Received: 15 March 2022 | Accepted: 1 July 2022

DOI: 10.1111/1365-2664.14249

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Activity of forest specialist bats decreases towards wind turbines at forest sites

Julia S. Ellerbrok[1,2] | Anna Delius[1] | Franziska Peter[3] | Nina Farwig[1] | Christian C. Voigt[2]

[1]Conservation Ecology, Department of Biology, University of Marburg, Marburg, Germany

[2]Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

[3]Natural Resource Conservation, University Kiel, Kiel, Germany

Correspondence
Julia S. Ellerbrok
Email: julia.ellerbrok@biologie.uni-marburg.de

Funding information
Deutsche Bundesstiftung Umwelt

Handling Editor: Silke Bauer

Abstract

1. Worldwide, wind turbines are increasingly being built at forest sites to meet the goals of national climate strategies. Yet, the impact on biodiversity is barely understood. Bats may be heavily affected by wind turbines in forests, because many species depend on forest ecosystems for roosting and hunting and can experience high fatality rates at wind turbines.
2. We performed acoustic surveys in 24 temperate forests in the low mountain ranges of Central Germany to monitor changes in the acoustic activity of bats in relation to wind turbine proximity, rotor size, vegetation structure and season. Call sequences were identified and assigned to one of three functional guilds: open-space, edge-space and narrow-space foragers, the latter being mainly forest specialists.
3. Based on the response behaviour of bats towards wind turbines in open landscapes, we predicted decreasing bat activity towards wind turbines at forest sites, especially for narrow-space foragers.
4. Vertical vegetation heterogeneity had a strong positive effect on all bats, yet responses to wind turbines in forests varied across foraging guilds. Activity of narrow-space foragers decreased towards turbines over distances of several hundred metres, especially towards turbines with large rotors and during mid-summer months. The activity of edge-space foragers did not change with distance to turbines or season, whereas the activity of open-space foragers increased close to turbines in late summer.
5. *Synthesis and applications*. Forest specialist bats avoid wind turbines in forests over distances of several hundred metres. This avoidance was most apparent towards turbines with large rotors. Since forests are an important habitat for these bats, we advise to exclude forests with diverse vegetation structure as potential wind turbine sites and to consider compensation measures to account for habitat degradation associated with the operation of wind turbines in forests.

KEYWORDS
acoustic monitoring, avoidance, bats, distance effect, foraging guilds, habitat degradation, temperate forests, wind farms

1 | INTRODUCTION

Global carbon dioxide emission is the main driver of climate change (Solomon et al., 2009), threatening biodiversity and human economies worldwide (Bellard et al., 2012; Walther et al., 2002). To mitigate this threat, many countries are promoting wind energy production as a sustainable form of energy from renewable sources (Gielen et al., 2019). However, a growing body of literature indicates that the construction and operation of wind turbines may lead to habitat loss and an increased mortality risk for wildlife (Grünkorn et al., 2017; Kuvlesky et al., 2007; Saidur et al., 2011). For instance, past studies documented high fatality rates of bats and birds at wind turbine rotors (Arnett et al., 2016; Thaxter et al., 2017). Indeed, it was suggested that wind turbines may be the most significant anthropogenic factor causing multiple mortality events in bats (O'Shea et al., 2016). Consistent with this notion, past studies estimated that annual losses of bats at wind turbines may reach several hundred thousand in countries of the temperate zone (Hayes, 2013; Voigt et al., 2015; Zimmerling & Francis, 2016). This is mirrored in observed and modelled population declines of high collision risk species in North America and Europe (Frick et al., 2017; Friedenberg & Frick, 2021; Printz et al., 2021).

Our current understanding of the wind energy–bat conflict is based almost exclusively on studies conducted at wind turbines operating in open landscapes. However, over recent years, turbines have been increasingly built at forest sites throughout Europe, particularly in Central and Northern Europe (Gaultier et al., 2020), despite guidelines recommending the contrary when alternative sites are available (Rodrigues et al., 2014). For instance, in Germany, more than 2,000 wind turbines (7.5% of all onshore turbines) operate currently at forest sites (Mackensen, 2019; Quentin & Tucci, 2021). To reduce further greenhouse gas emissions, recent pledges aimed at doubling the share of renewable energy production by increasing the area assigned for wind energy development from 0.8% (as of 2021) to 2.0% of the total surface area until 2030 (BMWK, 2022). Since land use pressure on open landscapes is already high and critical distances between wind turbines and settlements need to be maintained, several German federal states expand wind energy production in forests.

Although non-primary forests of the temperate zone are usually managed for timber production, they offer valuable habitats for many species (Götmark, 2013; Hilmers et al., 2018; Spiecker, 2003). Forests constitute important hunting grounds for forest specialist bats and provide shelter for many more bat species (Dietz & Kiefer, 2014; Müller et al., 2013; Plank et al., 2012). Thus far, it is largely unknown how wind turbines in forests affect forest-associated bats. Although not at high risk of colliding with turbine rotors, forest specialist bats foraging below the canopy may be impacted by indirect wind turbine effects (Hurst et al., 2020). For instance, studies in open landscapes documented a reduced bat activity close to wind turbines compared to control sites without turbines, suggesting an avoidance behaviour and an indirect habitat loss for several species (Millon et al., 2015). Another study documented decreased bat activity along transects towards turbines (Barré et al., 2018), an observation that was confirmed for small wind turbines (Minderman et al., 2017). The underlying cause for this avoidance remains unclear, but bats may respond to turbine-generated noise (Allen et al., 2021; Finch et al., 2020) or potentially to artificial light (Bennett & Hale, 2014). Turbine construction in forests is further accompanied by fragmentation and degradation (Lesiński et al., 2007), while the creation of clearings and aisles is leading to a loss of foraging habitats and daytime roosts in trees (Hurst et al., 2020). However, forest fragmentation may also lead to increased activity of those bats which are more adapted to open and edge habitats and to an increased collision risk for these species at forest wind turbines (Kirkpatrick et al., 2017).

