Biological Conservation 302 (2025) 110968

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Wind turbines displace bats from drinking sites

Carolin Scholz, Hannah Klein, Christian C. Voigt *

Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany
Universität Potsdam, Am Mühlenberg 3, 14476 Potsdam, Germany

ARTICLE INFO

Keywords:
Acoustic activity
Avoidance
Casualties
Displacement
Green-green dilemma
Habitat degradation
Human wildlife conflict
Wildlife

ABSTRACT

Bats depend on water for drinking and foraging, but the increasing number of wind turbines may pose a problem for bats, as operating wind turbines are known to displace bats over long distances. We asked whether turbines displace bats from critical habitats, namely small ponds where bats drink and forage. We recorded the acoustic activity and foraging activity of three functional guilds of bats, i.e. open space, edge space and narrow space foraging bats, using automated detectors at 59 ponds located at varying distances (~50 to 5000 m) from wind turbines. We observed that edge space foraging bats were most abundant at focal ponds compared to narrow and open space foraging bats. The overall acoustic activity of open and narrow space foraging bats decreased with decreasing distance to wind turbines, whereas the activity of edge space foraging bats was unaffected by wind turbines. The feeding activity of bats at focal ponds decreased for open space foraging bats in proximity to wind turbines. For narrow space foraging bats, we observed a trend towards reduced feeding activity at ponds close to wind turbines, whereas we did not observe any effect of wind turbines on the feeding activity of edge space foraging bats. The siting of wind turbines close to drinking sites may degrade the resource landscape for bats, which could lead to population declines. Avoiding the proximity of turbines to important bat habitats is essential to protect biodiversity on farmland.

1. Introduction

The use of wind energy is an important sector of renewable energy generation with global growth rates between 2 and 10 % (Global Wind Energy Council, 2023). Wind energy production is expected to contribute to the reduction of anthropogenic greenhouse gas emissions, but wind energy production can also have detrimental effects on habitats (e.g., Baidya Roy and Traiteur, 2010; Zhou et al., 2012; Diffendorfer et al., 2022) and wildlife such as birds and bats (e.g., Voigt et al., 2012; Pylant et al., 2016; Thaxter et al., 2017; Thaker et al., 2018; Frick et al., 2017; Conkling et al., 2022; Scholz et al., 2023; Voigt et al., 2024; Vander Zanden et al., 2024). To minimise these negative effects, it is important to use optimal siting strategies when constructing wind turbines (Balotari-Chiebao et al., 2023; Feng et al., 2023), for example by maintaining threshold distances from important habitats for nesting and wintering birds (Leddy et al., 1999; Stevens et al., 2013) or daytime roosts for bats (Reusch et al., 2022, 2023; Voigt et al., 2024). In addition, the number of fatalities at operating wind turbines should be minimised by appropriate countermeasures, such as automated detection systems to prevent bird collisions (May et al., 2012) or curtailment to protect bats from collisions with the rotating blades during periods of high bat activity (Arnett et al., 2011; Voigt et al., 2024). While optimal siting and mitigation of wind turbine casualties are of central importance, wind turbines can also have more subtle but far-reaching effects on neighboring ecosystems that extend beyond the immediate area of a wind turbine platform (Niebuhr et al., 2022). These far-reaching effects on ecosystems and wildlife have been poorly addressed, if at all, by standard planning, monitoring and permitting processes (e.g. Barré et al., 2018). Some of these effects include noise-induced displacement of animals (Tolvanen et al., 2023), wake-induced changes in local atmospheric conditions (Baidya Roy and Traiteur, 2010; Zhou et al., 2012; Diffendorfer et al., 2022; Wang et al., 2023), and some are associated with cascading effects in food webs (Thaker et al., 2018). These negative impacts may extend to areas that contain important wildlife habitats or that have been prioritised for biodiversity conservation (Pérez-García et al., 2022). Ignoring these impacts may lead to avoidable biodiversity losses during the expansion of wind energy production, which is undesirable given the ultimate goal of environmentally friendly energy production. Therefore, understanding the extent and ecological impact of the displacement of vulnerable species by wind turbines is key to a green

---

* Corresponding author at: Leibniz Institute for Zoo and Wildlife Research, Alfred-Kowalke-Str. 17, 10315 Berlin, Germany.
E-mail address: voigt@izw-berlin.de (C.C. Voigt).

https://doi.org/10.1016/j.biocon.2025.110968
Received 3 September 2024; Received in revised form 14 November 2024; Accepted 3 January 2025

transition from conventional to renewable energy sources (Smeraldo et al., 2020; Tesfahunegny et al., 2020).

The displacement of bats by wind turbines has been documented for species of different functional guilds, over a wide geographical range including boreal, temperate and subtropical zones (Millon et al., 2018; Barré et al., 2018; Ellerbrok et al., 2022; Gaultier et al., 2023; McKay et al., 2023), and for a variety of landscapes including farmland and forests (Barré et al., 2018; Ellerbrok et al., 2022). Similar to other sensitive taxa, bats can be displaced several hundred metres to more than one kilometre away from wind turbines (Barré et al., 2018; Ellerbrok et al., 2022; Reusch et al., 2022, 2023; Tolvanen et al., 2023). Previous studies have shown that bat activity decreases in the vicinity of small wind turbines as a function of wind speed (range: 0–15 m/s) and distance (close proximity 0–5 m, distance 20–25 m) (Minderman et al., 2012). These effects disappeared when the turbines were not operating (Minderman et al., 2012). Follow-up studies showed that for larger wind turbines, the decrease in bat activity was noticeable at even greater distances (Millon et al., 2018; Barré et al., 2018). For example, in France, Barré and colleagues observed significant declines in the activity of bats specialised in insect hunting in the forest interior and at forest edges, so-called narrow space and edge space foraging bats, respectively, at distances of up to 1 km from wind turbines on farmland (Barré et al., 2018). A strong negative effect of wind turbines on narrow space foraging bats has also been documented for wind turbines at forested sites in Germany (Ellerbrok et al., 2022, 2024). In particular, the avoidance response of narrow space foraging bats - a functional group not at risk of collision with wind turbines - increased with the size of wind turbines (Ellerbrok et al., 2022, 2024) and was only observed when turbines were in operation (Ellerbrok et al., 2024). In two GPS tracking studies with noctule bats, a European species that forages in open areas, avoidance of wind turbines occurred over distances of several kilometres (Reusch et al., 2022, 2023). Wind turbine configuration, operating mode and size parameters influenced the activity of several bat species from different functional guilds (Leroux et al., 2023). In addition, species flying at intermediate altitudes responded to wake turbulence generated by wind turbines (Leroux et al., 2024). The potential confounding effect of landscape features was minimised in these studies by the use of comparable control sites or appropriate statistical tests, suggesting that wind turbine operation was causal for the displacement of bats.

