



Coastal onshore wind turbines lead to habitat loss for bats in Northern Germany

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ABSTRACTS

Wind energy production is particularly rewarding along coastlines, yet coastlines are often important as migratory corridors for wildlife. This creates a conflict between energy production from renewable sources and conservation goals, which needs to be considered during environmental planning. To shed light on the spatial interactions of a high collision risk bat species with coastal wind turbines (WT), we analysed 32 tracks of 11 common noctule bats (*Nyctalus noctula*) in Northern Germany with miniaturized global positioning system units yielding 6266 locations. We used three spatial models to infer on the preferred and avoided landscape features in interaction with WT. We found 3.4% of all locations close to WT, with bats preferring areas with high levels of impervious surface, identified as farmhouses. Common noctule bats were also more present close to WT adjacent to paths and waterbodies. At the local scale, >70% of common noctule bats avoided WT, yet if bats approached WT we counted more positions at large WT, specifically close to known roosts. Our study highlights that coastal WT should not be placed next to feeding grounds and bat roosts. Additionally, avoidance of WT by bats indicates that foraging bats may suffer from habitat loss in coastal landscapes with high turbine densities. To mitigate the conflict between wind energy power production and conservation goals at coastal sites, wind turbines should be placed at distance to habitat features preferred by bats and turbine densities should be limited.

1. Introduction

Onshore wind farms are frequently built along coastlines (e.g., Katinas et al., 2009; Mackensen, 2019), because wind energy production is highest in areas with prevailing strong winds (Barthelmie and Palutikof, 1996; Nunalee and Basu, 2014). However, coastal areas are also important breeding grounds, migration flyways, and stopover sites of animals, and thus, the expansion of coastal wind energy production may come at the expense of wildlife conservation (e.g., Lamb et al., 2018; Li et al., 2020). In Germany, density of onshore wind turbines (WT) is highest along the North Sea coastline (Mackensen, 2019). This coastline, also known as the Wadden Sea, is a designated UNESCO World Heritage Site because of its importance for breeding, migration and stopover of

birds (Reise et al., 2010; Boere and Piersma, 2012). It is less known, although well established, that coastal areas are also used by bats for migration (Ahlén, 1997; Rydell et al., 2014), specifically also along the North Sea coastline of Germany and the Netherlands (Rydell et al., 2014). Thus, onshore wind farms could be in conflict with bat migration when habitats get degraded because of WT and, specifically, when bats collide with and die at these WT (Rydell et al., 2010).

In most European countries, bats are protected by the E.U. Habitat Directive (92/43/EWG (Annex II and IV)) and also by national legislation. Additionally, bats benefit in Europe from a strict protection by the U.N. convention on migratory species as specified in the UNEP/EURO-BATS agreement (signed in Bonn 1979; London 1991). Thus, impact assessments have to be performed before WT are constructed, and

Abbreviations: WT, wind turbine; GPS, Global Positioning System; U.N., United Nations; ARM, Area Restricted Movements; COM, Commuting; HMM, Hidden Markov Model; MCP, Minimum Convex Polygon; RSF, Resource Selection Function; SSF, Step Selection Function; AICc, Akaike information criteria corrected for small sample sizes; SD, Standard Deviation.

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mitigation schemes implemented during operation to reduce the negative impacts of WT on bats (Brinkmann et al., 2011). These surveys usually involve acoustic monitoring of bats at nacelles, where bat activity is recorded in part of the risk zone, namely the rotor swept area. However, the recording of ultrasonic calls of bats at nacelle height is impaired by the atmospheric and geometric attenuation of high frequency echolocation calls so that only a small fraction of the risk zone is surveyed, particularly at WT with large rotor diameter and for species with high frequency calls (Voigt et al., 2021). These limitations in combination with the elusive lifestyle of bats limit our understanding of how bats interact with WT. Three-dimensional tracking via thermal imaging suggested that bats approach WT mostly from the leeward side (Cryan et al., 2014), yet such studies are usually limited to a few turbines because of the time-consuming analysis, and they do not link flight trajectories to landscape features (Cryan et al., 2014; Gorresen et al., 2017).

To obtain insights into the movements of bats around WT, we conducted a study with miniaturized GPS (Global Positioning System) units with on-board ultrasonic microphones. GPS units are a promising tool to elucidate bat movements in relation to WT because of the various spatial scales GPS data are covering. In a pilot study conducted in northeastern Germany, we observed that male common noctules (*Nyctalus noctula*) avoided WT and females were attracted (Roeleke et al., 2016). However, it remained unclear whether the sex-specific response to WT was confounded by season. Here, we aimed at identifying factors that are relevant for bats when flying close to WT. Such information could inform stakeholders about whether certain turbine features, such as turbine size, correlate with a higher bat activity, or whether certain landscape features, such as waterbodies or forests, increase the likelihood of bats for being present at WT. During the planning process, stakeholders could then focus on those locations and types of WT that cause the least level of interaction between WT and bats. This could reduce revenue losses caused by curtailing the operation of turbines (Voigt et al., 2015).