In temperate forests, diverse vegetation structure and vertical stratification facilitate the cohabitation of three foraging guilds: open-space foragers which hunt insects above the canopy and in clearings, edge-space foragers which hunt along structures like forest edges or within gaps, and narrow-space foragers which hunt in dense vegetation and are especially adapted to life in forests (Denzinger & Schnitzler, 2013). The effect of habitat changes related to turbine construction and operation on bats may be guild specific due to different ecological requirements. The activity of open- and edge-space bats could even increase towards wind turbines caused by their attraction to clearings and forest edges (Kirkpatrick et al., 2017). Conversely, narrow-space foragers might respond negatively or not at all to the turbine-related habitat changes as they do not profit from open or semi-open habitats. In addition, a structure-rich forest vegetation could influence how far turbine effects on bats may extend into the surrounding forest, as dense vegetation may block visual signals and mitigate noise pollution. Lastly, turbine effects on bats may depend on the season, since bat activity varies throughout the year (Heim et al., 2016). For instance, most fatalities at turbines have been reported in late summer, coinciding with the post-weaning period of juveniles and the migration season (Kruszynski et al., 2022). Here, we asked how wind energy production affects bat assemblages in non-primary forests of Central Europe. This is a critical question since all bat species are protected by national and international legislation. Knowledge of factors that impact forest-associated bats is key to formulate adequate mitigation and compensation measures to protect bats when expanding wind energy production in forests.

In our study, we used call activity as a proxy for the abundance of bats and thus conducted acoustic surveys along distance gradients towards wind turbines in 24 forests. Compared to earlier distance-gradient studies on bat activity at wind turbines, our focus on forest sites is novel and offers new insights about the consequences of wind turbine integration in forests accounting for vegetation structure. We predicted (I) that bat activity decreases with increasing proximity to the nearest turbine and that this effect will be stronger at larger wind turbines, where sensory pollution is presumably stronger. Moreover, we expected (II) that bat responses differ across functional guilds with strongest impacts for the activity of forest specialists, that is, narrow-space foragers and (III) that bat responses may vary across seasons and with vertical vegetation heterogeneity as a measure of forest structure. Our study aims to contribute to a sustainable wind energy development in forests from the perspective of bat conservation. Ultimately, this will help to reconcile the two important environmental goals of mitigating climate change and protecting biodiversity.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted our study in Hesse, a federal state in Central Germany characterized by temperate low range mountains and a forest cover of 42% (316–545 m a.s.l., 50°81′N, 8°81′W, Figure 1). We selected 24 forests ranging from coniferous monocultures to mixed and deciduous stands. Forest patch size varied between 184 and 6,337 ha (1,798 ha ± 1,745 ha; mean ± standard deviation, hereafter). Wind turbines in our study sites had been erected between 2006 and 2017 (6 ± 3 years). Tower height ranged between 145 and 212 m (194 m ± 16 m; $N = 24$) while rotor diameter ranged between 82 and 126 m (mean: 112 m ± 11 m). Studied turbines were located individually in cleared forest patches that ranged in size between 0.16 and 11.77 ha (median: 1.75 ha). To minimize the confounding effects of other anthropogenic disturbances and edge effects, we excluded study sites adjacent to highways and factories and established all transect points at a distance of more than 473 m (median) to the forest edge (91–1,884 m). Fieldwork permits were obtained from the respective forest owners. Ethical approval was not required.

2.2 | Sampling of bat echolocation calls

At each forest site, we used a distance-gradient study design with sampling points at 80, 130, 250 and 450 m distance to our focal turbine at the edge of the wind farm. In one study site each, one 80, 130 and 250 m point had to be skipped because of smaller clearings. For acoustic monitoring, we used automated bat recorders (BATLOGGER A+; Elekon). At each sampling point, we installed one recorder per forest stratum: near-ground in the clutter-free understorey (approx. 2.5 m height) and a second recorder in the lower canopy, where height varied according to forest succession stage (range: 4 m–22 m; 13 m ± 4 m). Recordings were conducted in 45 nights between mid-May and mid-September 2020, from 9 pm to 5 am. Per night, we recorded simultaneously at two geographically close transects and at each sampling point in the two designated forest strata. At every recording point, we recorded bat calls once per sampling period (1: May 17–June 5; 2: June 8–July 7: 3: July 13–August 15; 4: August 18–September 17) with intervals of 17–58 days (33.29 ± 11.26 days) in between. Some exceptions were caused by technical failures and unforeseeable logging activities (four recording nights at 156 recording points, three at 15 points, two at 1 point and one at 14 points). We employed BATLOGGER default settings with a trigger frequency between 15 and 155 kHz, thus covering the call frequency range of species expected in the local bat assemblage. We set a pre-trigger time of 500 ms, a post-trigger time of 1,000 ms and a recording intersection time of 20s. We used the CrestAdvanced trigger algorithm to enhance the recording probability of quiet calls and minimize sensitivity towards disturbing noise (Elekon AG, 2020).

2.3 | Sampling of covariates

At each sampling point, we assessed four environmental variables that were assumed to influence bat activity: As a proxy for habitat heterogeneity, we estimated vegetation cover at heights of 0, 0.5, 1, 2, 4, 8, 16 and 32 m to the nearest 5% within a 10 m radius

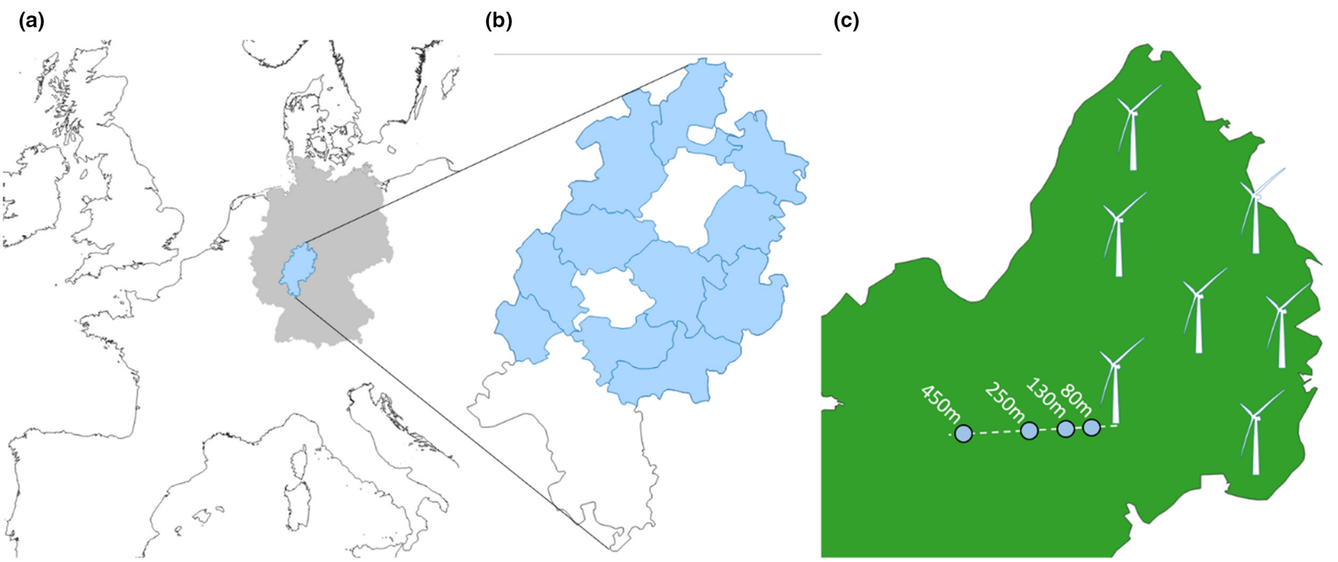

FIGURE 1 Map of the study area. Location of the sampling sites in (a) Germany and (b) Hesse are marked in blue. (c) Example transect at the edge of a forest wind farm with sampling points set up in increasing distances to the focal turbine.