Recent studies have recommended that wind turbines should only be installed in locations where their wide-ranging effects are unlikely to affect the use of key habitats by bats (Leroux et al., 2023; Voigt et al., 2024). Ponds are such important habitats because bats depend on them for drinking and foraging (Korine et al., 2016; Heim et al., 2018; Ancillotto et al., 2019; Kukka et al., 2024). The accessibility of ponds for drinking is particularly important in times of global warming, when droughts become more frequent (Cook et al., 2018) and ecosystems face higher levels of desertification (Huang et al., 2020), which may threaten the access of bats to drinking sites (Adams and Hayes, 2021), and thus the viability of local bat populations. Here, we asked whether the proximity of wind turbines to ponds alters the activity of bats at these drinking sites. In our study, we focused on three functional guilds, namely the narrow, edge and open space foraging guilds, whose members are abundant adjacent to or above arable fields in Central Europe (Denzinger and Schnitzler, 2013; Heim et al., 2017). The open space foraging bat guild includes the genera *Nyctalus*, *Eptesicus* and *Vespertilio*, the edge space foraging guild includes the genera *Pipistrellus* and *Barbastella*, and the narrow space foraging guild includes the genera *Plecotus* and *Myotis* (Denzinger and Schnitzler, 2013). We hypothesised that the activity of bats at ponds would be affected by the presence of wind turbines. Considering the results of previous studies from Germany (Ellerbrok et al., 2022, 2024; Reusch et al., 2022, 2023), we predicted that general activity and also the foraging activity of narrow- and open-field foraging bats would be lower at ponds close to wind turbines. Our study is relevant for reconciling the two important environmental goals of combating climate change and reversing biodiversity loss. The results of our study have important implications for planning and monitoring procedures during the construction of wind turbines in Europe and beyond, as all European bats are protected by national legislation and international directives (EU Habitats Directive) and conventions (UNEP/EUROBATS Agreement of the Convention on Migratory Species of Wild Animals, signed Bonn 1979, London 1991).

2. Material and methods

2.1. Study area

We investigated the acoustic activity of bats at ponds in the Quillow catchment area of Uckermark (northern Brandenburg, Germany) (Fig. 1). Except for the vicinity of the Quillow stream, where grassland predominates, most of the area is used for intensive agriculture (74 %). Small patches of woodland and small villages are scattered across the landscape. The Quillow catchment is characterised by >1000 small ponds, known as kettle holes, kettle lakes or pothole lakes (Heim et al., 2018), which are depressions created by glaciers in past geological eras that are now filled with water, either permanently or temporarily. Due to its relatively flat topography and openness, the Uckermark is an important area for wind energy production in Brandenburg, as evidenced by several hundred wind turbines of varying rated capacity (range: 0.25–7.5 MW; mean = 2.8 MW), hub height (36–169 m, mean = 120 m) and rotor diameter (31–164 m, mean = 99 m) (Landesamt für Umwelt Brandenburg, Appendix 1).

2.2. Data collection

We exclusively selected ponds with permanent water throughout the year for acoustic monitoring. For each focal pond, we estimated the pond size itself, the distances to the nearest wind turbine, forest edge, road, and neighboring water body using R (version 4.4.0) and freely available geographic layers (see Electronic Supplement: Appendix 1). We selected 60 ponds for which the aforementioned variables were not significantly correlated (see Electronic Supplement: Appendix 2). To assess this, we calculated the correlation between each numeric variable using the R package ‘corrplot’ (Wie and Simko, 2021). As the ultrasonic recording (see below) failed to work at one site, we ended up with 59 study sites. We constructed a correlation matrix for these 59 study sites by calculating the correlation between each numerical landscape feature variable using the R package ‘corrplot’ (Wie and Simko, 2021). We assessed the vegetation cover around the focal ponds by grouping them into the categories ‘none’ with no trees and shrubs (but grass and crops), ‘low’ (<25 % of the pond edge was surrounded by trees and shrubs) and ‘medium’ (25–50 % of the pond edge was surrounded by trees and shrubs) (Appendix 2).

We recorded the acoustic activity of bats during seven nights around the new moon at the beginning and end of July 2022. We avoided full moons, as bats may change their habitat use during full moon nights (Roeleke et al., 2018). We chose this particular month because local female bats are in late lactation and weaning, which is the most energetically demanding time of the year for females (Heim et al., 2016). Also, many water bodies dry up in summer, so we expected a higher dependence of bats on permanent water bodies. For the given recording nights, we obtained weather data from the local research station of the Leibniz Centre for Agricultural Landscape Research which measures, among other parameters, the prevailing ambient temperature and wind speed every 10 min. During the recording nights, environmental conditions were relatively similar, with an average ambient temperature of 12 °C (range 10 °C - 15 °C) and a wind speed of 10.4 m/s (range 9.9–12.2 m/s). We avoided recording on nights with storms or rain. We recorded bat activity from 21:00 to 05:00 each night at up to ten ponds simultaneously, but each pond was only sampled for one night. We used a custom R script to randomly select focal ponds during a given night, taking into account a relatively even distribution of distances to the