Here, we tested at a coastal landscape with high WT density whether common noctules prefer certain land cover categories, such as waterbodies and meadows (Roeleke et al., 2016, 2018, 2020; Voigt et al., 2020). Additionally, we tested whether common noctules are attracted to large, and thus more visible WT, because it was suggested that bats foraging at dusk may mistake large WT for tall trees with potential roosts (Cryan et al., 2014). Accordingly, we expected large WT to attract more common noctules than small WT. Alternatively, WT may represent prominent landscape elements where bats interact socially. Thus, we used acoustic data from on-board microphones to reveal the behaviour of bats at WT, especially with respect to feeding and the presence of conspecifics (Cvikel et al., 2015; Roeleke et al., 2020). Lastly, we tested whether females are more attracted to WT than males as suggested by our pilot study (Roeleke et al., 2016). The outcome of this study will provide valuable information for wind energy companies, conservation managers, and authorities about where to build wind turbines and how to operate them in order to reduce bat fatalities at coastal multi-use landscapes.

2. Material and methods

2.1. Study site and field work

Our work was conducted between August and early September 2020 under the animal care and welfare permit 33.19-42502-04-19/3163 and the conservation permit IV-60-610-96/2019. The study area close to the coastline of the North Sea is dominated by crop farming (~39%), meadows (~46%), small villages, a coastal climate, and a high density of WT. We focused on two small forests in the county of Aurich (Fig. S1) with natural roosts of common noctules. We captured bats by setting up mistnets (8–10 m length, 10 mm mesh size, Solida, Steinbach, Germany; 6–9 m length, 16 mm mesh size, Ecotone, Gdynia, Poland) at various

heights in flight corridors and in front of roosts. We noted the sex and age (based on epiphyseal closure) of captured bats. Additionally, we measured the forearm length (0.1 mm, calliper, Ecotone, Gdynia, Poland) and body mass (precision 0.1 g, electronic scale, Ecotone, Gdynia, Poland). In total, we tagged 16 common noctules. The body mass of these bats averaged 31.7 g (range 28.0–39.0 g). We used GPS loggers with an integrated ultrasonic microphone (ASDevelopments, Haifa, Israel). Additionally, we attached a single VHF transmitter (Telemetrie-Service Dessau, Dessau, Germany) to each tag which helped us to retrieve the unit. By attaching the unit to the fur at only two small spots using skin glue (Torbot, Cranston, USA), we ensured that they would fall off the bat within about 5 days. For retrieving the unit, we located the VHF signal of the radio-transmitter by homing in using a receiver and an antenna (ICOM IC-R30, ICOM, Japan; Australis 26K Receiver, Titley Scientific, Australia). Units made up about 10% of the bat's body mass. This was in the range of earlier studies which reported no negative impacts on bats (Cvikel et al., 2015; Roeleke et al., 2016, 2018, 2020; Voigt et al., 2020).

GPS units started recordings in the subsequent night to allow habituation of bats to the attached units. Then, GPS loggers sampled spatial positions every 30 s, starting at 20:30 or 21:00 h (CET; depending on sunset) and lasting until 02:00 h (CET), the presumed latest return time of bats to their roost (Roeleke et al., 2016; Voigt et al., 2020). The ultrasonic microphone was set to record every 10 s for 1.5 s with a sampling rate of 160 kHz (Roeleke et al., 2020).

2.2. Data preparation and environmental predictor variables

We excluded data from units with less than 10 GPS locations ($n = 1$). For the remaining tracks we measured the distance to starting point (roost), total travel distance, flight duration, step lengths (distance between subsequent spatial positions of a track), and turning angles (angle between three subsequent spatial positions). We used Hidden-Markov models (HMM) to assign spatial positions to one of two movement modes, Area Restricted Movement (ARM) or COMmuting behaviour (COM), based on step lengths and turning angles (fitHMM function, R-package 'moveHMM') (Michelot et al., 2016). We set mean step lengths to starting values of 40 m (± 40 m standard deviation; SD; state one/ARM) and 200 m (± 200 m SD; state two/COM). Furthermore, turning angle means were set to π (state one/ARM) and 0° (state two/COM). We fitted the HMM with a gamma distribution for step length and von Mises distribution for turning angles. A threshold of 0.75 was set to correctly assign one of the states to a GPS location. We characterized GPS locations below this certainty level as undefined. Short step lengths and larger turning angles were used to identify foraging behaviour (hereafter called ARM) and large step lengths and small turning angles to identify search behaviour or commuting (hereafter called COM).

In each acoustic file, we identified echolocation calls indicating search flights, social calls, and feeding buzzes (stereotypic sequences of echolocation calls with decreasing interval lengths and main frequencies of subsequent calls) indicating an insect hunt (Roeleke et al., 2020). Additionally, we noted the presence of conspecific calls and noise of unknown origin. Usually, we collected three acoustic files for each GPS location. We categorized a GPS location as hunting when at least one of the recordings assigned to this location contained a feeding buzz.