around distance points. We then calculated the diversity of the layers at each distance point using the Shannon–Weaver index to obtain vertical vegetation heterogeneity (Bibby et al., 2000). Furthermore, as a proxy for age structure, we measured the average tree canopy height in the immediate surrounding of sampling points with the help of a laser rangefinder (Forestry 550; Nikon) and used aerial photographs (Google Ireland Limited) to measure the distance between sampling points and the nearest outer forest edge. Finally, we calculated the proportion of deciduous and coniferous trees based on the Copernicus land cover map (ESA, 2018) within a 200 m radius around distance points, hereafter called tree composition. To capture differences in turbine characteristics, we retrieved the rotor diameter of each turbine from the publicly accessible database of Hessian environmental agency (HLNUG, 2019).

2.4 | Call analysis

We used the software BatExplorer (version 2.1.7.0; Elekon) to manually assign echolocation calls to bat species, only relying on the automatic call identification for *Pipistrellus pipistrellus*. We identified bat species based on echolocation call characteristics such as peak frequencies and call shapes from the literature (Barataud, 2020; LFU Bayern, 2020; Skiba, 2009). We subsequently grouped all call sequences into one of three ecological guilds (Denzinger & Schnitzler, 2013): open-space foragers (consisting of the genera *Eptesicus*, *Vespertilio* and *Nyctalus*), edge-space foragers (*Pipistrellus* ssp. and *Barbastella barbastellus*) and narrow-space foragers (genera *Myotis* and *Plecotus*). Sequences that could not be identified because of poor recording quality were discarded (0.4%). To obtain a proxy for the local bat abundance and prevent overestimation of single bats, we calculated the number of bat activity minutes for each of the three ecological guilds per night, sampling point and stratum. We divided recordings of all nights into 60-s intervals and counted minutes with at least one echolocation call, hereafter called activity minutes (Heim et al., 2016). If calls of more than one bat species appeared in one interval, they were considered as two separate activity minutes. Recordings with only social calls were discarded to avoid a bias towards species with higher detection and identification probability for social calls. In the following, we use the amount of activity minutes as a metric measure to describe bat activity.

2.5 | Data analysis

We conducted all statistical analyses with the software R (version 4.0.3; R Core Team, 2021). First, we split the dataset into three subsets, one for each foraging guild, because recorded activities were quantitatively too different between guilds to be fitted in the same model. For each guild, we tested if bat activity (response variable) decreases with increasing proximity to wind turbines. Due to the nested structure of our data, we used generalized linear mixed models (glmmTMB package; Brooks et al., 2017) with sampling points nested in study site as random effects. We used a negative binomial distribution to account for overdispersion (nbinom1 for open- and edge-space foragers, nbinom2 for narrow-space foragers) and, apart from that, applied the same model structure for all guilds. Models included turbine distance, vertical vegetation heterogeneity, canopy height, tree composition, rotor size, forest stratum and sampling period as fixed effects. Moreover, we added forest edge distance as fixed factor to correct for its potential influence on the distribution of bats in the studied forests, as well as the interactions of turbine distance with sampling period and rotor size. We checked the variance-inflation factor (VIF) of the regression, which assesses for each coefficient whether a correlation with other predictors may lead to an increased variance. VIF was below 2 for all predictors and we thus excluded multicollinearity (car package; Akinwande et al., 2015; Fox & Weisberg, 2019). All numerical predictors were standardized to allow direct comparison of estimates (Schielzeth, 2010). We worked with full models (Tredennick et al., 2021) and ensured their goodness-of-fit with the DHARMa package for residual diagnostics (Hartig, 2020). We checked that all models were informative looking at the difference in AIC value compared to null models and marginal R^2 values (Table S1). Rotor diameters were not randomly distributed across forest sites and small rotors were biased towards deciduous forests. To exclude misinterpretations, we repeated above described analyses with only the data obtained from deciduous forests, thereby obtaining a balanced representation of rotor sizes. Additionally, we tested for potential confounding edge effects of the turbine clearing on bat activity by applying our model to a subset including only data sampled at 250 and 450 m distance to the wind turbine. Results did not qualitatively change in the additional analyses compared to models based on the complete data set (Tables S2 and S3). Accordingly, we considered our original results to be robust.

3 | RESULTS

During 5 months of data sampling, we obtained 678 recordings of complete nights, out of which 17 did not contain any bat calls. In total, we recorded 61,988 activity minutes of which 83% belonged to edge-space foragers, 12% to narrow-space foragers and 5% to open-space foragers (Table 1).

The activity of narrow-space foragers was almost halved at the distance points closest to wind turbines (80 m) compared to 450 m distance points (Figure 2, Figure S1). This distance effect showed temporal variation, as it was apparent for the first three sampling periods (mid-May to mid-August) and absent for the last sampling period (mid-August to mid-September, Figure 3). Furthermore, the activity decrease was only observed towards turbines with rotors larger than 93 m diameter (Table 2, Figure 4). Activity increased with vertical vegetation heterogeneity, but no difference was observed

TABLE 1 Absolute and median numbers of activity minutes for each foraging guild at the distance points and pooled across recording levels

Turbine distance [m]	*N* sites	All bats		Open-space foragers		Edge-space foragers		Narrow-space foragers	
		N activity minutes	Median (per recording)	*N* activity minutes	Median (per recording)	*N* activity minutes	Median (per recording)	*N* activity minutes	Median (per recording)
80	23	13,879	3	688	2	8,609	26	1,263	2
130	24	15,686	4	588	1	9,452	35	1,821	5
250	24	13,161	3	665	2	7,935	35	1,088	4
450	24	18,958	4	700	1	12,838	36	1,989	5

