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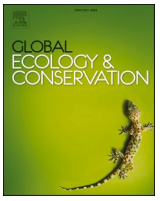

Forest bat activity declines with increasing wind speed in proximity of operating wind turbines

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ABSTRACT

The increasing use of onshore wind energy is leading to an increased deployment of wind turbines in structurally rich habitats such as forests. Forest-affiliated bats, in turn, are at risk of colliding with the rotor blades. Due to the legal protection of bats in Europe, it is imperative to restrict the operation of wind turbines to periods of low bat activity to avoid collisions. However, bats have also been observed to avoid wind turbines over several hundred meters distance, indicating a displacement that cannot solely be explained by modifications to the habitat. This avoidance suggests a displacement of bats by indirect factors related to wind turbine operation, e.g., wake turbulences and noise emissions. Therefore, we investigated whether the activity of forest-affiliated bats is influenced by operation mode (on/off) under variable wind conditions along transects from 80 to 450 m distance to wind turbines. We divided recordings by foraging guild, i.e., either narrow-space (*Myotis*, *Plecotus*), edge-space (*Pipistrellus, Barbastella*), or open-space foraging bats (*Nyctalus, Eptesicus, Vespertilio*), and analyzed the effects of wind turbine operation and wind speed on the recorded bat guild activity with mixed effects models. The acoustic activity of narrow-space foraging bats decreased by 77% with increasing wind speed when wind turbines were operating, while bat activity remained unaffected by wind speed when turbines were not operating. This was neither observed for open-space foraging bats nor for edge-space foraging bats, and neither wind turbine operation nor wind speed (ranging between 0 – 4 m/s at 10 m height above ground) were found to affect bat activity when considered alone. Wind turbine noise emissions are known to increase with rotor speed and consequently, wind speed, thus presenting a likely explanation for the interactive negative effect of turbine operation and wind speed specifically on noise-sensitive narrow-space foraging bats. To understand potential ecological long-term consequences for bat populations in forest areas with wind turbines and to design effective conservation measures, future research should focus on disentangling the effects of different disturbances related to turbine operation.

1. Introduction

Wind energy is globally promoted as more and more governments are committing to ambitious policy targets with the aim to reduce greenhouse gas emissions (UNFCCC, 2015). As of June 2022, wind turbines with a capacity of 874 GW had been installed

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worldwide, presenting a 13% increase to the year before (WWEA, 2022). The deployment of wind turbines impacts local wildlife as, for example, the construction and maintenance of wind turbines require space which can lead to habitat loss and fragmentation, particularly within forests, where wind turbines are increasingly built (FA Wind, 2022; Gaultier et al., 2020; Schöll and Nopp-Mayr, 2021; Xiarchos and Sandborn, 2017; Ellerbrok et al., 2023). Furthermore, birds, bats and flying insects may die from collisions with the moving blades of wind turbine rotors (Arnett et al., 2016; Thaxter et al., 2017; Voigt, 2021). Most of the obvious negative impacts of wind turbines on wildlife are well documented. Recent studies, however, have found that some bird and mammal species additionally show decreased activity levels in the vicinity of wind turbines, indicating that indirect influences may cause these animals to avoid wind turbines (Pearce-Higgins et al., 2009; Rehling et al., 2023; Skarin et al., 2018; Tolvanen et al., 2023). Bats seem to be especially sensitive to both direct and indirect effects of wind turbines, as they have been found to be susceptible to collisions as well as displacement at wind turbine sites.

Convergent research from various countries demonstrates an avoidance behavior of different bat taxa towards wind turbines (e.g., Ellerbrok et al., 2022; Barré et al., 2018; Gaultier et al., 2023; Leroux et al., 2022; Millon et al., 2015, 2018; Minderman et al., 2017; Reusch et al., 2022, 2023). This avoidance behavior seems to vary among habitats as well as among foraging guilds, a commonly used concept of grouping bat species with similar foraging style and habitat use (Denzinger and Schnitzler, 2013). For example, bats foraging in dense forest vegetation (narrow-space foraging bats) or open airspace (open-space foraging bats) avoid wind turbines in forests and open landscapes over several hundred meters (Ellerbrok et al., 2022; Gaultier et al., 2023; Reusch et al., 2022, 2023). Bats hunting along linear structures (edge-space foraging bats) have been observed avoiding wind turbines in open landscapes, where activity was reduced over more than one kilometer distance from turbines (Barré et al., 2018). Several hypotheses have been put forward to explain the avoidance of bats towards wind turbines (Barré et al., 2018; Gaultier et al., 2023). It was suggested that the avoidance is caused by habitat modifications associated with the deployment of wind turbines, especially in forests where clearings need to be created or extended to create sufficient space (FA Wind, 2022). However, studies have shown that bats were not less active in wind turbine clearings than in the surrounding forest (Ellerbrok et al., 2023) and that decreased bat activity towards wind turbines was independent of canopy openness and forest structure (Ellerbrok et al., 2022; Gaultier et al., 2023). These results suggest that the avoidance response of bats might instead be caused by factors related to the operation of the wind turbine.