Based on a 20 m raster of the Corine land cover map ("Digitales Landbedeckungsmodell für Deutschland", 2018 (LBM-DE2018)), we assigned the main underlying land cover type within a buffer of 50 m to each GPS location. Land cover types included sealed surface, urban green, agricultural areas, meadows and shrubs, forest, open natural areas, wetland, and waterbodies. After estimating the proportion of each land cover category within the 50 m buffer based on a 5 x 5 raster window surrounding the GPS location, we selected the category with the highest proportion inside the buffer. If the main category represented >50% of the 50 m buffer, the GPS location was assigned to this land cover type, otherwise it was characterized as "diverse". We retained the

proportion of sealed surface, forest and water within the buffer as separate numeric predictor variable. Furthermore, we calculated the distances of the GPS locations to paths (based on Layer 15 and 35 of the “Digitales Basis-Landschaftsmodell” (Ebenen) 2015 (Basis-DLM)) and the closest WT (Eichhorn et al., 2019). We defined paths as linear elements such as paved or unpaved paths, walking tracks, and roads.

2.3. Statistical analyses

We analysed the data with R 3.6.2. (R Core Team, 2019). We implemented a use-versus-availability design for feature selection to compare the observed GPS locations with the available predictor variables consisting of land cover categories, distance to linear landscape elements and WT, WT characteristics, and sex. We created five random points per observed GPS location in three different methodological approaches to cover different landscape scales (Fig. 1). We used resource selection functions (RSF) to assess preference/avoidance behaviour of bats at the landscape scale (Signer et al., 2018). We distinguished between two RSF: In a regional approach, we included all GPS positions and the total area covered by all tagged bats (Fig. 1A, D). The RSF compared observed GPS locations with points randomly distributed within the 100% minimum convex polygon (MCP) of spatial positions of all bats (hereafter abbreviated as $RSF_{GeneralMCP100}$). To be sure to only analyse locations that were on a bat's foraging trip and not related to homing behaviour, we excluded all locations <1.5 km distance around roosts (hereafter $RSF_{GeneralMCP100\ GPS>1.5km}$). We decided for this filter because one of the large wind farms was located close to a roosting site, which might bias the model outcome because bats commute to and from the roost independent of nearby wind turbines. In our local approach, we compared observed GPS locations with points randomly distributed within the 100% MCP of an individual's flight path (hereafter abbreviated as $RSF_{MCP100/flight\ path}$; Fig. 1B, E). In a local approach that included

information on the specific behaviour of bats, we used a step selection functions (SSF) to compare each observed step with random locations sharing the same focal point (local/behaviour approach, individual location level; Fig. 1C, F). The random locations are defined by randomly assigned step lengths and turning angles drawn from maximum likelihood fitted distributions based on the observed steps, with gamma distribution for step length and von Mises distribution for turning angles (Signer et al., 2018).

We investigated feature selection using generalized linear mixed effects models with Template Model Builder (glmmTMB function from R-package ‘glmmTMB’; Brooks et al., 2017), with binomial error distribution in case of the RSF. We included a random slope at individual level for the distance to WT in the RSF models to discern individual reaction norms of selection. The SSF used a conditional logistic regression model with step-id as stratum (clogit function from R-package ‘survival’; Therneau and Grambsch, 2000; Therneau, 2015). All models included the main land cover categories as well as the proportion of sealed surface, forest and waterbodies within 50 m of the GPS location, distance to paths, distance to closest WT, movement mode (ARM or COM), presence of feeding buzzes or conspecifics and sex as fixed effects. To assess whether movement mode or presence of feeding buzzes or conspecifics resulted in a better estimation of bat presence, we did not use these in the same model. We further tested different two-way interactions and three-way interactions between land cover categories, distance to closest WT, movement mode, presence of feeding buzzes or presence of conspecifics. All tested candidate models are specified in the supplement (Tables S1-S4).

Model selection was based on the Akaike information criterion corrected for small sample sizes (AICc). We selected simpler models whenever $dAICc_i < 2$, for $dAICc_i = AICc_i - AICc_{min}$ (Burnham et al., 2011; Culina et al., 2017). Numeric variables included as fixed effects in the model selection were tested for multicollinearity and only one of the