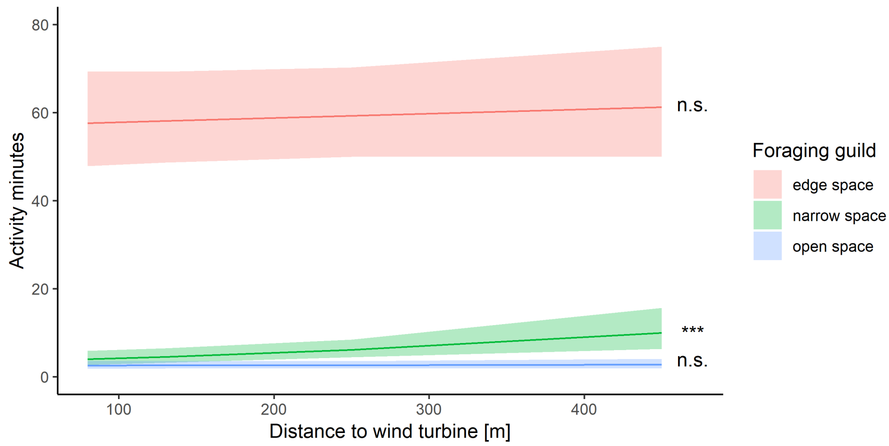

FIGURE 2 Effects (lines) and 95% confidence intervals (shades) of wind turbine distance on activity of three foraging guilds. Asterisks denote the significance level of effects (***<0.001 < **<0.01 < *<0.05 < n.s.).

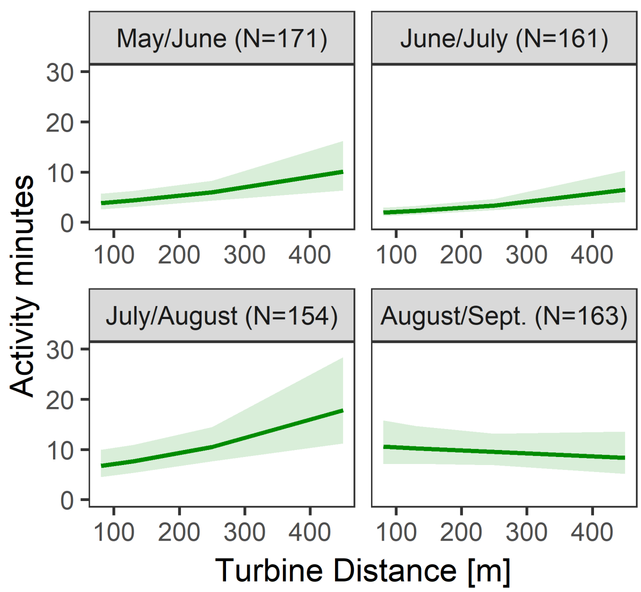

FIGURE 3 Interactive effect (lines) and 95% confidence intervals (shaded area) of turbine distance and sampling period on the activity of narrow-space foragers.

between recordings made at the canopy and ground level. Bats were most active between mid-July and mid-September (Table 2, Figures S4–S8).

The activity of edge-space foragers did not vary with turbine distance or rotor size (Figure 2, Figure S2). However, activity was higher at the canopy level than at ground level and increased with vertical vegetation heterogeneity and with tree height. Edge-space foragers were most active between mid-July and mid-August (Table 2, Figures S4–S8).

The overall activity of open-space foragers did neither change with the distance to the wind turbine (Figure 2, Figure S3) nor with rotor size. Yet, in the last sampling period (mid-August to mid-September), we observed an increase in activity minutes close to turbines (Figure 5). Activity of open-space foragers was higher at canopy than ground level and increased with the proportion of coniferous trees in the forest. Bats were most active between mid-July and mid-August (Table 2, Figures S4–S8).

4 | DISCUSSION

We studied bat activity at wind turbines in 24 temperate forests in Central Germany and discovered a relationship with turbine distance, season and turbine size, but different patterns depending on bat foraging guild. Strikingly, activity of narrow-space foragers decreased with increasing proximity to turbines. This effect was notable over distances of several hundred metres. Our findings highlight that forest-dwelling bats, being at low risk of colliding at turbines, might still be affected by wind turbines in forests. This complements research from open landscapes, where narrow-space foraging bats showed a similar negative response towards wind turbines (Barré et al., 2018; Millon et al., 2015). However, our study is the first to

TABLE 2 Estimates and *p*-values of the effects on call activity of three foraging guilds. Significant effects (*p*-value < 0.05) are shown in bold

Variables	*df*	Open-space foragers		Edge-space foragers		Narrow-space foragers	
		Chi²	*p*-value	Chi²	*p*-value	Chi²	*p*-value
Turbine distance	1	1.6	0.202	0.4	0.521	18.0	**<0.001**
Recording level 'canopy'	1	27.5	**<0.001**	35.5	**<0.001**	3.1	0.080
% conifers in forest	1	8.9	**0.003**	3.6	0.057	0.1	0.765
Vertical vegetation structure	1	1.3	0.258	21.1	**<0.001**	10.9	**0.001**
Rotor diameter	1	0.3	0.560	1.4	0.238	0.2	0.898
Canopy height	1	1.6	0.201	14.5	**<0.001**	0.4	0.733
Forest edge distance	1	0.7	0.387	1.2	0.288	2.6	0.106
Sampling period	3	51.1	**<0.001**	41.9	**<0.001**	75.7	**<0.001**
Turbine distance × sampling period	3	10.9	**0.012**	0.3	0.955	19.4	**<0.001**
Turbine distance × rotor diameter	1	1.99	0.158	3.6	0.057	4.7	**0.0295**

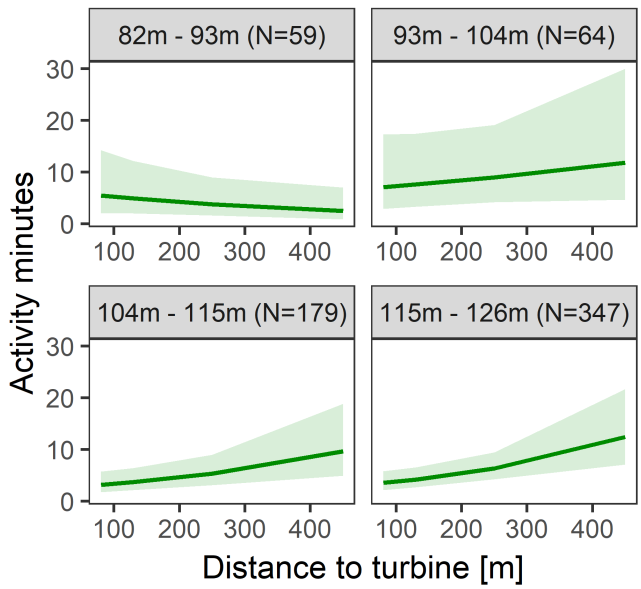

FIGURE 4 Interactive effect (lines) and 95% confidence interval (shaded area) of wind turbine distance and rotor size on the activity of narrow-space foragers.