When wind turbines are operating, the rotor blades are in constant motion presenting a potential visual disturbance that can startle wildlife (Saidur et al., 2011). Visual disturbances might be relevant for bats flying above the forest canopy in moonlit nights only. Rotor movements of operating wind turbines also interact with incoming air currents leading to wake turbulences that could affect bats flying downwind from turbines (Cryan et al., 2014). Additionally, the interaction between the spinning rotor blades and air currents creates aerodynamic noise which together with the mechanic noise emitted during turbine operation might deter bats (Heimann, 2018; Katinas et al., 2016). Potential disturbances by noise, wake turbulences or visual cues would increase with rotor speed and might therefore be amplified by increasing wind speed. Noise emission in particular were found to be louder at operating than at non-operating wind turbines with sound pressure levels increasing with wind speed (Heimann, 2018; Katinas et al., 2016). This is supported by a study on small wind turbines (< 50 kW) which demonstrated that the avoidance response of bats towards turbines depends on the operation status. In that study, bats of all foraging guilds decreased activity with increasing wind speeds but only when wind turbines were operating and stronger next to turbines than at 25 m distance (Minderman et al., 2012). Further, recent studies found a reduction in bat activity with increasing blade rotation speed at nacelle height as well as at the landscape scale (Barré et al., 2023; Leroux et al., 2023). Specifically, negative effects on the activity of pipistrelle bats were observed downwind from wind turbines, which could support wake turbulences or noise emissions as underlying drivers for avoidance responses rather than visual disturbances (Heimann, 2018; Leroux et al., 2023). Here we ask whether bat activity at large wind turbines in temperate forests can be explained by the interplay of operation mode, wind speed and wind direction.

We investigated the effect of the operation mode of wind turbines on the acoustic activity of bats at twelve wind turbine sites in forests of Hesse, Central Germany. In Germany, the operation of modern wind turbines is curtailed at times of predicted high bat activity to avoid collisions with high-flying bats. Widely applied algorithms trigger the starting and stopping of wind turbines in 10-min intervals throughout the night, depending on the hour and season, as well as wind speed and air temperature at nacelle height (Behr et al., 2017). In our study area, wind turbines equipped with a curtailment algorithm are not operating at night from April to October if wind speeds are below 6 m/s and ambient temperature above 10 °C at nacelle height (FA Wind, 2020). Operation phases of these wind turbines are logged each night which presents the opportunity to relate recorded acoustic bat activity to the logged operation times of wind turbines in the same night. With this approach, we expected to see (1) that the acoustic activity of bats is reduced in proximity to wind turbines when those are operating, but not when turbines are not operating. Since disturbances originating from the wind turbine, especially noise emissions and wake turbulences, might additionally be amplified by wind speed and wind direction, we further predicted (2) stronger avoidance of bats with increasing wind speed and at the downwind side of wind turbines compared to the upwind side.

2. Material & methods

2.1. Study area

Our study took place in the temperate low mountain ranges of Hesse in Central Germany (316 m to 509 m a.s.l.; Fig. 1). Bat and vegetation data were collected at 22 study sites (previously published in Ellerbrok et al., 2022, 2023) but protocols of nightly wind turbine operations were only obtainable for a subset of twelve of these sites. The chosen study sites were located in predominantly deciduous (seven study sites) or coniferous forests (five study sites) with a forest patch size between 1.84 ha and 25.95 ha (12.28 ha ±

6.91 ha; mean ± standard deviation, hereafter). Study sites were at a minimum distance between 9 km and 31 km (16 km ± 7 km) to each other, to ensure that bat recordings at different study sites were independent of each other. Further, study sites were as far as possible from anthropogenic infrastructure other than focal wind turbines and from forest edges to prevent confounding effects on bat activity. Each study site consisted of one wind turbine built on a cleared forest patch of 0.44 ha to 3.15 ha (1.15 ha ± 0.76 ha) and positioned at the margins of a wind farm. Focal wind turbines ranged in nominal rated power between 1.5 MW and 3.3 MW (2.8 MW ± 0.4 MW) and in rotor size between 97 m and 126 m diameter. The rotor diameter was correlated with the tower height (182 m – 212 m, mean: 199 m ± 8 m; $r = 0.59$, $p < 0.005$) and age of wind turbines (number of years between first year of operation and first year of data sampling: 1.5 – 19.0 years, mean: 4.8 ± 3.4 years; $r = -0.25$, $p < 0.005$). Information on focal wind turbines were retrieved from the publicly accessible data base of Hessian environmental agency (HLNUG, 2019).

2.2. Bat call sampling and analysis

At each study site, we recorded acoustic bat activity along a distance gradient, starting at the wind turbine and leading into the forest, away from other turbines of the wind farm. Sampling points were established with increasing intervals at 80 m, 130 m, 250 m, and 450 m from wind turbines, because the influence of a wind turbine was expected to be strongest close to the facility and to diminish with increasing distance. The starting distance of the sampling gradient was set at 80 m distance to turbines due to the approximate average size of the cleared area around turbines where recordings would not have been comparable to sites within the forest. The farthest sampling point was set at 450 m distance to turbines because forest patches in Germany are mostly small and would often not allow for larger recording distances without exiting the forest (Mann et al., 2023). We installed automated bat recorders (BATLOGGER A+, Elekon, Lucerne, Switzerland) at each sampling point in the lower tree canopy (height: 5 m – 29 m, mean: 16 m ± 6 m) and recorded for whole nights from 9 pm to 5 am. Recordings were carried out between May and September 2020 and 2021. Within each year, every sampling point was covered four times in randomized order with intervals of 17 to 61 days (33 ± 12 days) in between. We used BATLOGGER default settings with a trigger frequency between 15 kHz and 155 kHz, which covered the typical call frequency range of expected bat species. With the software BatExplorer (version 2.1, Elekon, Lucerne, Switzerland), we manually identified recorded bat call sequences based on their call shape, end frequencies and peak frequencies (Barataud, 2020; LFU, 2020; Skiba, 2009). Call sequences were either assigned to the functional guild of narrow-space foraging bats (*Myotis* ssp., *Plecotus* ssp.), edge-space foraging bats (*Pipistrellus* ssp., *Barbastellus* ssp.) or open-space foraging bats (*Eptesicus* ssp., *Nyctalus* ssp., *Vespertilio* ssp.; Denzinger and Schnitzler, 2013). To match the temporal resolution of wind turbine operation data, we divided recording nights into 10-minute intervals and calculated the number of minutes in which bat calls were present for each interval.