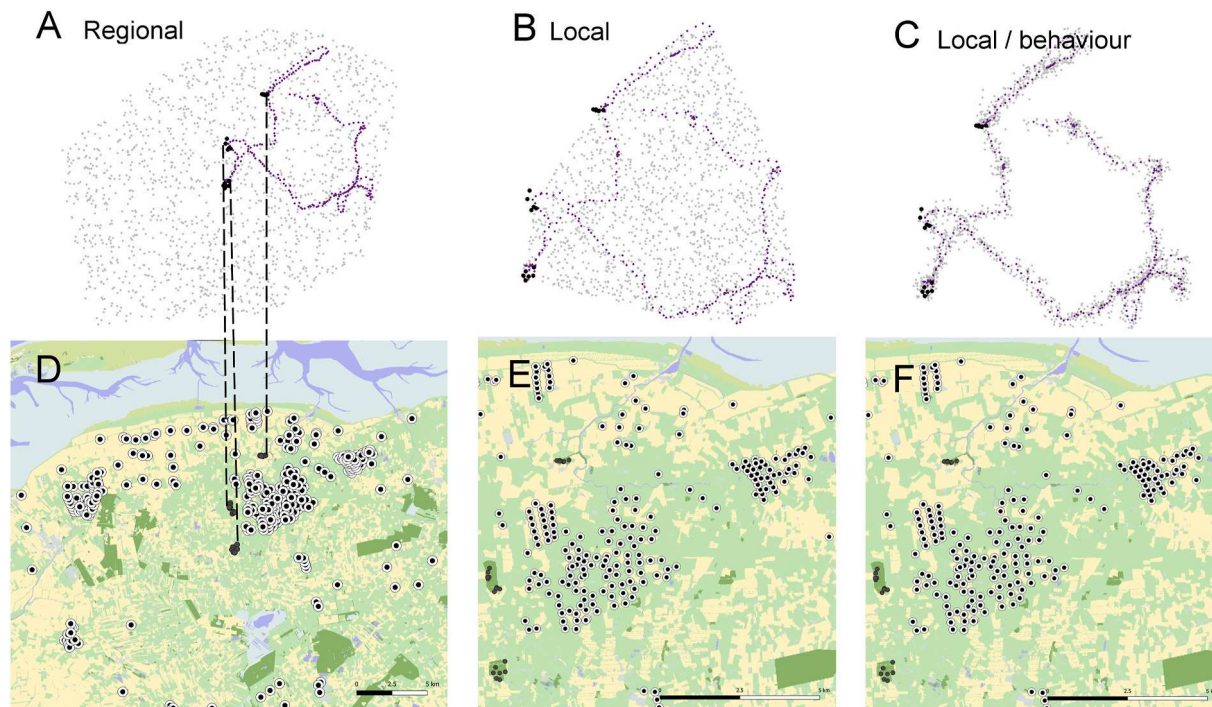


Fig. 1. Model description for one individual flight path: (A, D) regional scale with a resource selection function (RSF) based on random points generated in the MCP100 encompassing all GPS tracks ($RSF_{GeneralMCP100}$), (B, E) local scale with RSF based on random points generated in the MCP100 of individual MCP covering all spatial positions of a focal individual's flight path ($RSF_{MCP100/flight\ path}$), and (C, F) local scale considering individual behaviours based on step selection function (SSF). Random points are depicted in grey and observed GPS locations in violet. The background map was obtained from Corine land cover map (Digitales Landbedeckungsmodell für Deutschland, 2018 (LBM-DE2018), 20m raster). Information on wind turbines (WT; symbol: white circle with black dot in the centre) was obtained from Eichhorn et al. (2019). Larger dark-grey points characterize tree roosts used by the individuals. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

compared variables was included in the model if $|\text{Kendall's tau}| > 0.7$ (Mukaka, 2012). To assess model quality we determined the area under the curve (AUC) or explained variance (R^2).

2.4. Attraction effect of wind turbines

To investigate the behaviour of bats in close proximity to WT, we counted the GPS locations within 100 m distance of WT and created generalized linear models with Poisson error distribution. Similar to the previous feature selection models, land cover category, as well as proportion of sealed surface, forest and waterbodies within the 50 m buffer around the WT and distance to paths were included as fixed effects. Additionally, we tested a possible effect of turbine size (diameter of rotor blades), distance to assumed roosts, number of neighbouring WT within 1 km of WT to account for potential cumulative effects of WT within wind farms, as well as the interaction between the last two factors (Table S5).

3. Results

3.1. General flight behaviour

Out of 16 tagged bats, we retrieved GPS tags from eleven individuals (six males/five females). In total, we recorded 32 flight paths from these bats, which resulted in 6.266 GPS locations (Fig. 1), with 3.4% of locations recorded at distances <100 m to the nearest WT. We analysed data from 20 nights resulting in 32 round-trip flight paths. During a given night, bats travelled on average 29 ± 18 km (mean \pm one SD) (Table 1). The assignment of movement modes to spatial positions revealed that about 48% belonged to commuting (COM), 43% to hunting (ARM), i.e. area restricted movement, and 9% to undefined movements. For further analyses, we used the acoustic information (feeding buzzes, search calls, social calls, presence of conspecifics, noise) assigned to spatial positions. Focusing on feeding buzzes, movement modes showed a similar distribution across land cover categories with a slightly higher proportion of ARM over forests and sealed surfaces and of COM over farmland and meadows (Fig. S2A). For the acoustic classes of conspecific presence and social calls, we observed the same pattern, but the differences between ARM and COM were more pronounced for the aforementioned land cover classes (Fig. S2B).

3.2. Feature selection

All three methodological approaches (Fig. 1A–F) yielded similar results for the two-way interaction of features as well as for distance to paths, with the regional approach excluding locations around roosts yielding the clearest signal in discriminating bat locations from random points (AUC = 0.79; Table S7). Owing to this consistency, we present only results from the SSF model for overall effects, as this is the latest development for analysing high-throughput tracking data, while we use the random effect models (both RSFs) for visualizing differences amongst individuals in their behaviour towards WT. All model results are reported in the supplemental information (Figs. S3–S14, S17; Tables S6–S9).

The presence of common noctules increased significantly with increasing proportion of sealed surface within distances <100 m to WT,

while sealed surfaces were not attractive for bats when being far away from WT (i.e., at distances >2 km) (Fig. 2, Table S7). Additionally, common noctules were more likely to be present close to paths than expected by random movements (Fig. S13). Furthermore, common noctules were most likely present at distances <100 m to WT when waterbodies were present, irrespective of whether bats showed ARM or COM (Fig. S6). During ARM, indicating aerial hunts, common noctules were most likely present over forests, waterbodies and wetlands close to WT (Figs. S3–S9; Tables S6–S9). Although the majority of GPS locations were found above farmland and meadows, these land cover types were mostly avoided considering their relative availability within the study area (Figs. S3–S6, S15). Sex did not explain variation in the used land cover categories.