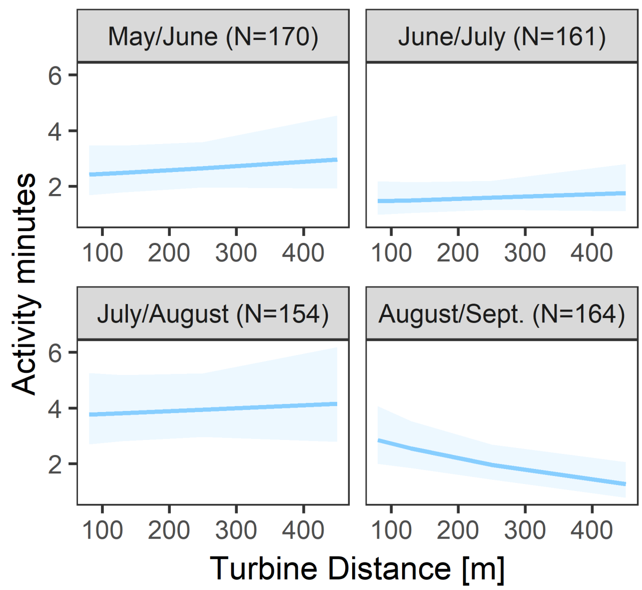

FIGURE 5 Interactive effect (lines) and 95% confidence intervals (shaded area) of turbine distance and sampling period on the activity of open-space foragers.

confirm this pattern for forests, a highly important habitat from the perspective of bat conservation.

4.1 | Narrow-space foragers: Avoidance of large wind turbines

We found that the activity of narrow-space foragers, mainly *Myotis* bats in our study area, decreased significantly towards turbines. This is in line with earlier studies on *Myotis* activity in open landscapes (Barré et al., 2018), even when focussing on small wind turbines (Minderman et al., 2012), highlighting the sensitivity of narrow-space foragers to wind turbines both in forests and open landscapes.

Furthermore, we found that the activity decline of narrow-space foragers towards wind turbines was weaker in late summer, which confirmed the results of another open landscape study comparing wind turbine sites to control sites (Millon et al., 2015). In our study, we observed a distance effect particularly at turbines with large rotors. This suggests that avoidance might be caused by turbine-generated noise, which is presumably related to turbine size and diminishes over distance (Katinas et al., 2016). An adverse effect of noise on *Myotis* activity is also implied by a study on small wind turbines, where bats were particularly repelled by operating turbines (Minderman et al., 2012). Many narrow-space foragers locate their prey passively by detecting acoustic cues (Denzinger &

Schnitzler, 2013). Therefore, these bats tend to avoid noisy environments, suggesting either a masking of prey sounds by anthropogenic sound emissions (Schaub et al., 2009) or a startling effect (Luo et al., 2015). In conclusion, we found a hitherto unknown avoidance behaviour of narrow-space foragers towards wind turbines in forests, indicating an indirect habitat loss for bats of this functional guild, possibly caused by noise.

4.2 | Edge-space foragers: No effect of wind turbines

For edge-space foragers, which were mostly *P. pipistrellus* in our study, we neither found support for avoidance of, nor attraction towards wind turbines in forests. In contrast, recent open landscape studies observed a strong decrease in the activity of *P. pipistrellus* at hedgerows with decreasing distances to turbines on the one hand (Barré et al., 2018), and an increased activity at wind turbine sites in comparison to control sites on the other hand (Richardson et al., 2021). Possibly, the discrepancy between findings may be explained by different habitat matrices. Specifically, the erection of wind turbines in forests creates clearings and a network of edge structures which is an ideal foraging habitat for edge-space foragers. Indeed, it was observed that members of the edge- and open-space foraging guild were more active in spruce plantation after clear-cuttings (Kirkpatrick et al., 2017). In conclusion, clear-cutting for turbine construction probably poses a spatially restricted benefit for edge-space foragers.

4.3 | Open-space foragers: Seasonal attraction to wind turbines

Activity of open-space foragers did not change in relation to turbine distance except for an activity increase with increasing turbine proximity in late summer. Our overall findings contrast with a previous open-landscape study that showed decreased activity for *N. leisleri*, but not for *N. noctula* and *E. serotinus* close to turbines (Barré et al., 2018), suggesting that open-space foragers might not be coherent in their responses to wind turbines. Different responses may even be related to intraspecies variation across bat individuals, as was suggested by GPS tracking studies on *N. noctula* around wind turbines (Reusch et al., 2022; Roeleke et al., 2016). In contrast, our finding of open-space foragers being attracted to wind turbines in late summer aligns with numerous previous studies suggesting an attraction effect of wind turbines on open-space foragers, hypothesizing various, yet untested causes (Guest et al., 2022). Given the seasonality of the attraction, open-space foragers possibly confuse forest turbines with tall trees, when searching for orientation points or stop-over roosts during fall migration (Cryan et al., 2014; Jameson & Willis, 2014). However, a recent study from Northern Germany shows an avoidance behaviour of *N. noctula* in late summer towards wind turbines, which argues against a general attraction of open-space foragers towards turbines in this season (Reusch et al., 2022). In conclusion, we could not confirm avoidance behaviour towards turbines for the entire guild. Yet, our findings of a seasonal attraction to turbines in forests are of high relevance in context of collision risks for open-space foragers.

4.4 | Diverse vegetation structure enhances bat activity

High activity of edge- and narrow-space foragers coincided with heterogeneous vertical vegetation structure. Similar positive effects of different measures of vegetation structure on forest-associated bats have been shown before and can be explained by a higher availability of microhabitats (Adams et al., 2009; Langridge et al., 2019; Müller et al., 2013). Furthermore, activity of edge-space foragers increased with tree height, suggesting a preference for more mature forest stands, probably due to their dependency on semi-open foraging habitats which rarely occur in early succession stages. In contrast, activity of open-space foragers was not affected by vertical vegetation structure or tree height, indicating that forest vegetation parameters are less important for aerial hawkers. For most bats, we observed a higher activity in the canopy than near-ground, confirming that the forest canopy is an important bat habitat (Adams et al., 2009; Erasmy et al., 2021; Müller et al., 2013; Plank et al., 2012). Lastly, we found a similar activity of most bats in mixed and coniferous forests which is consistent with a recent study suggesting that bats can find suitable roosts even in monocultural forest plantations (Buchholz et al., 2021). In conclusion, our findings indicate that forests with diverse vegetation structure present valuable habitats for a variety of bats, while forest type alone seems to be less important. The high activity of open-space foragers in conifer-dominated forests is likely related to high proportions of standing deadwood and clearances in these forests, leading to reduced attenuation of echolocation calls and an increased recording probability (Lawrence & Simmons, 1982).