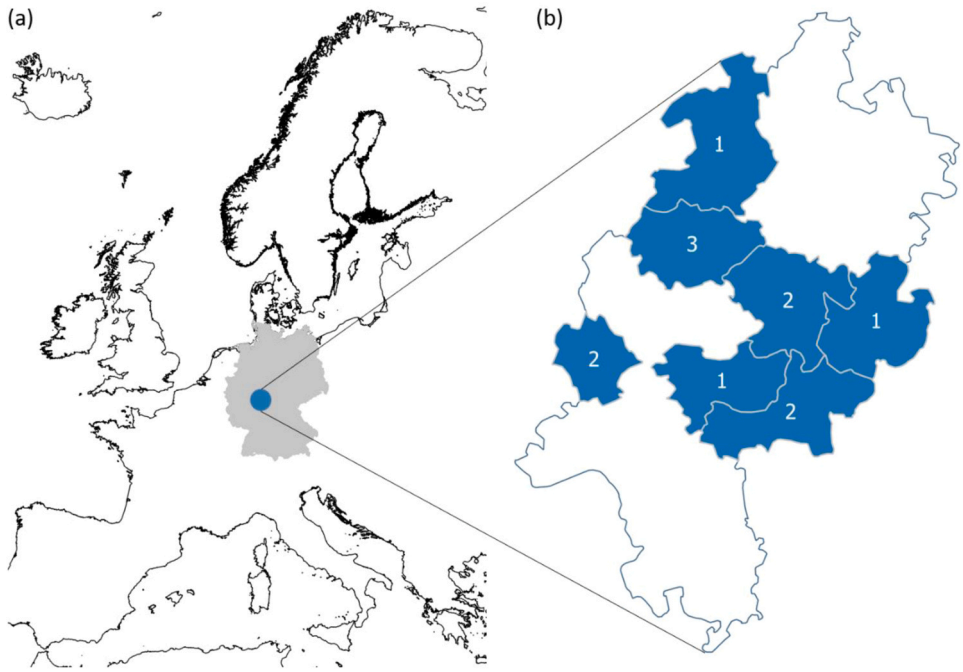

Fig. 1. Location of the study area. (a) The study was conducted in temperate forests of Central Germany. (b) Within the federal state of Hesse bat activity was sampled at twelve wind turbines across seven districts. White numbers state the number of investigated wind turbine sites per district. Due to agreements with forest owners, the exact location of wind turbines must not be disclosed.

2.3. Sampling of covariates

In Germany, the operation of modern wind turbines is usually curtailed at nights during predicted periods of high bat activity to reduce collision risk. Automated curtailments are based on algorithms which are fine-tuned for individual wind turbines (Behr et al., 2017). Due to legal requirements, wind energy companies need to document these curtailments. We merged the various operation logs, resulting in a documentation of nightly wind turbine operation and standstill phases in a 10-min resolution for each focal wind turbine which we matched with the 10-min intervals for which we recorded acoustic bat activity. Further, weather data in hourly resolution and based on a combination of observations and model data were downloaded from Copernicus Climate Change Service for each study site (Muñoz Sabater, 2019). Based on these simulated data, we calculated ambient temperature at 2 m above surface as well as wind speed and wind direction at 10 m above surface which we expected to influence bat activity at canopy height. We expected a correlation of our simulated wind speed and temperature data with measurements at nacelle height where data are gathered for automatic operation curtailments (Tizgui et al., 2017), but not necessarily a strong correlation with turbine operation since curtailment algorithms integrate several criteria (Fig. 2). Since activity levels of bats above 4 m/s wind speed at 10 m above ground were few, we discarded them as outliers and only recorded bat activity along a continuum of wind speeds up to 4 m/s. Wind direction was determined in relation to the geographic orientation of the recording transect for each study site and classified as downwind when the wind was blowing from the wind turbine down the transect and as upwind when the wind was blowing in the opposite direction (with an accepted deviation of $\pm$ 22.5°). All other relations of wind direction and transect orientation were classified as crosswind. Lastly, to account for variation in forest habitat structure and its effects on bat activity at each recording point, we estimated vegetation cover at ground level, 0.5 m, 1 m, 2 m, 4 m, 8 m, 16 m, and 32 m above ground to the nearest 5% within a 10 m radius. Subsequently, we calculated vertical vegetation heterogeneity across the layers using the Shannon-Weaver index (Bibby et al., 2000).

2.4. Data analysis

All statistical analyses were done with R (version 4.2.2; R Core Team, 2022). The analyses described in the following sections were done with separate models for each bat foraging guild, because activity levels differed considerably among guilds and could not be fitted in a single model. First, we analyzed bat activity data at a temporal resolution of 10 min to capture immediate effects. Then, we analyzed bat guild activity data at a temporal resolution of full nights to capture potential cumulative effects which might only become evident when conditions persist over longer periods.