3.3. Individual responses of bats to wind turbines

We found large individual variation in movement responses toward WT (distance to closest WT; integrated as individual random slopes in both RSF models). At the regional level (RSF_{GeneralMCP100}), common noctules seemed to be attracted to WT (Fig. S17), yet this effect disappeared when excluding locations close to roosts (RSF_{GeneralMCP100 GPS>1.5km}) and variation across individuals increased (Fig. S14). This suggests that our finding of an attractive effect at the regional scale was mostly caused by the forests situated right next to a large wind farm which caused bats to pass by the wind farm at close distance when flying to and from daytime roosts in the forest. Our local model approach was expected to be insensitive to this artefact, and accordingly, we observed for the RSF_{MCP100/flight path} that bats avoided WT (Fig. 3). The acoustic data did not improve model quality (Tables S1–4), which is probably due to the lack of correlation between acoustic data and land cover categories (Fig. S2) and distance to closest WT (Fig. S16), especially in case of feeding buzzes.

3.4. GPS locations at wind turbines

In total, 3.4 percent of GPS locations were recorded at distances <100 m to the nearest WT in our study area, ranging from 0 to 15 for a given WT (Fig. 4). We detected significantly more GPS locations within 100 m of WT with large rotor diameter and especially when WT were located next to daytime roosts. When accounting for the distance to roosts, a central or peripheral position of WT within a wind farm or specific landscape elements had no effect on the model outcome (Fig. 5, Table S10, $R^2 = 0.47$). However, there was no effect of rotor diameter but centrality of the WT when compared to the number of bat locations versus RSF_{MCP100/flight path} random locations inside the buffer due to the placement of the wind park inside the main hunting grounds of the bats (Fig. S18, Table S11).

4. Discussion

Our study is the first to describe the movement responses of bats toward onshore wind turbines (WT) at a coastal site that is known for its high energy yield from wind power and for its high conservation status as a migratory corridor for wildlife. Common noctules are migratory bats in Europe and at the same time a species with high collision risk at WT (Rydell et al., 2010; Lehnert et al., 2014). Knowing how these bats interact with WT at a coastal migratory corridor is pivotal for informing conservation agencies about effective management measures and wind farm developers about how to best avoid conflicts with bat conservation. Using miniaturized GPS units with on-board microphones, we established fine-scale flight tracks for eleven bats in a landscape with high WT density. Our three model approaches, the step selection function and resource selection functions at a regional and local landscape scale, yielded convergent results, which supports the robustness of our results and the general nature of our findings.

We observed that common noctules were likely present at WT when

Table 1

Description of flight paths of common noctules across all 32 flight paths.

Movement parameter	Mean (range)
Flight path per individual:	3 (2–4)
Total flight distance per flight path (km):	29 (4–71)
Maximal distance to start per flight path (km):	6 (1–20)
Flight duration (min):	169 (19–288)
Minimal distance to closest WT (m):	123 (7–1570)

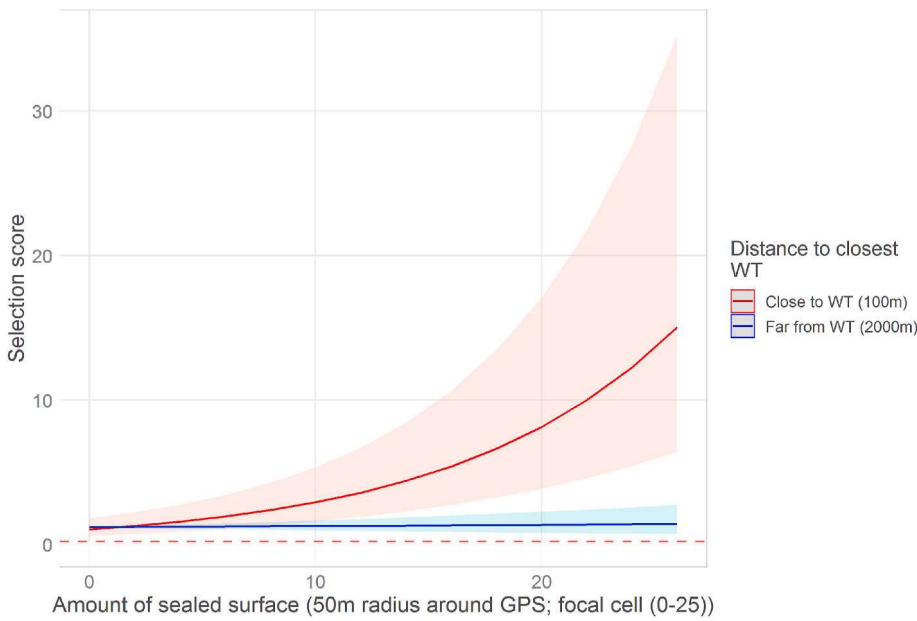


Fig. 2. Estimated selection score (relative selection against the strata-averages of the SSFs; originally termed ‘risk score’ in the R-package survival) for common noctules in relation to the amount of sealed surface within a 50 m radius around the GPS location, calculated for two distance categories in relation to wind turbines: Close to turbines (~100 m; red line) and far away from turbines (~2000 m; blue line) with corresponding 95% confidence interval. The remaining variables in the model were set constant (main land cover = meadow; distance to closest path = 0.12 km, logarithm of step length = 4.74, step-id = 1850714E_2020/08/27_10). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

