suggesting that these variables had no consistent effect on the occurrence of collision fatalities (Table 1). As a test of confidence, we investigated the effect of using different spatial resolutions (ranging from grid sizes of 5 km × 5 km to 25 km × 25 km) on the results of our analysis (Table S3). The analysis yielded similar results across all considered grid sizes, suggesting that our conclusions are unaffected by the underlying spatial scale.

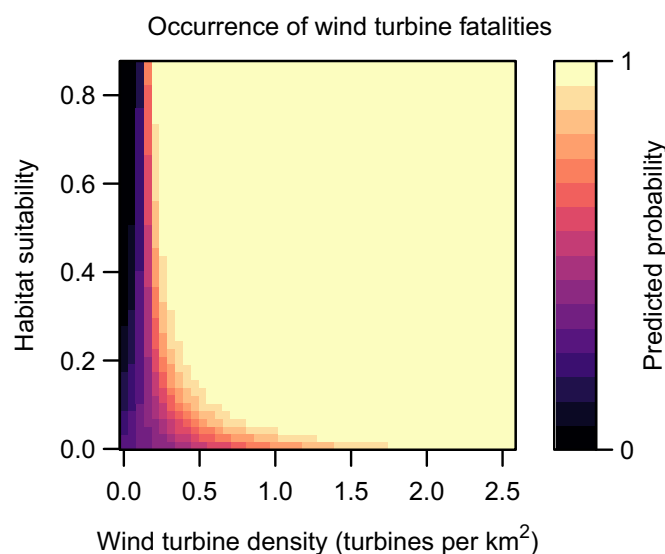


Fig. 3. Predicted probability of occurrence of wind turbine fatalities in response to wind turbine density (turbines per km²) and habitat suitability. Model predictions are based on the model-averaged parameter estimates from the model selection procedure (see Table 1).

4. Discussion

4.1. Occurrence of wind turbine collision fatalities

Here we used data for the WTE in Northeast Germany to assess whether collision mortality increases with wind turbine density and whether a high population density or habitat suitability in the vicinity of wind turbines amplify the effect of wind turbine density on collision mortality. Before discussing our findings, we would like to emphasize again that our study does not rely on systematically collected data on the occurrence of collision fatalities but on opportunistic data collected by the public. Therefore, although our records cover a wide area, we do not know if the search regime was comparable across the study area. This limitation should be kept in mind when interpreting the results of our study. Yet, we can rule out that the collision mortality data are not biased towards wind turbines, because the public reports all dead eagles to regional authorities and not just wind turbine collision fatalities. We found that wind turbine density and habitat suitability had synergistic effects on the occurrence of collision fatalities. The occurrence of collision fatalities increased with the density of wind turbines and this effect was stronger in areas of high habitat suitability. Moreover, combining wind turbine density and habitat suitability allowed for better predictions of collision mortality than combining wind turbine density and nest site density. These results indicate that considering a combination of data on wind turbine densities and habitat suitability allows for improved assessments of collision mortality at large spatial scales. The results also suggest that wind turbines in highly suitable foraging or breeding habitats may have disproportionately strong effects on the mortality of sensitive bird species.

As expected from previous work (Schaub, 2012), wind turbine density was the main predictor of collision mortality in our study. The finding that the best model including wind turbine density, habitat suitability and their interaction outperformed the equivalent model based on nest site density (Table 1) indicates that habitat suitability may better reflect actual habitat use – and thus collision mortality – than the density of nest sites. We are aware of the fact that our habitat suitability model is based on nest site locations and thus, both approaches (i.e., nest site density and habitat suitability) are not independent. However, the aim of the present study was not to compare independent samples, but to compare the performance of both approaches in predicting spatial patterns of collision mortality. One possible explanation for the superior performance of the collision mortality models based on habitat suitability is that the shape and size of individual home ranges of breeding eagles is related to the distribution of suitable habitat. For example, previous work has shown that home range size decreases with an increase in habitat suitability (Krone et al., 2013), which suggests that habitat suitability is an important determinant of movement behaviour, habitat use and potentially collision mortality. In addition, habitat suitability may implicitly take the presence of floaters (non-breeding adults) and dispersing young birds into account (Penteriani et al., 2011), assuming that breeding birds, floaters and dispersing birds have similar habitat preferences (according to unpublished ring recovery data). The contribution of floaters and dispersing young birds to wind turbine collision fatalities might be particularly important within our study population of the WTE. First, the species is a long-lived raptor that becomes sexually mature at the age of four to five years, which naturally leads to a high proportion of non-breeding birds within the population (Penteriani et al., 2011). Second, due to density-dependent effects the number of non-breeding adults in the German population has increased within the last years (Sulawa et al., 2010; Heuck et al., 2017). We hence assume that the models including habitat suitability had a better predictive power than the models including nest site density, because habitat suitability provides a more integrative measure that accounts for the habitat use of breeders as well as for the potential occurrence of non-breeding birds within a population.