We assessed how bat activity was affected by the operation mode of wind turbines using generalized linear mixed models (GLMMs, package glmmTMB; Brooks et al., 2017). First, we built one model for each foraging guild with bat activity as a response variable and wind turbine operation mode ("off" or "on") as predictor variable (fixed effect). Sampling points were nested in study sites and recording nights which was specified as random effect. As further fixed effects, we included distance to the next wind turbine (80 m, 130 m, 250 m, or 450 m), diameter of the wind turbine rotor, time of night as well as vertical vegetation heterogeneity and weather covariates (ambient temperature at 2 m above surface, wind speed and wind direction relative to transect at 10 m above surface). All continuous fixed factors were standardized with a z-transformation.

For the GLMMs at 10-min resolution, we used a binomial error distribution based on presence and absence data, because an examination of the response variable revealed that only a small percentage of all 10-intervals contained more than one minute of bat activity (4.2% in narrow-space foragers, 27.0% in edge-space foraging bats, 2.6% in open-space foragers). However, within the edge-space foraging guild the residuals for a binomial model deviated severely from normal distribution, which is why we performed a truncated poisson (hurdle) model for this guild. Moreover, we included an autoregressive covariance structure in all GLMMs at 10-min

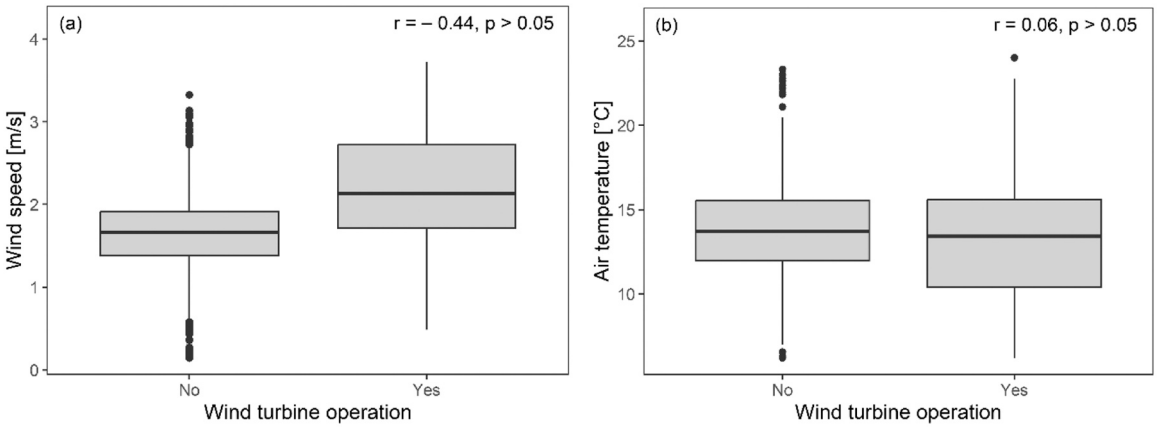

Fig. 2. Recorded operation of wind turbines at different wind speeds and ambient temperatures. Neither wind speed at 10 m (a) nor ambient temperature at 2 m above surface (b) significantly differed between intervals of wind turbine operation and standstill. Bars depict mean values and shades depict interquartile ranges of weather variables. Correlation coefficients and p-values are the results of a point-biserial correlation test.

resolution to account for temporal autocorrelation of bat activity between consecutive 10-min intervals (Durbin-Watson test for temporal autocorrelation in narrow-space foraging bats: DW = 0.86, $p < 0.005$; edge-space foraging bats: DW = 0.24, $p < 0.005$; open-space foraging bats: DW = 0.58, $p < 0.005$; package DHARMa, Hartig, 2022). As a result, models were built in the following way:

Bat activity ~ wind turbine operation mode + wind turbine distance + wind turbine size + weather covariates + vertical vegetation heterogeneity + time of night + ar1(time of night+0|night/plot) + 1|night/plot

To run GLMMs on full-night resolution, we first calculated the proportion of each night when wind turbines had been operating as well as the summed amount of bat activity minutes for each night. For numerical site variables which varied throughout the night (wind speed, ambient temperature) we calculated mean values for the corresponding nights. The same fixed effects were included in models both on 10-min and nightly resolution, except time of night and wind direction in relation to transects, where a scaling to full nights was not possible. Based on the structure of the new response variable, we used a negative binomial error distribution. As a result, models were built the following way:

Bat activity ~ wind turbine operation % + wind turbine distance + wind turbine size + weather covariates + vertical vegetation heterogeneity + 1|night/plot

To improve the model fit we ran a model selection for the GLMMs both on 10 min and full night resolution and retained only the most relevant predictor variables (fixed effects). Accordingly, we built candidate models with all possible combinations of fixed effects, always containing wind turbine operation as our variable of interest. Interactions between wind turbine operation and other covariates were included. Models were then ranked by AICc and the model with the lowest AICc was selected for further analyses (package MuMIn; Bartoń, 2022; Appendix S1).

We performed model diagnostics for all full and selected models to ensure robustness of results. We checked for multicollinearity by calculating variance inflation factors with the car package (Fox and Weisberg, 2019) and ensured that the factor was below two for all given combination of variables. We checked for homoscedasticity and normally distributed residuals with the DHARMa package (Hartig, 2022). P-values and estimates for fixed effects, calculated with Wald-χ2-tests from the car package, were compared between full and selected models (Appendix S4). For significant interactive effects with wind turbine operation status we calculated the within-group p-values with least-squares means (package lsmeans; Lenth et al., 2016).

3. Results

Wind turbines were operating during 49% of all recorded 10-min intervals, with highest numbers of operation periods in June and lowest in September (Fig. 3). In total, we recorded 28,856 min with bat presence over 297 full night recordings, sampled over the peak bat season (May to September) of two years. Narrow-space foraging bats made up 14% of all recorded bat activity minutes. Bats of this foraging guild were active in 12% of all recorded 10-min intervals. Edge-space foraging bats made up 78% of activity minutes and were active in 42% of 10-min intervals. Open-space foraging bats made up 8% of activity minutes and were active in 8% of 10-min intervals. Bat activity levels varied in the course of the night and between foraging guilds (Appendix S2).