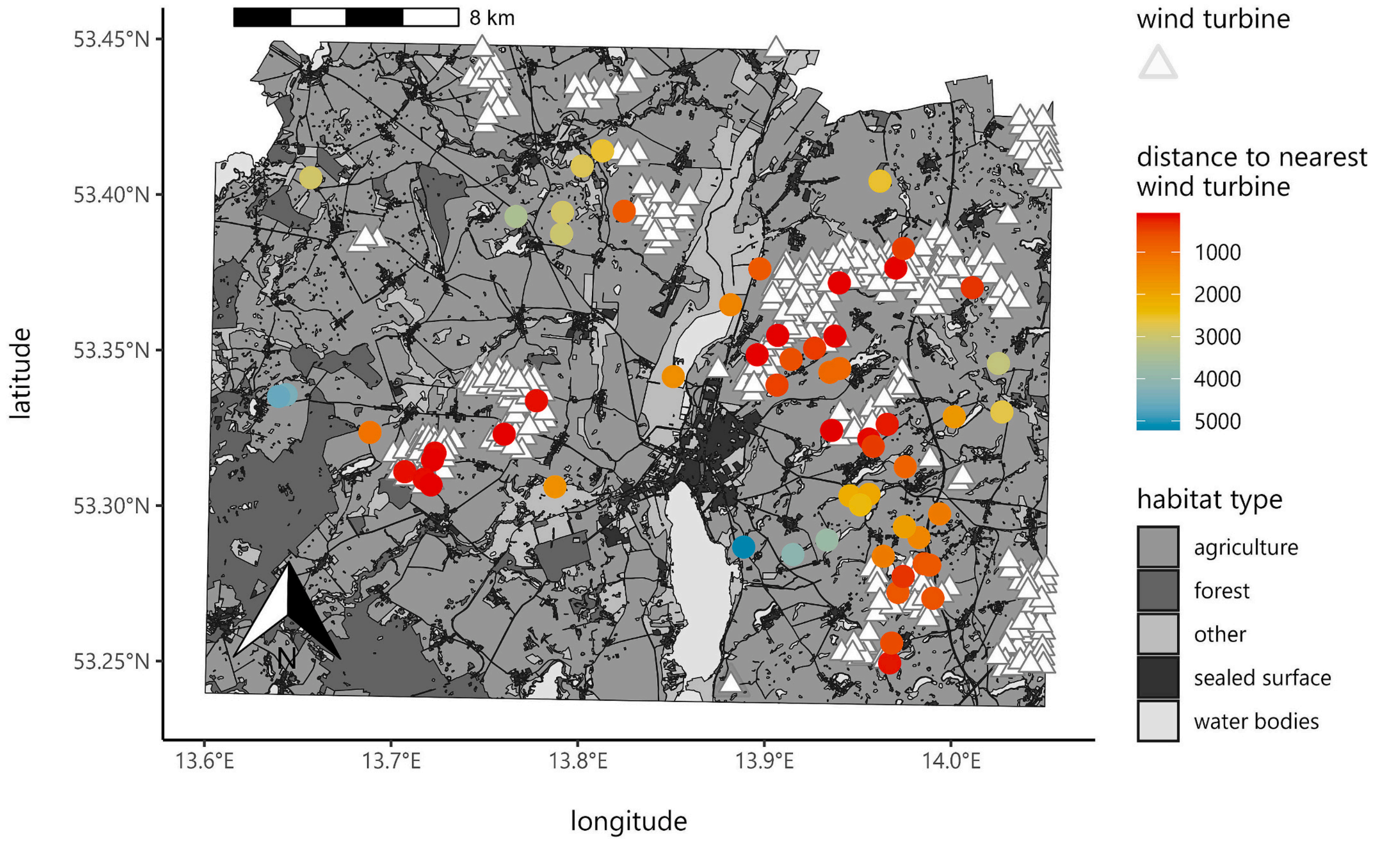

Fig. 1. Study area in the Quillow catchment area in northeastern Brandenburg, about 100 km north of Berlin. White triangles represent wind turbines and colored circles our sampling sites (red circles showing ponds close to wind turbines, blue circles those far away from wind turbines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

nearest wind turbines and pond sizes. In addition, we maintained a minimum distance of 1 km between focal ponds on a recording night to limit spatial and temporal autocorrelation.

We measured the acoustic activity of bats using automatic ultrasonic recorders (Batcorder 3.1, ecoObs, Nürnberg, Germany) attached to a metal pole at a height of 1–1.5 m and at a distance of about 5–10 m from the pond water surface. The following settings were used for recording Quality: 20, Threshold: −36 dB, Post-trigger: 400 ms, critical frequency: 14 kHz. The quality setting of 20 is optimal for discriminating bat calls, balancing sensitivity and the risk of missing calls, i.e. increasing the quality setting will capture more detailed sounds but may exclude some bat calls. The threshold setting affects the sensitivity of the recorder, i.e. for our purposes the sensitivity has been reduced from the default setting of −27 dB to −36 dB in order to maximise the recording distance. The post-trigger value, set at the recommended 400 ms, defines the maximum time interval between bat calls within a single recording file. If the interval between calls exceeds this value, a new recording file is initiated. The critical frequency, the minimum frequency that is automatically recorded, was set at 14 kHz to ensure that the low frequency calls of the bat genera *Nyctalus*, *Eptesicus* and *Vespertilio* were recorded.

2.3. Identification of bat species based on echolocation calls

All audio files were visualised as sonagrams using the BatExplorer software (Batlogger, version 2.1.11.2) and calls were manually analysed and assigned to one of the three functional guilds. In addition to general bat activity, we also counted the number of foraging calls in order to be able to analyse foraging activity separately at a later stage.

When analysing bat calls, we used minutes of activity as a unit rather than the total number of recorded echolocation calls to provide a more accurate and standardised measure of bat activity. We consider activity minutes to be more representative for estimating the activity of individual bats at a given study site, as individual bats usually forage for some time in a small habitat patch. By counting all recorded echolocation calls, the data collection is prone to pseudo-replication, as recordings from only one or a few bats were recorded. Counting activity minutes does not necessarily solve the problem of pseudo-replication, but it greatly reduces it. We therefore consider activity minutes to be a more reliable proxy for the activity of individual bats at a given recording site. We summed the active minutes per night (and therefore per site) for general and foraging activity (recordings including foraging calls). Therefore, these are not actual activity minutes, but minutes in which activity was recorded, i.e. at least 1 bat call per minute. As the detection probability of different bat guilds differs, we corrected the number of activity minutes for general and foraging activity per guild by a factor of 1, 1.875 and 0.44 for edge, narrow and open space foraging bats, respectively (Barataud, 2015).

2.4. Statistical analysis

We used the lme4 package (Bates et al., 2015) and the glmer function in R for a generalized linear mixed effects model (GLMM), with log as the link function, to test our prediction that bat activity at ponds decreases in proximity to wind turbines. We included foraging guild as an interaction and site as a random factor in our Poisson regression model, assuming that the response of bats depends on guild membership (number_of_active_minutes ∼ distance_to_nearest_windturbine*foraging_guild +1| site −1). By adding the "-1" we have omitted the intercept term. This results in exactly the same fit as without the '-1', but the interpretation of the parameter estimates is more straightforward. In particular, each estimate associated with foraging_guild directly gives the intercept for each bat guild, and each estimate associated with dist_nearest_wt_km:

foraging_guild directly gives the slope for each bat guild. Thus, our approach directly indicates which guild is affected by distance to wind turbines. We built one model for the general activity and a second for the foraging activity of bats at ponds. In our study, each site was measured only once, which minimises the possibility of temporal autocorrelation within sites. Also, in our study design, with a single measurement per site, the random factor for site captures the variability between sites, simplifying the model structure and analysis. We assumed that site as a random factor accounted for the variation in bat activity due to site-specific factors, implicitly accounting for spatial heterogeneity and thus increasing the robustness of our analysis of the relationship between bat activity and distance from wind turbines. The random factor also covers variability in, for example, distance to vegetation such as forest or wind turbine features, and therefore accounts for variability between sites. As we assigned records to foraging guilds for each site, we ended up with 177 observations (3 foraging guilds * 59 sites = 177 observations). We generated model estimates using the summary() function and incidence rate ratios (IRR), their confidence intervals (CIIRR) and *p*-values using the tab_model function of the sjPlot package (Lüdecke, 2024). The IRR is a measure used in count data models, such as Poisson regression, to express the effect of a predictor variable on the rate of occurrence of an event. It is the exponential form of the coefficient from the regression model and gives an intuitive interpretation of how the rate of the outcome changes with a unit increase in the predictor variable. An IRR of 1 indicates that the predictor variable has no effect on the incidence rate. An IRR >1 indicates a positive association between the predictor and the outcome rate, e.g. an IRR of 1.5 means that a one-unit increase in the predictor is associated with a 50 % increase in the incidence rate of the outcome. On the other hand, an IRR <1 indicates a negative association and, for example, a value of 0.75 means that a one-unit increase in the predictor is associated with a 25 % decrease in the incidence rate of the outcome. All statistical analyses were performed in R Studio using R version 4.4.0 (R core group, 2024).

3. Results

We recorded 8391 audio files of bat echolocation calls, of which 3056 were attributed to *Pipistrellus pipistrellus*, the most abundant species, followed by 1738 recordings attributed to *Pipistrellus pygmaeus* and 800 to *Pipistrellus nathusii*. The acoustic activity of bats of the genus *Pipistrellus* and 1 recording of *Barbastella barbastellus* were lumped into the guild of edge space foraging bats. We recorded 2264 records from bats of the genera *Nyctalus*, *Eptesicus* and *Vespertilio*, which we classified as bats of the open space foraging guild. Finally, 516 records were assigned to *Myotis* spp. and 16 to *Plecotus* spp., all of which were assigned to the narrow space foraging guild. The 8391 recordings resulted in 2956 total activity minutes and 352 foraging minutes for all 59 sites (corrected for detection probability).

The Poisson mixed model included site as a random factor (Table 1, top). The overall explanatory power of the model is 0.95 (conditional R^2), and the explanatory power of the fixed effects alone is 0.38 (marginal R^2). At the focal ponds, bats foraging in narrow and open spaces were less active than those foraging at edge structures. The distance between the focal ponds and the nearest wind turbine had no effect on the acoustic activity of edge space foraging bats (Fig. 2, Table 1). In contrast, the acoustic activity of narrow and open space foraging bats decreased significantly as the distance from the focal pond to the nearest wind turbine increased (Fig. 2, Table 1). Compared to the predicted activity of bats at a distance of 5 km to the wind turbines, the acoustic activity of open space foraging bats decreased by 53 % and that of narrow space foraging bats by 63 % at ponds close to wind turbines.

Model results for feeding activity were similar to those for total bat acoustic activity. The overall explanatory power of the feeding activity model (Table 1, bottom) was 0.77 (conditional R^2) and the explanatory power of the fixed effects alone was 0.23 (marginal R^2). Narrow and open space foraging bats foraged less than edge space foragers, and there was no significant effect of distance from the focal pond to the nearest wind turbine on the foraging activity of edge space foragers. However, open space foragers hunted significantly less close to wind turbines than far away (Fig. 2, Table 1, bottom). For narrow space foraging bats, we observed a trend towards reduced feeding activity at focal ponds close to wind turbines (Fig. 2, Table 1, bottom). Relative to the predicted activity of bats at a distance of 5 km to wind turbnies, the hunting activity of open space foraging bats decreased by 87 % and the feeding activity of narrow space foraging bats tended to decrease by 76 % at ponds near wind turbines.

Table 1

Model summary for the overall activity at ponds (top) and feeding activity (bottom). The intercept corresponds to the foraging guild "edge space foragers" and distance to nearest wind turbine was measured in kilometres. Estimates were obtained by the model summary, incidence rate ratios (IRR), Conficence Intervals (CI) and *p*-values were generated with the tab_model function of the sjPlot package in R (Lüdecke, 2024).

	Overall acoustic activity			
Predictors	*Estimate*	*IRR*	*CI_{IRR}*	*p*
dist nearest wind turbine	−0.06	0.94	0.76–1.18	0.610
foraging guild [edge]	3.12	22.55	15.56–32.70	<0.001
foraging guild [narrow]	1.53	4.60	3.12–6.77	<0.001
foraging guild [open]	0.93	2.53	1.69–3.80	<0.001
dist nearest wind turbine x foraging guild [narrow]	0.26	1.30	1.20–1.40	<0.001
dist nearest wind turbine x foraging guild [open]	0.21	1.23	1.12–1.36	<0.001
Random Effects				
σ^2	0.09			
$\tau_{00\ site}$	1.02			
ICC	0.92			
N_{site}	59			
Observations	177			
Marginal R^2 / Conditional R^2	0.380/ 0.948			

	Feeding activity			
Predictors	*Estimate*	*IRR*	*CI_{IRR}*	*p*
dist nearest wind turbine	0.03	1.03	0.70–1.53	0.882
foraging guild [edge]	0.14	1.15	0.56–2.34	0.703
foraging guild [narrow]	−2.30	0.10	0.04–0.24	<0.001
foraging guild [open]	−2.35	0.10	0.04–0.22	<0.001
dist nearest wind turbine x foraging guild [narrow]	0.26	1.29	0.98–1.71	0.074
dist nearest wind turbine x foraging guild [open]	0.39	1.47	1.14–1.89	0.003
Random Effects				
σ^2	1.10			
$\tau_{00\ site}$	2.61			
ICC	0.70			
N_{site}	59			
Observations	177			
Marginal R^2 / Conditional R^2	0.229/ 0.772			