The relatively high predictive power of the best model of collision mortality ($r^2 = 0.54$, Table 1) suggests that large-scale assessments of collision mortality for WTEs may be improved by using a combination of data on wind turbine densities and habitat suitability. Therefore, our results support and encourage the use of models that combine data on the distribution of wind turbines with data on habitat suitability as a tool for the analysis of conflict potential on larger spatial scales as it has already been done for a selection of bird species (e. g. Fielding et al., 2006; de Lucas et al., 2012; Reid et al., 2015; Vasilakis et al., 2016, 2017). In particular, the knowledge of conflict potential gained by such models could be used as an initial criterion for the identification of areas, where wind power development should be avoided for reasons of species conservation on a regional planning level. Furthermore, due to the intensive monitoring of rare species (e.g., eagles) the spatial coverage of nest site data is comparatively good, at least in some regions. But for more abundant species, such as the Red Kite, nest sites are difficult to monitor comprehensively across larger spatial scales (Heuck et al., 2013). In regions or for species for which data on the distribution of breeding pairs are incomplete, information from habitat suitability models may provide a reasonable alternative to the use of nest site data for the assessment of conflict potential. Overall, our results highlight that strategic planning of wind farm development on regional scales benefits from models that combine data on the distribution of wind turbines with data on habitat suitability, because these models allow the identification of areas in which species conservation should be given priority.

However, we would like to note that despite their usefulness for regional planning processes habitat suitability models are neither a substitute for detailed population monitoring nor for site-specific Environmental Impact Assessments in the course of project planning. On the one hand, long-term population monitoring provides comprehensive data on the distribution and abundance of the birds in space and time, which is required for habitat suitability models. On the other hand, site-specific Environmental Impact Assessments are crucial to ground-proof the actual habitat use of a focal species in proximity to planned wind turbines. Apart from this, Environmental Impact Assessments are essential to evaluate the potential local impact of wind farms on other species for which habitat suitability models are not available or feasible.

4.2. Conclusions and application

We found that the occurrence of collision fatalities increased with the density of wind turbines and this effect was amplified in areas of high habitat suitability. These synergistic effects indicate that placing wind turbines in core population areas with high habitat suitability can cause a disproportionate increase in mortality when compared with peripheral population areas characterized by low habitat suitability. Furthermore, our results show that models combining wind turbine density and habitat suitability perform significantly better at predicting collision fatalities than equivalent models based on nest site density. Thus, our findings show that combining data on the distribution of wind turbines and habitat suitability provides a reasonable alternative to the use of nest site data for predicting spatial patterns of collision mortality in wide-ranging birds, such as large raptors. In practice, this has some advantages for the planning process of wind energy farms on regional scale. First, habitat suitability is temporally stable when compared with annually varying occupation of nest sites and thus nest site density. And second, data on habitat parameters are freely available and collision mortality can be assessed on regional scale without comprehensive monitoring data. We conclude that assessments of the spatial occurrence of collision fatalities based on models that integrate data on wind turbine densities and habitat suitability can be useful for the strategic planning of wind farm development on regional scales. In particular, our study highlights that wind turbines should not be placed in core population areas of sensitive bird species as disproportionate effects on

mortality may undermine the positive effects of parallel conservation efforts.

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Appendix A. Supplementary data

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