The time series model revealed that the acoustic activity of bats was not affected by the operation mode of wind turbines, regardless of foraging guild. However, acoustic activity of narrow-space foraging bats decreased by 77% (95% confidence interval [−78%, −75%]) with increasing wind speed when wind turbines were operating ($p = 0.036$), while the activity remained unaffected by wind speed when wind turbines were not operating ($p = 0.65$; Fig. 4). This interaction did not appear as significant in the full model

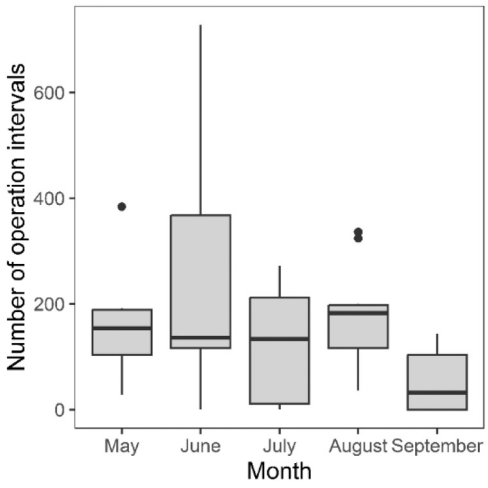

Fig. 3. Recorded operation of wind turbines across sampling points throughout the year. Mean number (bars) and interquartile range (shades) of recorded 10-min intervals with wind turbine operation.

($p = 0.265$; Appendix S3). Additionally, narrow-space foraging bats were less active close to wind turbines than far from wind turbines (−48%, CI [−49%, −47%]; Fig. 5a). The activity of bats decreased with increasing rotor size (−78%, CI [−76%, −78%]) and increased with increasing vertical vegetation heterogeneity (+193%, CI [+184%, +199%]; Table 1).

Acoustic activity of edge-space foraging bats recorded closest to wind turbines decreased by 8% (CI [8%, −8%]) in comparison to the recording points most distant to wind turbines (Fig. 5b). In addition, acoustic activity increased with decreasing vegetation heterogeneity (13%, CI [−2%, +12%]) and decreased over the course of the night (−28%, CI [−27%, +8%]; Table 1). All but the effect of time was supported by the full model (Appendix S4).

Open-space foraging bats were more active at study sites with larger rotors compared to sites with smaller rotors (+167%, CI [+117%, +228%]), and their activity increased with vertical vegetation heterogeneity at the recording points (+499%, CI [+485%, +510%]). Additionally, we observed a marginally significant trend of reduced activity in open-space foraging bats with increasing proximity to wind turbines, especially when wind turbines were operating (Fig. 5c, Table 1, Appendix S3). Only in the full model we found a positive effect of ambient temperature on the activity of open-space foraging bats (Appendix S4).

The GLMMs at the resolution of full nights did not reveal any further effects of turbine operation on summed bat activity. Still, these models showed that high mean ambient temperature had a positive effect on the activity of narrow-space (+614%, CI [+596%, +633%]), edge-space (+170%, CI [164%, +176%]) and open-space foraging bats (+3681%, CI [+3488%, +3883%]). High mean wind speed reduced the activity of narrow-space (−97%, CI [−99%, −93%]) and edge-space foraging bats (−82%, CI [−68%, −90%]; Table 1). In the full model, the negative effect of increasing wind speed on edge-space foraging bats was not significant ($p = 0.265$), while wind speed as a quadratic term had a significant effect ($p = 0.018$; Appendix S4).

4. Discussion

We investigated the activity of bats around wind turbines at twelve forested sites in Germany to elucidate the causal mechanisms driving avoidance of wind turbines by bats. We argued that disturbances of operating wind turbines (noise, wake turbulences or visual cues) might be responsible for the avoidance and assessed differences between activity of three bat foraging guilds at operating and non-operating wind turbines. We found no overall effect of wind turbine operation mode on activity levels of any of the local bat foraging guilds. Activity of narrow-space foraging bats decreased with increasing wind speed in a range between 0 and 4 m/s measured at 10 m above surface, but only when wind turbines were operating and regardless of distance to wind turbines. Additionally, narrow-space and edge-space foraging bats reduced their activity towards wind turbines over distances of at least 450 m, regardless of wind turbine operation mode.

Overall, bat activity did not differ between times when wind turbines were operating and times when they were not operating, independent of distance to wind turbines, although theoretically wind turbines were switched off by algorithms when bat activity was predicted to be high (Behr et al., 2017). However, curtailment algorithms use environmental variables measured at the nacelle and mainly aim to reduce collisions with high-flying open-space and edge-space foraging bats (Behr et al., 2017; Rodrigues et al., 2014). However, in our study we recorded bat activity at forest canopy height where low-flying narrow-space foragers are more active and wind conditions are less harsh, which might explain why turbines were operating even though recorded bat activity levels were high. In addition, a time lag between turbine operation and responses in bat activity could have disguised a potential correlation of both