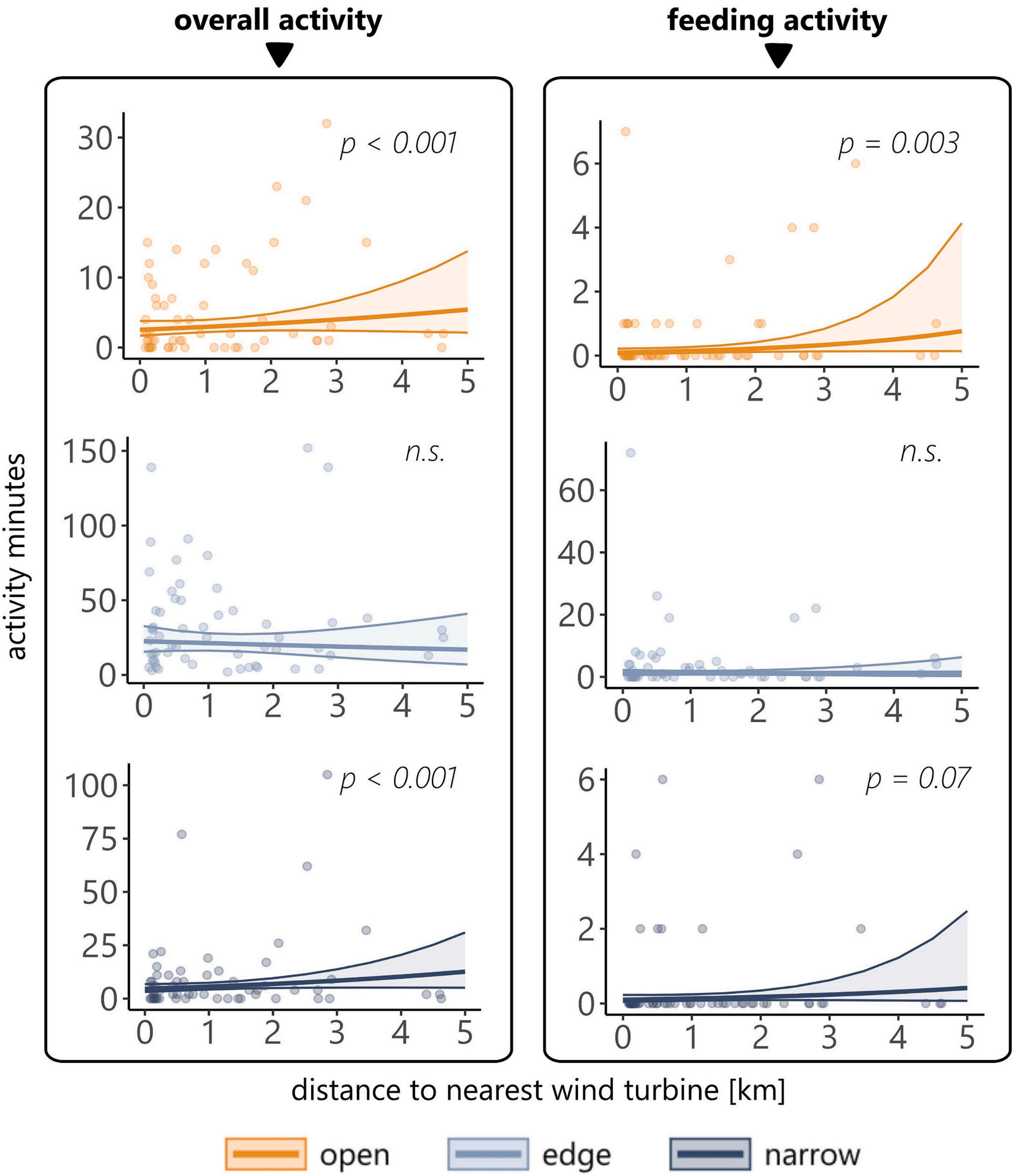

Fig. 2. Effect plots of the Generalized Linear Mixed-Effects Models (GLMM) for overall acoustic activity (left panels) and feeding activity (right panels) in minutes (with activity) per night at ponds in relation to wind turbine distance for open (orange; top row), edge (light blue, middle row) and narrow (dark blue, bottom row) space foraging bats. The plot illustrates the predicted values and confidence intervals based on the respective model using the "ggeffects" (Lüdecke, 2018) and "ggplot2" (Wickham, 2016) packages in R and the raw data. The random factor "site" is included to account for the variability at sampling locations. Significant effects can be observed for narrow and open space foragers in the overall acoustic activity model and for open space forages in the feeding model, indicating avoidance behaviour of bat towards wind turbines for species of different functional guilds. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

We investigated whether wind turbines displace bats from drinking sites during the critical lactation and weaning period of females in early summer. Our study was conducted in northeastern Germany, an area characterised by intensive agriculture, increasing drought (Zink et al., 2016, Boeing et al., 2021), a high density of wind turbines (FA Wind, 2023, Voigt et al., 2015), and high rates of bat mortality at wind turbines (Kruszynski et al., 2022; Voigt et al., 2022). At the same time, many small ponds are scattered across the landscape, providing drinking and foraging sites for local bats. We found that both general activity and hunting activity of narrow and open space foraging bats decreased with decreasing distance from wind turbines, even in highly attractive habitats such as drinking sites; however, we acknowledge a trend in hunting activity of narrow space foraging bats. Overall, our observations are consistent with the idea that bats avoid ponds in close proximity to wind turbines (see also Barré et al., 2018; Ellerbrok et al., 2022, 2024; Reusch et al., 2022, 2023). Previous studies in the same or nearby regions confirmed that bats of these two functional guilds are highly sensitive to the presence and operation of wind turbines (Roeleke et al., 2016; Ellerbrok et al., 2022, 2024; Reusch et al., 2022, 2023). Bat species of the edge space foraging guild may show a more variable response to wind turbine operation, firstly because they are attracted to edge-like landscape features such as hedgerows and vegetation at ponds (Ellerbrok et al., 2023), and secondly because their flight behaviour is altered by wake turbulence in the tailwind of turbines (Leroux et al., 2023). Thus, the lack of a displacement effect for edge space foraging bats may be due to the fact that opposing factors may cancel each other out, i.e., edge space foraging bats may be attracted by the physical structure of turbines, may alter their flight according to the prevailing wake turbulence in the tailwind of turbines, and may also be repelled by turbine-generated noise. This may result in more variable context-specific effects that are difficult to quantify.