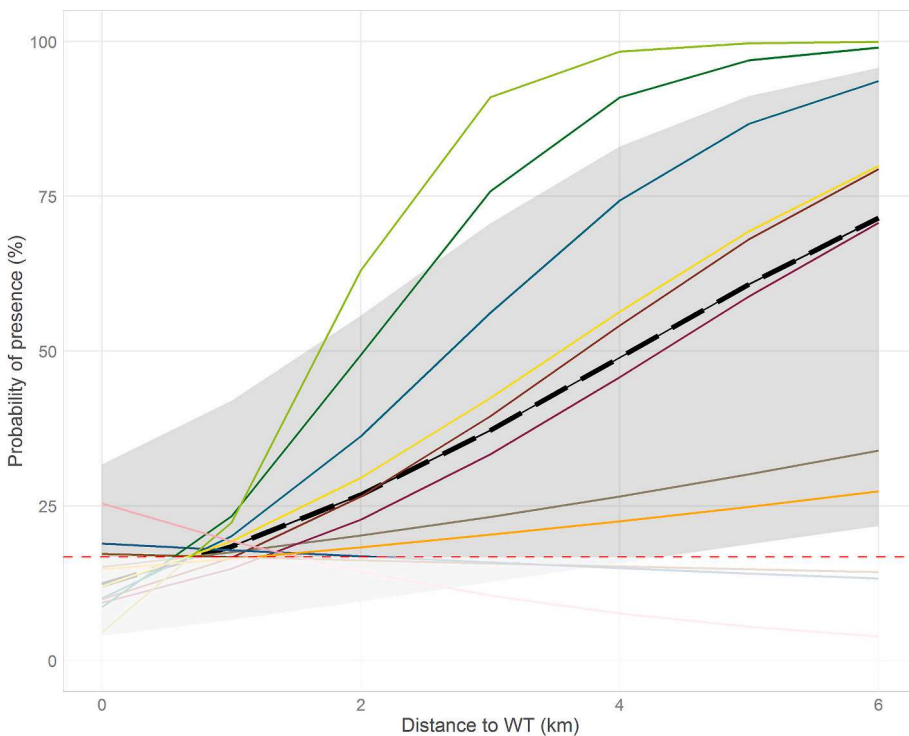


Fig. 3. Estimated probability of presence in relation to the distance (km) to wind turbines (WT) for common noctules based on the random effects of the best fitted model. The random points for comparison were generated within a MCP100 encompassing all GPS positions of individual flight paths (RSF_{MCP100/flight path}). The response curve is shown on the population level (black, long dashed line) and individual level (solid lines, colours representing individuals). The underlying grey polygon shows the prediction interval on population level. The red dashed line describes the threshold of 16.7% (observed:random points = 1:5) separating habitat avoidance (below) from preference (above). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

these were situated in an area with a high level of impervious surfaces. These areas represent mostly uninhabited farmhouse complexes where livestock are kept in stables. We assume that a high insect abundance at these sites may have turned these areas attractive for foraging bats. Accordingly, we recommend erecting WT only at some distance to farmhouses, a suggestion that has already been put forward for the reason of human safety and for reducing WT related annoyance by local inhabitants. We also observed common noctules close to WT when paths and waterbodies were present. Paths could be used by commuting common noctules as a guiding landscape structure (Roeleke et al., 2016, 2020). Waterbodies produce many insects with aquatic larval stages, thus they present suitable foraging grounds for aerial-hawking bats such

as common noctules (Voigt et al., 2020). Our observation suggests that WT should only be erected at far distances from waterbodies to reduce the level of interaction of foraging and commuting bats with WT.

At the local scale, the population of studied common noctules avoided WT, yet we also observed a high level of inter-individual variation, with some individuals avoiding WT and few others being attracted to WT. This high level of inter-individual variation in response to WT confirms an earlier study conducted with the same species (Roeleke et al., 2016). Sex did not explain this variation, and thus the underlying causes for this high inter-individual variation remains elusive. We speculate that the avoidance or attractant behaviour toward WT could be related to the geographic origin of individual bats. Bats that are