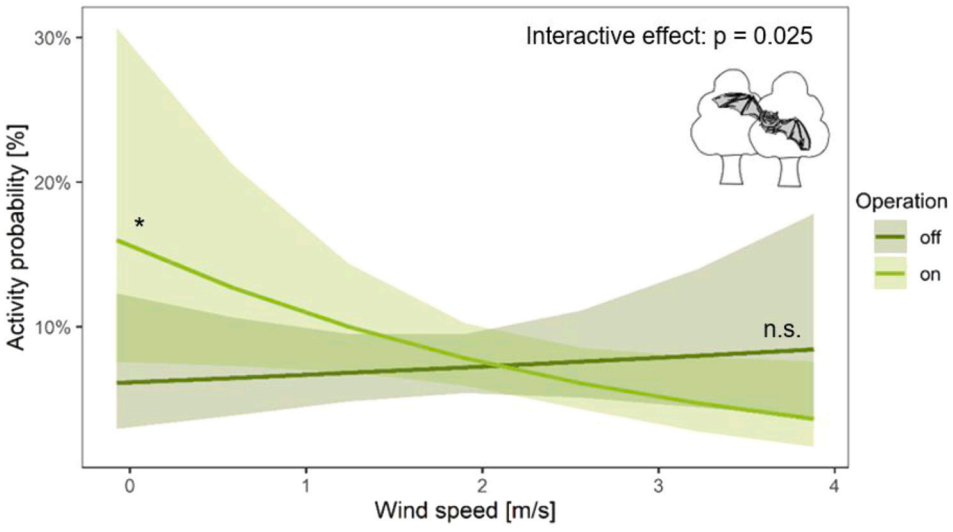

Fig. 4. Activity probability of narrow-space foraging bats in relation to wind speed around operating and non-operating wind turbines. Mean estimates (lines) and 95%-confidence intervals (shades) of activity probability in narrow-space foraging bats depending on wind speed at times of wind turbine operation ('on') and standstill ('off') in 10-min intervals of the night. Asterisks denote the significance level of the effect for different turbine operation modes (*** < 0.001 < ** < 0.01 < * < 0.05 < n.s.).

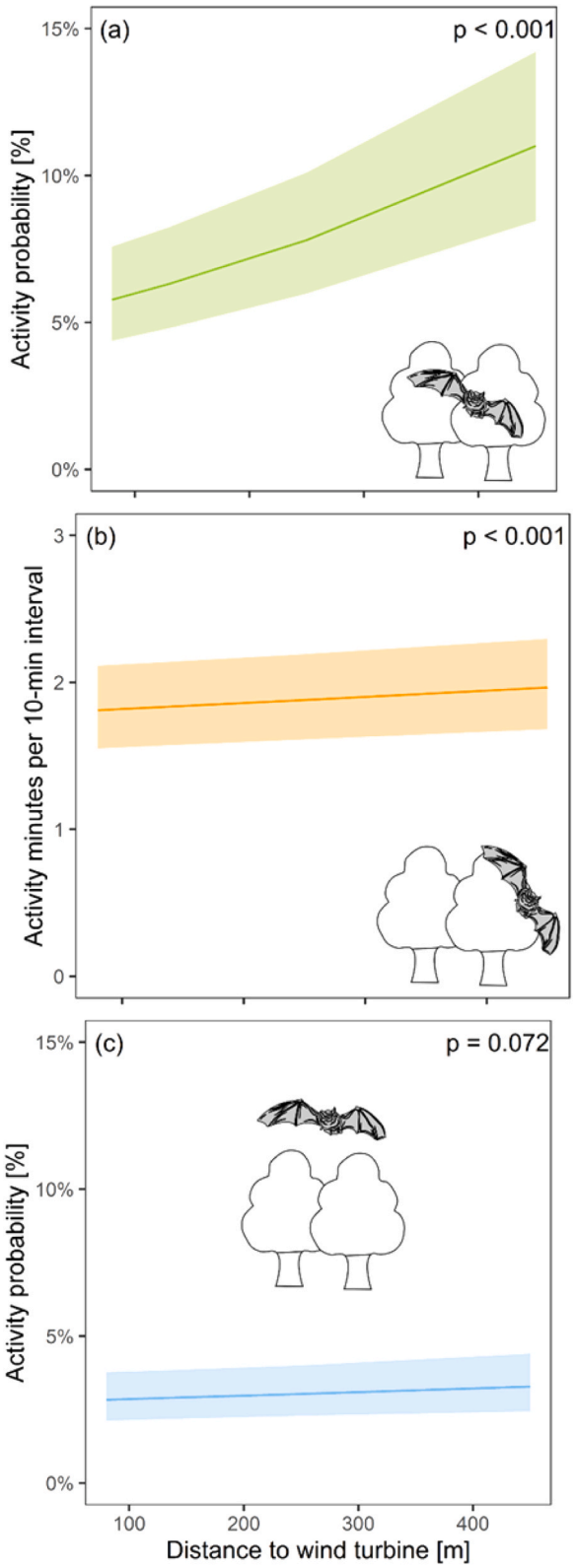

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Fig. 5. Bat activity at increasing distances to wind turbines regardless of operation mode. Mean estimates (lines) and 95%-confidence intervals (shades) of bat activity depending on the distance to wind turbines for (a) narrow-space, (b) edge-space, and (c) open-space foraging bats in 10-min time intervals of the night. (a) and (c) are on a binomial scale, while a hurdle model is underlying (b). The hurdle model was performed to achieve a normal distribution of residuals in the model for edge-space foraging bats.

factors. This was, however, not supported by investigations of total bat activity throughout the night where no correlation with total wind turbine operation time was found either. Noticeably, weather parameters, i.e., wind speed at 10 m and ambient temperature at 2 m above surface, did not explain the variation in bat activity in our main models At first sight, this seems to contradict a series of studies which showed that bat activity strongly depends on weather, specifically wind speed, ambient temperature, and precipitation (e.g., Behr et al., 2017; Erickson and West, 2002; Voigt et al., 2011). However, while bats are generally known to fly less with increasing wind speed, a strong activity decrease is only expected for wind speeds of more than 6 m/s (e.g., Erickson and West, 2002; Voigt et al., 2015). Still, models based on averaged wind speed and ambient temperature of whole nights confirmed the significance of weather parameters as a factor explaining total nightly bat activity.