Two potential causes of bat displacement, which are not mutually exclusive, are currently discussed in the literature. Both depend on the operation of wind turbines: Turbulence in the wake of wind turbines and turbine-generated noise (Teff-Seker et al., 2022; Tolvanen et al., 2023). In our study, we did not have access to the operating protocols of the local wind turbines and therefore cannot confirm or exclude that the operating mode played a role in the displacement of bats, as observed in a previous study (Ellerbrok et al., 2024). However, the mitigation measures commonly used in Germany do not rely on a complete shutdown at night during the summer months, but rather regulate the operation by turning the turbines on and off depending on suitable weather conditions, time of night and season (Ellerbrok et al., 2024). In general, wind turbines installed before 2010 also operate without curtailment measures (Voigt et al., 2022). We are therefore confident that the wind turbines in our study area were in operation, at least during part of the nights during our study period. Visual inspection in the field confirmed this assumption. Other studies have suggested that wake turbulence may alter the flight behaviour of bats near wind turbines, leading to reduced activity in the tailwind of turbines for some species (Leroux et al., 2023, 2024). Data on the presence of wake turbulences were not available in our study and we did not include wind direction in our model. Therefore, we cannot test for an effect of wake turbulence. Wake turbulence has been suggested to be more relevant for edge and open space foraging bats flying at medium to high altitudes (Leroux et al., 2023). Ellerbrok and colleagues documented that the mode of operation of turbines correlated with the avoidance response of narrow space foraging bats to wind turbines at forested sites (Ellerbrok et al., 2024). As the displacement of bats at forested sites was observed for bats foraging in dense vegetation, i.e. narrow space foraging bats, Ellerbrok and colleagues ruled out that wake turbulence played a role, and instead suggested that turbine-generated noise was relevant for displacement of narrow space foraging bats. We did not measure turbine noise in our study and therefore cannot confirm or refute the notion of noise-induced displacement of bats. Other factors, such as landscape features or turbine dimensions, may have contributed to the model (conditional R^2), but were controlled for by including site as a random factor. Both models yielded relatively high marginal R^2 values, indicating that distance from the wind turbine is a highly relevant factor in the model. A correlation matrix also suggests that landscape features such as distance to forest edge, pond size and others are not highly correlated with distance between ponds and wind turbines (electronic supplementary material: appendix 2d). In summary, we have documented reduced activity at ponds near wind turbines, independent of landscape features, suggesting that turbine-related factors play a central role in bat displacement.

In our study, we refrained from a species-specific approach due to the difficulty of identifying bat species with similar echolocation call characteristics from their echolocation calls (Russo and Voigt, 2016). We assumed that species of the same functional guild would respond similarly to wind turbines. As echolocation call features were similar between *Myotis* species specialised as narrow space foraging bats flying in forest interiors and *Myotis daubentonii*, a trawling bat, we may have increased the noise in our dataset if the response behaviour of these two functional guilds contrasted. *Myotis daubentonii* occurs regularly at our study site, but is more common at larger lakes than at ponds of the size we studied. Therefore, we assume that the erroneous inclusion of *M. daubentonii* in the guild response of space foraging bats may have little, if any, effect on the outcome of our analysis. We assume that the detection distance of ultrasonic detectors for open space and edge space foraging bats was greater than for narrow space foraging bats, as the detection distance decreases with increasing echolocation call frequency (Voigt et al., 2021). We attempted to account for this by including a correction factor following Barataud (2015), but we cannot be sure that this fully accounts for the sampling bias since detection distance also varies with flight direction relative to the ultrasonic microphone (Voigt et al., 2021).

5. Conclusions

We conclude from our results that the operation of wind turbines on farmland can contribute to a reduction in local bat diversity, not necessarily due to casualties at wind turbines, but rather due to displacement from wind turbines. This decline in the abundance of narrow and open space foraging bats near wind turbines is associated with a loss of their ecological function on farmland (Scholz and Voigt, 2022). Bats are known to provide ecosystem services by consuming insect pests (Kunz et al., 2011; Boyles et al., 2011; Williams-Guillén et al., 2016; Maslo et al., 2022; Russo et al., 2018). Therefore, displacement of bats over large areas around wind turbines may contribute to reduced crop production and the need for increased pesticide application to compensate. Displacement effects on wildlife caused by wind turbine operations may contribute to cryptic cascading trophic effects that have not been previously recognised (Thaker et al., 2018; Scholz and Voigt, 2022). Our results highlight the urgent need to consider the loss of critical habitats for vulnerable bats and other wildlife when planning wind turbines (Barré et al., 2018). We therefore argue that valuable bat habitats, such as ponds, should be considered at a distance of several kilometres from wind turbines when expanding wind energy production. Ignoring the need to protect critical bat habitats could jeopardise an environmentally friendly wind energy production.

CRediT authorship contribution statement

Carolin Scholz: Writing – review & editing, Visualization, Validation, Supervision, Methodology, Formal analysis, Data curation. **Hannah Klein:** Methodology, Investigation, Formal analysis, Data curation. **Christian C. Voigt:** Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding

Financial support was provided in part by Deutsche Forschungsgemeinschaft (DFG; Grant GRK 2118 Biomove (to CCV).

Declaration of competing interest

The authors declare no competing interest.

Acknowledgements

We gratefully acknowledge the ZALF research station for providing accommodation during the fieldwork. We extend our sincere thanks to the landowners and farmers of the Uckermark for their invaluable support and collaboration, which were crucial for the successful completion of this study. Thanks to the IZW R & Stats group for their insightful discussions on study design and the development of generalized linear mixed-effects models (GLMMs). We would like to thank Detlev Kelm for his careful revision of the draft manuscript and his suggestions. Special thanks Alexandre Courtiol, your expertise greatly enhanced the rigor and depth of our statistical analysis!

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.110968.

Data availability

Data and scripts are available at doi: 10.5281/zenodo.13684419

References

Adams, R.A., Hayes, M.A., 2021. The importance of water availability to bats: climate warming and increasing global aridity. In: Lim, B.K., et al. (Eds.), 50 years of bat research. Fascinating life sciences. Springer, Cham. https://doi.org/10.1007/978-3-030-54727-1_7.

Ancillotto, L., Bosso, L., Salinas-Ramos, V.B., Russo, D., 2019. The importance of ponds for the conservation of bats in urban landscapes. Landsc. Urban Plan. 190, 103607.

Arnett, E.B., Huso, M.M., Schirmacher, M.R., Hayes, J.P., 2011. Altering turbine speed reduces bat mortality at wind-energy facilities. Front. Ecol. Environ. 9 (4), 209–214.

Baidya Roy, S., Traiteur, J.J., 2010. Impacts of wind farms on surface air temperatures. Proc. Natl. Acad. Sci. 107 (42), 17899–17904.

Balotari-Chiebao, F., Santangeli, A., Piirainen, S., Byholm, P., 2023. Wind energy expansion and birds: identifying priority areas for impact avoidance at a national level. Biol. Conserv. 277, 109851.

Barataud, M., 2015. Acoustic Ecology of European Bats: Species Identification and Studies of their Habitats and Foraging Behaviour. University of Chicago Press, Chicago, Illinois, 352 pp. (cloth). ISBN: 987-2-85653-771-8.