5 | CONCLUSIONS

Our study highlights that the activity of forest-associated bats declines towards wind turbines at forest sites. Narrow-space foragers such as *Plecotus* spp. and *Myotis* spp. seemingly avoid wind turbines in forests and show reduced activity by about 50% from 450 to 80 m turbine distance. This avoidance is possibly caused by habitat degradation triggered by turbine-generated noise, since it was strongest towards turbines with large rotors. Consequently, legally protected forest bat specialists lose large habitat areas when wind turbines are erected at forest sites. Hence, we argue that this habitat loss should be compensated by taking nearby old forest stand out of forestry use, thus creating refugia for forest specialist bats. We also plead for a general caution when siting wind turbines in forests, since the response of bats was independent of vegetation structure and tree composition. We do not necessarily argue for a complete ban of wind energy production in forests, because in some countries there is little other option for renewable energies. Where absolutely necessary, turbines should only be built in managed forests with low vertical vegetation heterogeneity, as bat activity is expected to be low in these forests. This approach would most likely also account for birds and insects, which have been reported to die in considerable numbers through wind turbines (Thaxter et al., 2017; Voigt, 2021). However, as forest-related studies on birds and insects are still lacking, we urge to fill these research gaps to provide a basis for comprehensive recommendations on wind energy development in forests.

ACKNOWLEDGEMENTS

This research was funded by Deutsche Bundesstiftung Umwelt (DBU). We are grateful for study permissions and organizational support by Hessian nature conservation agencies and forest owners. We thank Laura de Vries, Lea Vetter, Marcel Becker and Nina Wallmann for supporting fieldwork, Katharina Rehnig and PGNU for helping with acoustic analyses and Finn Rehling for advises during data analysis and visualization. Open Access funding enabled and organized by Projekt DEAL.

AUTHORS' CONTRIBUTIONS

N.F., F.P. and C.C.V. conceived the ideas and designed the methodology; J.S.E. and A.D. collected the data; J.S.E. analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Our study relied on local authors and research assistants. We frequently presented our research progress to stakeholders and sought their feedback.

CONFLICT OF INTEREST

None of the authors have conflicting interests.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.m0cfxpp66 (Ellerbrok et al., 2022).

ORCID

Julia S. Ellerbrok https://orcid.org/0000-0002-1109-6947
Anna Delius https://orcid.org/0000-0001-5240-4486
Franziska Peter https://orcid.org/0000-0002-0494-9956
Nina Farwig https://orcid.org/0000-0002-0554-5128
Christian C. Voigt https://orcid.org/0000-0002-0706-3974

REFERENCES

Adams, M. D., Law, B. S., & French, K. O. (2009). Vegetation structure influences the vertical stratification of open- and edge-space aerial-foraging bats in harvested forests. *Forest Ecology and Management*, *258*(9), 2090–2100. https://doi.org/10.1016/j.foreco.2009.08.002

Akinwande, M. O., Dikko, H. G., & Samson, A. (2015). Variance inflation factor: As a condition for the inclusion of suppressor variable(s) in regression analysis. *Open Journal of Statistics*, *5*(7), 754–767. https://doi.org/10.4236/ojs.2015.57075

Allen, L. C., Hristov, N. I., Rubin, J. J., Lightsey, J. T., & Barber, J. R. (2021). Noise distracts foraging bats. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1944), 20202689. https://doi.org/10.1098/rspb.2020.2689

Arnett, E. B., Baerwald, E. F., Mathews, F., Rodrigues, L., Rodríguez-Durán, A., Rydell, J., Villegas-Patraca, R., & Voigt, C. C. (2016). Impacts of wind energy development on bats: A global perspective. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 295–323). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_11

Barataud, M. (2020). *Acoustic ecology of European bats: Species identification, study of their habitats and foraging behaviour* (2nd ed.). Biotope.

Barré, K., Le Viol, I., Bas, Y., Julliard, R., & Kerbiriou, C. (2018). Estimating habitat loss due to wind turbine avoidance by bats: Implications for European siting guidance. *Biological Conservation*, *226*, 205–214. https://doi.org/10.1016/j.biocon.2018.07.011

Bayerisches Landesamt für Umwelt (LFU Bayern). (2020). *Bestimmung von Fledermausrufaufnahmen und Kriterien für die Wertung von akustischen Artnachweisen: Teil 1*. Fledermausschutz in Bayern. https://www.lfu.bayern.de/publikationen/get_pdf.htm?art_nr=lfu_nat_00378

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Bennett, V. J., & Hale, A. M. (2014). Red aviation lights on wind turbines do not increase bat-turbine collisions. *Animal Conservation*, *17*(4), 354–358. https://doi.org/10.1111/acv.12102

Bibby, C., Burgess, N., Hill, D., & Mustoe, S. (2000). *Bird census techniques*. Academic Press.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Boelker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378–400. https://doi.org/10.32614/RJ-2017-066

Buchholz, S., Kelm, V., & Ghanem, S. J. (2021). Mono-specific forest plantations are valuable bat habitats: Implications for wind energy development. *European Journal of Wildlife Research*, *67*(1), article 1. https://doi.org/10.1007/s10344-020-01440-8

Bundesministerium für Wirtschaft und Klimaschutz (BMWK). (2022). Eröffnungsbilanz Klimaschutz. Retrieved from https://www.bmwk.de/Redaktion/DE/Downloads/Energie/220111_eroeffnungsbilanz_klimaschutz.html

Cryan, P. M., Gorresen, P. M., Hein, C. D., Schirmacher, M. R., Diehl, R. H., Huso, M. M., Hayman, D. T. S., Fricker, P. D., Bonaccorso, F. J., Johnson, D. H., Heist, K., & Dalton, D. C. (2014). Behavior of bats at wind turbines. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(42), 15126–15131. https://doi.org/10.1073/pnas.1406672111

Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, *4*, 164. https://doi.org/10.3389/fphys.2013.00164

Dietz, C., & Kiefer, A. (2014). *Die Fledermäuse Europas: Kennen, bestimmen, schützen. KosmosNaturführer*. Kosmos.