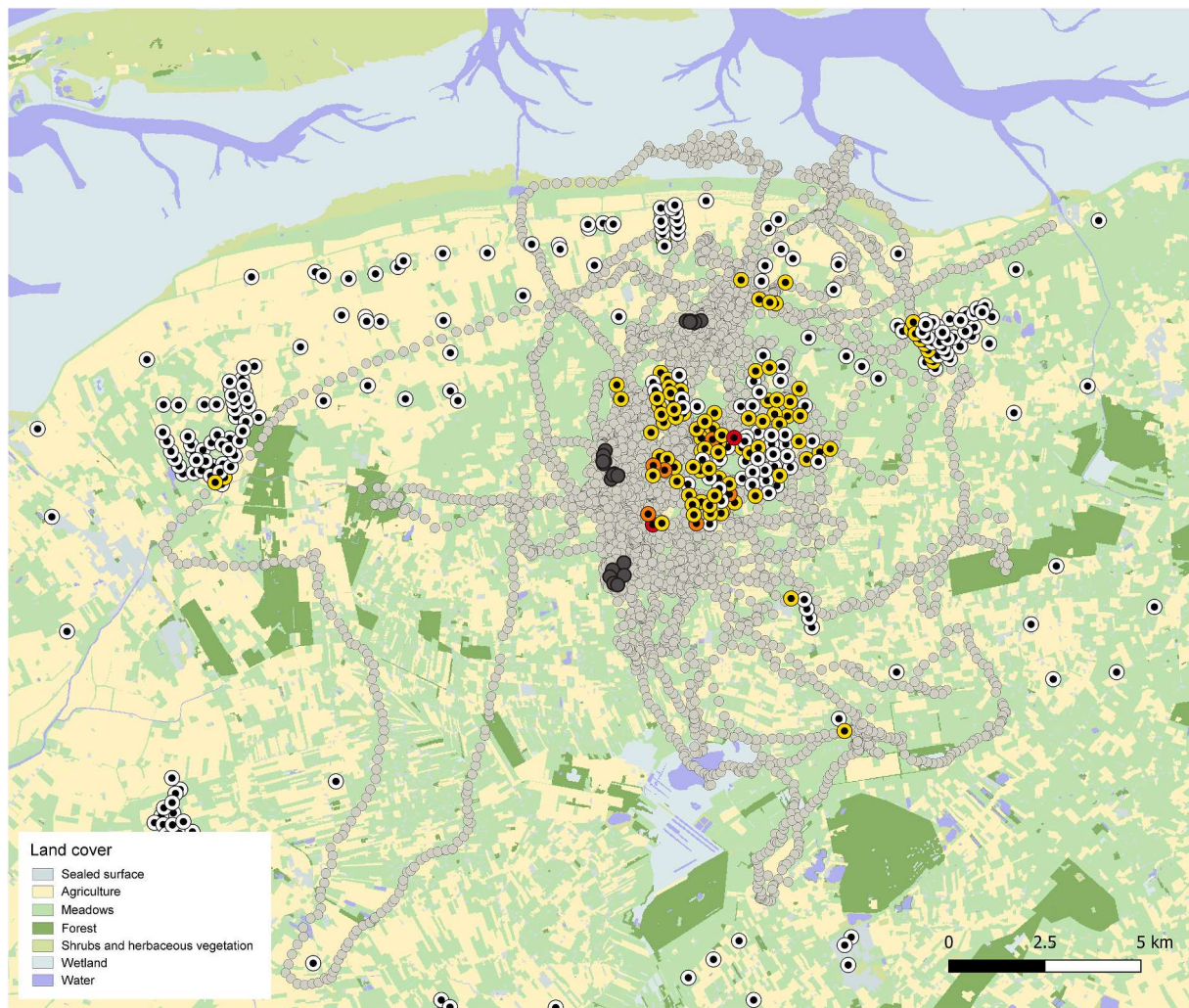


Fig. 4. Flight paths of common noctules (*Nyctalus noctula*) in late summer in Northern Germany. Each grey dot represents a spatial position of a bat. The background map was obtained from the same source as in Fig. 1. The colours of the WT symbols relate to the number of GPS locations within the 100 m buffer of the respective wind turbine (white – 0 (N = 293), yellow – 1–5 (N = 84), orange – 6–10 (N = 7), red – 11–15 (N = 2)). Dark grey points indicate tree roosts. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

present year-round may not explore WT as potential roosting sites, since they are likely to know natural roosts in the local area. In contrast, migratory conspecifics may explore WT when searching for daytime roosts in unknown terrain. Unfortunately, we were not able to differentiate between local and migrant bats in our study. The observed avoidance behaviour on the population level suggests that (1) bats do not access areas close to WT for foraging on a regular scale, and that (2) bats make detours while exploring the landscape for resource patches. Thus, wind farms may reduce the area available for foraging bats. As a consequence, a high WT density may further reduce the connectivity of habitats that bats may need on a daily basis. All in all, avoidance behaviour toward WT may lower the quality of habitats used by common noctules. Unfortunately, habitat degradation and loss is by and large not considered during wind turbine developments, yet our data shows that landscapes with high densities of WT may push bats away from areas that they may have used before for foraging, commuting, and most likely also migrating.

If common noctules approached WT, they were more likely to fly toward large than small WT, yet we cannot exclude the possibility that this is an effect of landuse of bats independent of turbine size. This pattern was more pronounced when roosts were present next to WT. We assume that the higher activity levels of common noctules at large WT may lead to stricter curtailment regulations as a mitigation measure, i.e.

the cut-in speed will have to be increased significantly to protect common noctules from colliding with the spinning blades. Since the presence probability of common noctules increased at large WT in proximity to daytime roosts, we recommend building WT only far away from areas with a high potential for roosts, e.g., forests. For large WT, we expect an intensified conflict between energy production from renewable sources and conservation goals, i.e. the protection of common noctules as a high collision risk species, because of the high activity levels of common noctules at large WT and the fact that larger WT generate more electricity at even low wind speeds compared to small WT (Voigt et al., 2015).