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. Biol. Conserv. 226, 205–214.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Boeing, F., Rakovech, O., Kumar, R., Samaniego, L., Schrön, M., Hildebrandt, A., Rebmann, C., Thober, S., Müller, S., Zacharias, S., Bogena, H., Schneider, K., Kiese, R., Attinger, S., Marx, A., 2021. High-resolution drought simulations and comparison to soil moisture observations in Germany. Hydrol. Earth Syst. Sci. Discuss. 1–35.

Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. Science 332, 41–42.

Conkling, T.J., Vander Zanden, H.B., Allison, T.D., Diffendorfer, J.E., Dietsch, T.V., Duerr, A.E., Fesnock, A.L., Hernandez, R.R., Loss, S.R., Nelson, D.M., Sanzenbacher, P.M., 2022. Vulnerability of avian populations to renewable energy production. R. Soc. Open Sci. 9 (3), 211558.

Cook, B.I., Mankin, J.S., Anchukaitis, K.J., 2018. Climate change and drought: from past to future. Curr. Clim. Chang. Rep. 4, 164–179.

Denzinger, A., Schnitzler, H.U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Front. Physiol. 4, 164.

Diffendorfer, J.E., Vanderhoof, M.K., Ancona, Z.H., 2022. Wind turbine wakes can impact down-wind vegetation greenness. Environ. Res. Lett. 17 (10), 104025.

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. J. Appl. Ecol. 59 (10), 2497–2506.

Ellerbrok, J.S., Farwig, N., Peter, F., Rehling, F., Voigt, C.C., 2023. Forest gaps around wind turbines attract bat species with high collision risk. Biol. Conserv. 288, 110347.

Ellerbrok, J.S., Farwig, N., Peter, F., Voigt, C.C., 2024. Forest Bat Activity Declines with Increasing Wind Speed in Proximity of Operating Wind Turbines. Glob. Ecol. Cons. 49, e02782.

Feng, X., Li, S., Kalies, E.L., Markus, C., Harrell, P., Patiño-Echeverri, D., 2023. Low impact siting for wind power facilities in the Southeast United States. Wind Energy 26 (12), 1254–1275.

Frick, W.F., Baerwald, E.F., Pollock, J.F., Barclay, R.M., Szymanski, J.A., Weller, T.J., Russell, A.L., Loeb, S.C., Medellin, R.A., McGuire, L.P., 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. Biol. Conserv. 209, 172–177.

Gaultier, S.P., Lilley, T.M., Vesterinen, E.J., Brommer, J.E., 2023. The presence of wind turbines repels bats in boreal forests. Landsc. Urban Plan. 231, 104636.

Heim, O., Schröder, A., Eccard, J., Jung, K., Voigt, C.C., 2016. Seasonal activity patterns of European bats above intensively used farmland. Agric. Ecosyst. Environ. 233, 130–139.

Heim, O., Lorenz, L., Kramer-Schadt, S., Jung, K., Voigt, C.C., Eccard, J.A., 2017. Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields. Ecol. Process. 6, 1–15.

Global Wind Energy Council, 2023. Global Wind Report 2023. Global Wind Energy Council. https://gwec.net/globalwindreport2023.

Heim, O., Lenski, J., Schulze, J., Jung, K., Kramer-Schadt, S., Eccard, J.A., Voigt, C.C., 2018. The relevance of vegetation structures and small water bodies for bats foraging above farmland. Basic Appl. Ecol. 27, 9–19.

Huang, J., Zhang, G., Zhang, Y., Guan, X., Wei, Y., Guo, R., 2020. Global desertification vulnerability to climate change and human activities. Land Degrad. Dev. 31 (11), 1380–1391.

Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., Jacobs, D., 2016. Bats and water: Anthropogenic alterations threaten global bat populations. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropo- Cene: Conservation of Bats in a Changing World. Springer, Heidelberg-Cham, pp. 215–241.

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. Ecol. Appl. 32 (2), e2513.

Kukka, P.M., Miller, H.A., Thomas, J.P., Schmiegelow, F.K., Jung, T.S., 2024. The best watering hole in town: characteristics of ponds used by an endangered bat in an urbanizing boreal landscape. Glob. Ecol. Conserv. 51, e02933.

Kunz, T.H., de Torrez, E.B., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. Ann. N. Y. Acad. Sci. 1223 (1), 1–38.

Leroux, C., Le Viol, I., Valet, N., Kerbiriou, C., Barré, K., 2023. Disentangling mechanisms responsible for wind energy effects on European bats. J. Environ. Manag. 346, 118987.

Leddy, K.L., Higgins, K.F., Naugle, D.E., 1999. Effects of wind turbines on upland nesting birds in Conservation Reserve Program grasslands. The Wilson Bulletin, pp. 100–104.

Leroux, C., Barré, K., Valet, N., Kerbiriou, C., Le Viol, I., 2024. Distribution of common pipistrelle (*Pipistrellus pipistrellus*) activity is altered by airflow disruption generated by wind turbines. PLOS ONE 19 (5), e0303368.

Lüdecke, D., 2018. Ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3 (26), 772. https://doi.org/10.21105/joss.00772.

Lüdecke, D., 2024. sjPlot: data visualization for statistics in social science. R package version, 2 (8), 16.

Maslo, B., Mau, R.L., Kerwin, K., McDonough, R., McHale, E., Foster, J.T., 2022. Bats provide a critical ecosystem service by consuming a large diversity of agricultural pest insects. Agric. Ecosyst. Environ. 324, 107722.

May, R.F., Hamre, Ø., Vang, R., Nygård, T., 2012. Evaluation of the DTBird Video-System at the Smøla Wind-Power Plant. In: Detection capabilities for capturing near-turbine avian behaviour. NINA rapport.

McKay, R.A., Johns, S.E., Bischof, R., Mathews, F., van der Kooij, J., Yoh, N., Eldegard, K., 2024. Wind Energy Development Can Lead to Guild-Specific Habitat Loss in Boreal Forest Bats. Wildl. Biol. 2, e01168.

Millon, L., Colin, C., Brescia, F., Kerbiriou, C., 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. Ecol. Eng. 112, 51–54.

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.

Niebuhr, B.B., Sant'Ana, D., Panzacchi, M., van Moorter, B., Sandström, P., Morato, R.G., Skarin, A., 2022. Renewable energy infrastructure impacts biodiversity beyond the area it occupies. Proc. Natl. Acad. Sci. 119 (48), e2208815119.

Pérez-García, J.M., Morant, J., Arrondo, E., Sebastián-González, E., Lambertucci, S.A., Santangeli, A., Serrano, D., 2022. Priority areas for conservation alone are not a good proxy for predicting the impact of renewable energy expansion. Proceedings of the National Academy of Sciences 119 (33), e2204505119.