Elekon AG. (2020). *Batlogger a/a+ manual.: Firmware version V 2.6*. Retrieved from https://downloads.batlogger.com/bla/BATLOGGER_A_Manual_en_190211.pdf

Ellerbrok, J. S., Delius, A., Peter, F., Farwig, N., & Voigt, C. C. (2022). Data from: Activity of forest specialist bats decreases towards wind turbines at forest sites. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.m0cfxpp66

Erasmy, M., Leuschner, C., Balkenhol, N., & Dietz, M. (2021). Three-dimensional stratification pattern in an old-growth lowland forest: How does height in canopy and season influence temperate bat activity? *Ecology and Evolution*, *11*(23), 17273–17288. https://doi.org/10.1002/ece3.8363

European Space Agency (ESA). (2018). *Copernicus Open Access Hub*. Retrieved from https://www.scihub.copernicus.eu/

Finch, D., Schofield, H., & Mathews, F. (2020). Traffic noise playback reduces the activity and feeding behaviour of free-living bats. *Environmental Pollution (Barking, Essex: 1987)*, *263*(Pt B), 114405. https://doi.org/10.1016/j.envpol.2020.114405

Fox, J., & Weisberg, S. (2019). An R companion to applied regression (3rd ed.). R package.

Frick, W. F., Baerwald, E. F., Pollock, J. F., Barclay, R., Szymanski, J. A., Weller, T. J., A. Russell, S. Loeb, R. Medellín, McGuire, L. P. (2017). Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation*, *209*, 172–177. https://doi.org/10.1016/j.biocon.2017.02.023

Friedenberg, N. A., & Frick, W. F. (2021). Assessing fatality minimization for hoary bats amid continued wind energy development. *Biological Conservation*, *262*, 109309. https://doi.org/10.1016/j.biocon.2021.109309

Gaultier, S. P., Blomberg, A. S., Ijäs, A., Vasko, V., Vesterinen, E. J., Brommer, J. E., & Lilley, T. M. (2020). Bats and wind farms: The role and importance of the Baltic Sea countries in the European context of power transition and biodiversity conservation. *Environmental Science & Technology*, *54*(17), 10385–10398. https://doi.org/10.1021/acs.est.0c00070

Gielen, D., Boshell, F., Saygin, D., Bazilian, M. D., Wagner, N., & Gorini, R. (2019). The role of renewable energy in the global energy transformation. *Energy Strategy Reviews*, *24*, 38–50. https://doi.org/10.1016/j.esr.2019.01.006

Götmark, F. (2013). Habitat management alternatives for conservation forests in the temperate zone: Review, synthesis, and implications. *Forest Ecology and Management*, *306*, 292–307. https://doi.org/10.1016/j.foreco.2013.06.014

Grünkorn, T., Blew, J., Krüger, O., Potiek, A., Reichenbach, M., von Rönn, J., Timmermann, H., Weitekamp, S., & Nehls, G. (2017). A large-scale, multispecies assessment of avian mortality rates at land-based wind turbines in northern Germany. In J. Köppel (Ed.), *Wind energy and wildlife interactions* (pp. 43–64). Springer International Publishing. https://doi.org/10.1007/978-3-319-51272-3_3

Guest, E. E., Stamps, B. F., Durish, N. D., Hale, A. M., Hein, C. D., Morton, B. P., Weaver, S. P., & Fritts, S. R. (2022). An updated review of hypotheses regarding bat attraction to wind turbines. *Animals: An Open Access Journal from MDPI*, *12*(3), 343. https://doi.org/10.3390/ani12030343

Hartig, F. (2020). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3.3.0. Retrieved from https://CRAN.R-project.org/package=DHARMa

Hayes, M. A. (2013). Bats killed in large numbers at United States wind energy facilities. *Bioscience*, *63*(12), 975–979. https://doi.org/10.1525/bio.2013.63.12.10

Heim, O., Schröder, A., Eccard, J., Jung, K., & Voigt, C. C. (2016). Seasonal activity patterns of European bats above intensively used farmland. *Agriculture, Ecosystems & Environment*, *233*, 130–139. https://doi.org/10.1016/j.agee.2016.09.002

Hessisches Landesamt für Naturschutz, Umwelt und Geologie (HLNUG) (2019). Windenergie in Hessen. Retrieved from https://www.hlnug.de/themen/luft/windenergie-in-hessen

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., & Müller, J. (2018). Biodiversity along temperate forest succession. *Journal of Applied Ecology*, *55*(6), 2756–2766. https://doi.org/10.1111/1365-2664.13238

Hurst, J., Biedermann, M., Dietz, C., Dietz, M., Reers, H., Karst, I., Petermann, R., Schorcht, W., & Brinkmann, R. (2020). Windkraft im Wald und Fledermausschutz—Überblick über den Kenntnisstand und geeignete Erfassungsmethoden und Maßnahmen. In C. C. Voigt (Ed.), *Evidenzbasierter Fledermausschutz in Windkraftvorhaben* (pp. 29–54). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-61454-9_2

Jameson, J. W., & Willis, C. K. (2014). Activity of tree bats at anthropogenic tall structures: Implications for mortality of bats at wind turbines. *Animal Behaviour*, *97*, 145–152. https://doi.org/10.1016/j.anbehav.2014.09.003

Katinas, V., Marčiukaitis, M., & Tamašauskienė, M. (2016). Analysis of the wind turbine noise emissions and impact on the environment. *Renewable and Sustainable Energy Reviews*, *58*, 825–831. https://doi.org/10.1016/j.rser.2015.12.140

Kirkpatrick, L., Oldfield, I. F., & Park, K. (2017). Responses of bats to clear fell harvesting in Sitka spruce plantations, and implications for wind turbine installation. *Forest Ecology and Management*, *395*, 1–8. https://doi.org/10.1016/j.foreco.2017.03.033

Kruszynski, C., Bailey, L. D., Bach, L., Bach, P., Fritze, M., Lindecke, O., Teige, T., & Voigt, C. C. (2022). High vulnerability of juvenile Nathusius' pipistrelle bats (*Pipistrellus nathusii*) at wind turbines. *Ecological Applications: A Publication of the Ecological Society of America*, *32*(2), e2513. https://doi.org/10.1002/eap.2513

Kuvlesky, W. P., Brennan, L. A., Morrison, M. L., Boydston, K. K., Ballard, B. M., & Bryant, F. C. (2007). Wind energy development and wildlife conservation: Challenges and opportunities. *Journal of Wildlife Management*, *71*(8), 2487–2498. https://doi.org/10.2193/2007-248

Langridge, J., Pisanu, B., Laguet, S., Archaux, F., & Tillon, L. (2019). The role of complex vegetation structures in determining hawking bat activity in temperate forests. *Forest Ecology and Management*, *448*, 559–571. https://doi.org/10.1016/j.foreco.2019.04.053

Lawrence, B. D., & Simmons, J. A. (1982). Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *The Journal of the Acoustical Society of America*, *71*(3), 585–590. https://doi.org/10.1121/1.387529

Lesiński, G., Kowalski, M., Wojtowicz, B., Gulatowska, J., & Lisowska, A. (2007). Bats on forest islands of different size in an agricultural landscape. *Folia Zoologica*, *65*(2), 153–161.