Strikingly, bats of the narrow-space foraging guild were negatively affected by increasing wind speeds at 10 m above surface around operating wind turbines, which was not observed at non-operating wind turbines, i.e., turbines with non-moving rotor blades. This implies that a potential avoidance of operating wind turbines by bats might indeed be caused or amplified by wind speed and, consequently, rotor speed (Barré et al., 2023; Leroux et al., 2023). An interactive negative effect of wind turbine operation and wind speed on bat activity is also consistent with a previous study conducted at small wind turbines (< 50 kW net energy production) in open habitats (Minderman et al., 2012). In that study, bats of all foraging guilds decreased activity with increasing wind speed ranging between 0 and 14 m/s and over distances of at least 25 m when wind turbines were operating. These convergent results suggest that the operation of wind turbines at relatively high wind speeds can indeed negatively affect bat activity in both forests and open habitats. Moreover, the strength of the adverse effect seems to increase with turbine dimensions, as we observed a stronger effect at modern, large wind turbines compared to older, small wind turbines, which extended over at least 450 m into forests. Yet, for edge-space and open-space foraging bats we could not confirm a negative effect of wind turbine operation depending on wind speed over similar spatial scales, possibly because the clearing required for turbine operation at forested sites creates a preferred habitat for bats of these guilds (Ellerbrok et al., 2023), which might counteract an avoidance response.

The interplay of wind turbine operation and wind conditions appears to be highly complex and may affect bats in different ways depending on guild and habitat (Leroux et al., 2023). Our observation of a reduced activity of narrow-space foraging bats with increasing wind speed exclusively at operating wind turbines confirms that avoidance towards turbines is likely driven by factors related to rotor speed, i.e., visual disturbances, wake turbulences or noise emissions. In windy conditions, wind direction is strongly influencing from what side bats are approaching a wind turbine, indicating that wake turbulences may be affecting bats near wind turbines (Cryan et al., 2014). It is still unclear to what extent wake turbulences could reduce bat activity on a landscape scale. However, in our study, reduced activity of narrow-space foraging bats at operating wind turbines was not related to wind direction and therefore probably not explained by wake turbulences. Moreover, narrow-space foraging bats mostly fly below the forest canopy (Denzinger and Schnitzler, 2013; Roemer et al., 2017) where wake turbulences, and visual disturbances like light emissions from wind turbines, seem less likely to penetrate than noise emissions. Although effects of noise emissions by wind turbines on bats have not been studied so far, it is known that bats are sensitive to anthropogenic noise, as has often been shown for bats being exposed to traffic noise. For example, bats avoid crossing roads especially when traffic noise is loud (Bennett and Zurcher, 2013; Zurcher et al., 2010) and decrease activity towards busy roads (Berthinussen and Altringham, 2012; Claireau et al., 2019). Further, experimental studies demonstrated that foraging success is impaired and prey search prolonged when bats are exposed to playbacks of traffic noise (Finch et al., 2020; Luo et al., 2015; Schaub et al., 2009; Siemers and Schaub, 2011).

Bats might be affected in similar ways by road traffic and wind turbine operation noise because both share certain acoustic features. Specifically, wind turbines generate non-continuous, i.e., pulsed sounds in broadband frequencies and with an unpredictable onset if turbines are switched on and off in the cause of the night. The hypothesis that bats avoid operating wind turbines due to noise emissions fits well with our finding of decreasing bat activity with increasing wind turbine rotor size, because modern larger wind turbines generate more noise than old and small turbines if not counteracted by modifications to the rotor blades, e.g., brushes on the trailing edge, or to the drivetrain, e.g., dampers (Deshmukh et al., 2019; Hansen and Hansen, 2020; Møller and Pedersen, 2011; Xu et al., 2021). Yet, we were unable to confirm that bat activity is affected stronger downwind than upwind from wind turbines, although wind turbine noise emissions should propagate more efficiently downwind from turbines (Heimann, 2018; Katinas et al., 2016; Leroux et al., 2023). Based on our findings, noise emissions of operating wind turbines are a likely explanation why bats avoid wind turbines, but we can ultimately not rule out that further factors, e.g., wake turbulences, may play a role in reducing the activity of narrow-space foraging bats. Further, we were not able to measure turbine-generated sounds at varying distances to wind turbines in our study area and can therefore only speculate how far wind turbine-related sounds propagate locally and how disturbing these sounds are for bats. We recommend conducting playback experiments similar to previous studies on birds (Szymański et al., 2017; Zwart et al., 2016) and evaluate the effect of wind turbine noise emission on the activity of forest-associated bats.

Finally, we found a negative effect of wind turbine operation with increasing wind speed only for narrow-space foraging bats, but not for bats from the open-space and edge-space foraging guild. On the one hand, different responses among bat foraging guilds might be related to their preferred use of habitat niches in forests. For example, open-space foraging bats fly above the tree canopy, where winds are stronger, and could therefore be more exposed to visual cues and turbulences originating from wind turbines. This may explain why open-space foraging bats tend to be less active close to operating wind turbines independent of wind speeds, while this was

Table 1
Results of selected GLMMs at 10-min and full night resolution. Estimates and p-values of the effects on bat echolocation activity of three bat foraging guilds. Significant effects (p-value < 0.05) are shown in bold. Predictors from the full model which were not included in the top AICc model are marked with an "x". Time of night and wind direction could not be assessed in the models for full nights (blank).