We acknowledge that our study is based only on a limited sample size, although being about equal in sex ratio, and that field data was obtained only during a single season and restricted to the summer migration period. Our temporal focus on the summer migration period pays tribute to the fact that most observed fatalities of common noctules are observed during migration (Rydell et al., 2010). Our data is consistent with earlier studies with respect to preferred foraging habitats of common noctules, such as waterbodies, forests and extensive farmland (Roeleke et al., 2016, 2018, 2020; Voigt et al., 2020). Also, a large inter-individual variation of response behaviour of common noctules to WT was observed before (Roeleke et al., 2016). Thus, while considering limitations that might emerge from a limited sample size, we

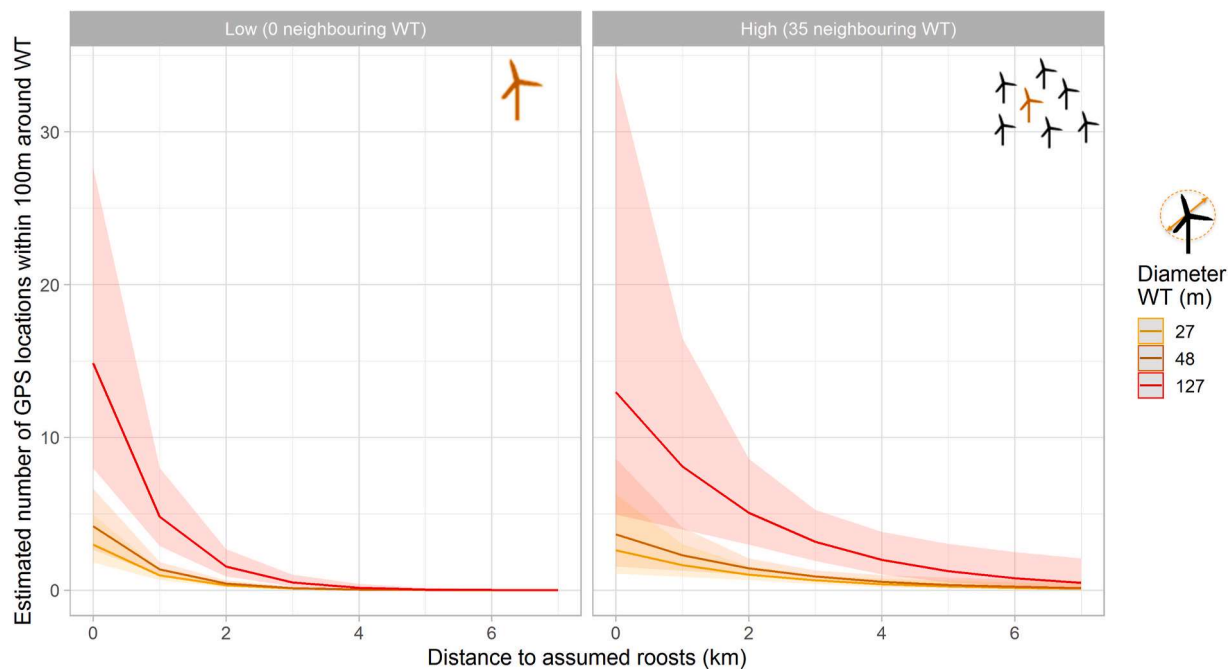


Fig. 5. Estimated number of GPS locations of common noctules (*Nyctalus noctula*) at < 100 m distance to wind turbines (WT) in relation to distance to known roosts (km), the number of neighbouring WT within 1 km distance and the diameter of rotor blades of the corresponding WT (diameter 27 m: orange lines; diameter 48 m: brown lines; diameter 127 m: red lines). The number of neighbouring WT in 1 km distance was illustrated for two scenarios (left graph: no neighbouring WT = low density; right graph: 35 neighbouring WT = high density). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

nonetheless see general patterns that remain consistent across studies.

4.1. Conclusions

We infer from our GPS tracking study of bats that coastal areas with a high density of WT are high risk areas for aerial-hawking bats such as common noctules. WT should not be erected close to foraging grounds and daytime roosts of common noctules to avoid high activity levels of bats at WT. Large WT may attract more bats than small WT, thus stronger curtailment regulations may counteract the higher energy yield of large WT; yet we cannot exclude an effect of wind park placement in relation to foraging grounds on this finding. At the population level, common noctules avoided WT. At a local scale, the response behaviour of common noctules toward WT was highly variable; and factors contributing to this variation remained unclear. Coastal areas with migratory corridors remain high conflict areas where environmental goals to protect the climate via the promotion of wind energy and the protection of biodiversity are difficult to balance. Habitat degradation and loss should be acknowledged as an important problem associated with the development of WT facilities in coastal areas, since wind farms may restrict the space available for bats for daily movements and migration.

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Credit author statement

Reusch: Data curation, Formal analysis, Field work, Data Formal analysis, Visualization, Writing, Editing. **Lozar:** Data Formal analysis, Commenting. **Kramer-Schadt:** Funding acquisition, Investigation, Data Formal analysis, Supervision; Validation, Comment and editing of manuscript. **Voigt:** Conceptualization, Funding acquisition,

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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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Appendix A. Supplementary data

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