Luo, J., Siemers, B. M., & Koselj, K. (2015). How anthropogenic noise affects foraging. *Global Change Biology*, *21*(9), 3278–3289. https://doi.org/10.1111/gcb.12997

Mackensen, R. (2019). *Windenergie Report Deutschland 2018*. Fraunhofer Verlag. https://publica.fraunhofer.de/entities/publication/c3cff226-62e8-4fa2-b9c2-c2e18fa9328a/details

Millon, L., Julien, J.-F., Julliard, R., & Kerbiriou, C. (2015). Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecological Engineering*, *75*, 250–257. https://doi.org/10.1016/j.ecoleng.2014.11.050

Minderman, J., Gillis, M. H., Daly, H. F., & Park, K. J. (2017). Landscape-scale effects of single- and multiple small wind turbines on bat activity. *Animal Conservation*, *20*(5), 455–462. https://doi.org/10.1111/acv.12331

Minderman, J., Pendlebury, C. J., Pearce-Higgins, J. W., & Park, K. J. (2012). Experimental evidence for the effect of small wind turbine proximity and operation on bird and bat activity. *PLoS ONE*, *7*(7), e41177. https://doi.org/10.1371/journal.pone.0041177

Müller, J., Brandl, R., Buchner, J., Pretzsch, H., Seifert, S., Strätz, C., Strätz, C., Veith, M., & Fenton, B. (2013). From ground to above canopy—Bat activity in mature forests is driven by vegetation density and height. *Forest Ecology and Management*, *306*, 179–184. https://doi.org/10.1016/j.foreco.2013.06.043

O'Shea, T. J., Cryan, P. M., Hayman, D. T. S., Plowright, R. K., & Streicker, D. G. (2016). Multiple mortality events in bats: A global review. *Mammal Review*, *46*(3), 175–190. https://doi.org/10.1111/mam.12064

Plank, M., Fiedler, K., & Reiter, G. (2012). Use of forest strata by bats in temperate forests. *Journal of Zoology*, *286*(2), 154–162. https://doi.org/10.1111/j.1469-7998.2011.00859.x

Printz, L., Tschapka, M., & Vogeler, A. (2021). The common noctule bat (*Nyctalus noctula*): Population trends from artificial roosts and the

effect of biotic and abiotic parameters on the probability of occupation. *Journal of Urban Ecology*, *7*(1), 1–7. https://doi.org/10.1093/jue/juab033
Quentin, J., & Tucci, F. (Eds.). (2021). *Entwicklung der Windenergie im Wald: Ausbau, planerische Vorgaben und Empfehlungen für Windenergiestandorte auf Waldflächen in den Bundesländern* (6th ed.). https://www.fachagentur-windenergie.de/veroeffentlichungen/publikationen/
R Core Team (2021): *A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/
Reusch, C., Lozar, M., Kramer-Schadt, S., & Voigt, C. (2022). Coastal onshore wind turbines lead to habitat loss for bats in northern Germany. *Journal of Environmental Management.*, *310*, 114715. https://doi.org/10.1016/j.jenvman.2022.114715
Richardson, S. M., Lintott, P. R., Hosken, D. J., Economou, T., & Mathews, F. (2021). Peaks in bat activity at turbines and the implications for mitigating the impact of wind energy developments on bats. *Scientific Reports*, *11*(1), 3636. https://doi.org/10.1038/s41598-021-82014-9
Rodrigues, L., Bach, L., Dubourg-Savage, M.-J., Karapandža, B., Kovac, D., Kervyn, T., Dekker, J., Kepel, A., Bach, P., Collins, J., Harbusch, C., Park, K., Micevski, B., & Minderman, J. (2014). Guidelines for consideration of bats in wind farm projects: Revision. https://www.eurobats.org/publications/eurobats_publication_series
Roeleke, M., Blohm, T., Kramer-Schadt, S., Yovel, Y., & Voigt, C. C. (2016). Habitat use of bats in relation to wind turbines revealed by GPS tracking. *Scientific Reports*, *6*, 28961. https://doi.org/10.1038/srep28961
Saidur, R., Rahim, N. A., Islam, M. R., & Solangi, K. H. (2011). Environmental impact of wind energy. *Renewable and Sustainable Energy Reviews*, *15*(5), 2423–2430. https://doi.org/10.1016/j.rser.2011.02.024
Schaub, A., Ostwald, J., & Siemers, B. M. (2009). Foraging bats avoid noise. *Journal of Experimental Biology*, *212*(18), 3174–3180. https://doi.org/10.1242/jeb.037283
Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x
Skiba, R. (2009). *Europäische Fledermäuse* (2nd ed.). VerlagsKGWolf.
Solomon, S., Plattner, G.-K., Knutti, R., & Friedlingstein, P. (2009). Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(6), 1704–1709. https://doi.org/10.1073/pnas.0812721106
Spiecker, H. (2003). Silvicultural management in maintaining biodiversity and resistance of forests in Europe—Temperate zone. *Journal of Environmental Management*, *67*(1), 55–65. https://doi.org/10.1016/S0301-4797(02)00188-3
Thaxter, C. B., Buchanan, G. M., Carr, J., Butchart, S. H. M., Newbold, T., Green, R. E., Tobias, J. A., Foden, W. B., O'Brien, S., & Pearce-Higgins, J. W. (2017). Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20170829. https://doi.org/10.1098/rspb.2017.0829
Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, *102*(6), e03336. https://doi.org/10.1002/ecy.3336
Voigt, C. C. (2021). Insect fatalities at wind turbines as biodiversity sinks. *Conservation Science and Practice*, *3*(5), e03336. https://doi.org/10.1111/csp2.366
Voigt, C. C., Lehnert, L. S., Petersons, G., Adorf, F., & Bach, L. (2015). Wildlife and renewable energy: German politics cross migratory bats. *European Journal of Wildlife Research*, *61*(2), 213–219. https://doi.org/10.1007/s10344-015-0903-y
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(6879), 389–395. https://doi.org/10.1038/416389a
Zimmerling, J. R., & Francis, C. M. (2016). Bat mortality due to wind turbines in Canada. *Journal of Wildlife Management*, *80*(8), 1360–1369. https://doi.org/10.1002/jwmg.21128

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Ellerbrok, J. S., Delius, A., Peter, F., Farwig, N., & Voigt, C. C. (2022). Activity of forest specialist bats decreases towards wind turbines at forest sites. *Journal of Applied Ecology*, *00*, 1–10. https://doi.org/10.1111/1365-2664.14249