			Temporal resolution			
			10 min intervals		full nights	
Foraging guild	Predictors	Df	Chisq	p-value	Chisq	p-value
Narrow-space	turbine operation	1	1.375	0.241	1.823	0.177
	turbine distance	1	104.474	**<0.001**	13.689	**<0.001**
	wind speed - linear	1	0.963	0.337	6.245	**0.012**
	wind speed - quadratic	1	X	x	x	x
	ambient temperature	1	X	x	6.417	**0.011**
	rotor diameter	1	9.590	**0.002**	7.418	**0.006**
	vertical vegetation heterogeneity	1	45.767	**<0.001**	x	x
	wind direction	2	X	x		
	time of night	1	3.047	0.081		
	turbine operation x turbine distance	1	X	x	x	x
	turbine operation x wind direction	4	X	x		
	turbine operation x wind speed - linear	1	5.351	**0.021**	x	x
Edge-space	turbine operation	1	1.563	0.211	0.376	0.540
	turbine distance	1	13.653	**<0.001**	x	x
	wind speed - linear	1	0.107	0.743	6.482	**0.011**
	wind speed - quadratic	1	X	x	x	x
	ambient temperature	1	X	x	6.064	**0.014**
	rotor diameter	1	3.527	0.060	2.819	0.093
	vertical vegetation heterogeneity	1	5.007	**0.025**	9.428	**0.002**
	wind direction	2	4.477	0.108		
	time of night	1	4.543	**0.033**		
	turbine operation x turbine distance	1	X	x	x	x
	turbine operation x wind direction	4	X	x		
	turbine operation x wind speed - linear	1	X	x	x	x
Open-space	turbine operation	1	0.290	0.590	0.013	0.911
	turbine distance	1	3.235	0.072	x	x
	wind speed - linear	1	2.102	0.147	2.532	0.112
	wind speed - quadratic	1	X	x	x	x
	ambient temperature	1	17.062	**<0.001**	21.136	**<0.001**
	rotor diameter	1	3.934	**0.047**	1.660	0.198
	vertical vegetation heterogeneity	1	82.931	**<0.001**	22.496	**<0.001**
	wind direction	2	X	x		
	time of night	1	X	x		
	turbine operation x turbine distance	1	3.732	0.053	x	x
	turbine operation x wind direction	4	X	x		
	turbine operation x wind speed - linear	1	X	x	x	x

not observed for narrow-space and edge-space foraging bats, that fly lower and prefer foraging habitats in forests and at forest edges (Denzinger and Schnitzler, 2013). On the other hand, observed differences among foraging guilds are in line with studies indicating that bat taxa differ in their sensitivity to anthropogenic disturbances and, specifically, that narrow-space foraging bats are more likely to avoid anthropogenic noises and lights than bats from other foraging guilds (Barré et al., 2022; Bonsen et al., 2015). Accordingly, a stronger avoidance response in narrow-space foraging bats compared to open-space and edge-space foraging bats might present additional evidence that decreased bat activity at operating wind turbines with increasing wind speed could be caused by noise emissions.

5. Conclusion

Our study confirms that bats in temperate forests generally avoid wind turbines and that sensitivity to wind turbine operation varies between foraging guilds. In particular, narrow-space foraging bats, which are especially dependent on the forest habitat, significantly reduced their activity with increasing wind speed when wind turbines were operating. Notably, we did not observe any significant changes in the activity levels of edge-space and open-space foraging bats in response to the operating mode of wind turbines. Consequently, guild-specific sensitivity of bats towards wind turbine operation may influence the composition of local bat communities. The interactive effect of turbine operation and wind speed on the activity of narrow-space foraging bats hints towards noise emissions as an underlying driver but this has to be verified by future research. Our study design focused on the short-term effects of wind turbine operation on bats. However, long-term effects beyond the timeframe of our study are possible and even likely should the decrease in bat activity close to wind turbines indeed be caused by noise emissions (Francis and Barber, 2013). For example, noise emissions could cause chronic stress, ultimately leading to fitness costs for bats, as previously shown for small birds (Kleist et al., 2018). Bats have an excellent spatial memory and might therefore remember areas with noise pollution at the landscape scale over extended

periods (Mueller and Mueller, 1979). Consequently, even occasional startling noises from wind turbines might lead to an avoidance by bats and thereby deteriorate available habitats and ultimately affect the viability of bat populations.

In conclusion, conservation actions should be considered which could include the reduction of wind turbine noise emissions by technical adjustments such as brushing the trailing edges of rotors. Further, an extension of curtailment algorithms to predict activity peaks also of narrow-space foraging bats flying below forest canopies may help to avoid displacements by wind turbines. Finally, playback experiments with noise recordings will help to better understand how bats react to wind turbine noises under controlled conditions, and might eventually contribute to estimate and offset the amount of habitat that is indirectly lost for bats around wind turbines.

CRediT authorship contribution statement

Peter Franziska: Conceptualization, Funding acquisition, Investigation, Methodology, Writing – review & editing. **Voigt Christian C.:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing – review & editing. **Farwig Nina:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Ellerbrok Julia S.:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Julia S. Ellerbrok reports financial support was provided by German Federal Environmental Foundation.

Data availability

The original data and R code this study is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.vx0k6djxg (Ellerbrok, 2023)

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02782.

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