Pylant, C.L., Nelson, D.M., Fitzpatrick, M.C., Gates, J.E., Keller, S.R., 2016. Geographic origins and population genetics of bats killed at wind-energy facilities. Ecol. Appl. 26 (5), 1381–1395.

R Core Team, 2024. R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reusch, C., Lozar, M., Kramer-Schadt, S., Voigt, C.C., 2022. Coastal onshore wind turbines lead to habitat loss for bats in northern Germany. J. Environ. Manag. 310. https://doi.org/10.1016/j.jenvman.2022.114715.

Reusch, C., Paul, A.A., Fritze, M., Kramer-Schadt, S., Voigt, C.C., 2023. Wind turbines in forests conflict with habitat use of tree-dwelling bats. Curr. Biol. https://doi.org/10.1015/j.cub.2022.12.050.

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. Sci. Rep. 6 (1), 1–9.

Roeleke, M., Teige, T., Hoffmeister, U., Klingler, F., Voigt, C.C., 2018. Aerial-hawking bats adjust their use of space to the lunar cycle. Mov. Ecol. 6, 1–10.

Russo, D., Voigt, C.C., 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: A cautionary note for a sound analysis. Ecol. Indic. 66, 598–602.

Russo, D., Bosso, L., Ancillotto, L., 2018. Novel perspectives on bat insectivory highlight the value of this ecosystem service in farmland: research frontiers and management implications. Agric. Ecosyst. Environ. 266, 31–38.

Scholz, C., Voigt, C.C., 2022. Diet analysis of bats killed at wind turbines suggests large-scale losses of trophic interactions. Cons. Sci. Pract. 4 (7), e12744.

Scholz, C., Ittermann, L., Brunkow, N., Voigt, C.C., 2023. Fehlende Betriebssteuerungen an alten Windenergieanlagen können hohe Schlagopferzahlen bei Fledermäusen verursachen. Nat. Lands. 55 (08), 28–33.

Smeraldo, S., Bosso, L., Fraissinet, M., Bordignon, L., Brunelli, M., Ancillotto, L., Russo, D., 2020. Modelling risks posed by wind turbines and power lines to soaring birds: the black stork (*Ciconia nigra*) in Italy as a case study. Biodivers. Conserv. 29, 1959–1976.

Stevens, T.K., Hale, A.M., Karsten, K.B., Bennett, V.J., 2013. An analysis of displacement from wind turbines in a wintering grassland bird community. Biodiversity and Conservation 22, 1755–1767.

Teff-Seker, Y., Berger-Tal, O., Lehnardt, Y., Teschner, N., 2022. Noise pollution from wind turbines and its effects on wildlife: A cross-national analysis of current policies and planning regulations. Renew. Sust. Energ. Rev. 168, 112801.

Tesfahunegny, W., Datiko, D., Wale, M., Hailay, G.E., Hunduma, T., 2020. Impact of wind energy development on birds and bats: the case of Adama wind farm, Central Ethiopia. J. Basic Appl. Zool. 81, 1–9.

Thaker, M., Zambre, A., Bhosale, H., 2018. Wind farms have cascading impacts on ecosystems across trophic levels. Nat. Ecol. Evol. 2 (12), 1854–1858.

Thaxter, C.B., Buchanan, G.M., Carr, J., Butchart, S.H., Newbold, T., Green, R.E., 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.

Tolvanen, A., Routavaara, H., Jokikokko, M., Rana, P., 2023. How far are birds, bats, and terrestrial mammals displaced from onshore wind power development? A systematic review. Biol. Conserv. 288, 110382.

Vander Zanden, H.B., Nelson, D.M., Conkling, T.J., Allison, T.D., Diffendorfer, J.E., Dietsch, T.V., Fesnock, A.L., Loss, S.R., Ortiz, P.A., Paulman, R., Rogers, K.H., 2024. The Geographic Extent of Bird Populations Affected by Renewable-Energy Development. Conserv. Biol. e14191.

Voigt, C.C., Popa-Lisseanu, A.G., Niermann, I., Kramer-Schadt, S., 2012. The catchment area of wind farms for European bats: a plea for international regulations. Biol. Conserv. 153, 80–86.

Voigt, C.C., Lehnert, L.S., Petersons, G., Adorf, F., Bach, L., 2015. Wildlife and renewable energy: German politics cross migratory bats. Eur. J. Wildl. Res. 61, 213–219.

Voigt, C.C., Russo, D., Runkel, V., Goerlitz, H.R., 2021. Limitations of acoustic monitoring at wind turbines to evaluate fatality risk of bats. Mammal Rev. 51 (4), 559–570.

Voigt, C.C., Kaiser, K., Look, S., Scharnweber, K., Scholz, C., 2022. Wind turbines without curtailment produce large numbers of bat fatalities throughout their lifetime: A call against ignorance and neglect. Glob. Ecol. Cons. 37, e02149.

Voigt, C.C., Bernard, E., Huang, J.C.C., Frick, W.F., Kerbiriou, C., MacEwan, K., Mathews, F., Rodriguez-Duran, A., Scholz, C., Webala, P.W., Welbergen, J., Whitby, M., 2024. Toward solving the global green–green dilemma between wind energy production and bat conservation. BioScience 74 (4), 240–252.

Wang, G., Li, G.Q., Liu, Z., 2023. Wind farms dry surface soil in temporal and spatial variation. Sci. Total Environ. 857, 159293.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wie, T., Simko, V., 2021. R Package 'corrplot': Visualization of a Correlation Matrix (Version 0.92).

Williams-Guillén, K., Olimpi, E., Maas, B., Taylor, P.J., Arlettaz, R., 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of Chiroptera and their ecosystem services in agricultural landscapes. In: Bats in the Anthropocene: Conservation of bats in a changing world. Springer, Cham, pp. 151–186.

FA Wind, 2023. Entwicklung der Windenergie im Wald. Fachagentur Windenergie an Land, Berlin. Eingesehen am 18.01.2024 unter: https://www.fachagentur-windenergie.de/ fileadmin/files/Windenergie_im_Wald/FA-Wind_Analyse_Wind_im_Wald_8Auflage_2023.pdf.

Zhou, L., Tian, Y., Baidya Roy, S., Thorncroft, C., Bosart, L.F., Hu, Y., 2012. Impacts of wind farms on land surface temperature. Nat. Clim. Chang. 2 (7), 539–543.

Zink, M., Samaniego, L., Kumar, R., Thober, S., Mai, J., Schäfer, D., Marx, A., 2016. The German drought monitor. Environ. Res. Lett. 11 (7), 074002.