



Research article

Disentangling mechanisms responsible for wind energy effects on European bats

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ARTICLE INFO

Handling Editor: Lixiao Zhang

Keywords:

Chiroptera

Passive acoustic monitoring

Wind turbine configuration

Wind turbine operation

Wind turbine size

Wake effect

ABSTRACT

Mitigating anthropogenic climate change involves deployments of renewable energy worldwide, including wind energy, which can cause significant impacts on flying animals. Bats have highly contrasted responses to wind turbines (WT), either through attraction increasing collision risks, or avoidance leading to habitat losses. However, the underlying mechanisms remain largely unknown despite the expected rapid evolution of WT size and densities. Here, using an extensive acoustic sampling (i.e. 361 sites-nights) up to 1483 m from WT at regional scale, we disentangle the effects of WT size (ground clearance and rotor diameter), configuration (density and distance), and operation (blade rotation speed and wake effect) on hedgerow use by 8 bat species/groups and one vertical community distribution index. Our results reveal that all WT parameters affected bat activity and their vertical distribution. Especially, we show that the relative activity of high-flying species in the community was lower for higher WT density and lower ground clearance. Medium-flying species were sensitive to wind turbine distance, with either attraction or avoidance depending on proximity to the wake area and wind conditions. Specifically, wind turbine distance, wake effect and their interaction each affected the activity of one, three, and three species out of eight, respectively. Blade rotation and rotor diameter affected the activity of four and three species/groups, respectively, and ground clearance affected the activity of five ones. Taken together, WT configuration, operation, and size parameters affected the activity of three, five, and seven out of eight species/groups, respectively. These results call for the consideration of all these factors when assessing the ecological sustainability of future wind farms. The study especially advocates to avoid high WT densities, large rotors, and to site WT as far as possible from optimal habitats such as woody edges and not between them and the source of prevailing winds, in order to limit bats-WT interactions.

1. Introduction

The world is facing an unprecedented biodiversity crisis (Ceballos et al., 2015; Pimm et al., 2014). Regardless of biodiversity metrics used, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and non-governmental organizations such as the International Union for Conservation of Nature (IUCN) and World Wide Fund for Nature (WWF) agreed to place the habitat loss and degradation as the main driver of biodiversity losses (Bellard et al., 2022). Furthermore, climate change and biodiversity loss have been shown to be interdependent (Pettorelli et al., 2021) and as such halting

these crises, often tackled separately, should form part of a global strategy. However, objectives and action levers underlying each crisis may be conflicting. For example, the transition from fossil to renewable energies has been identified as one of the main levers to reduce greenhouse gas emissions (Shukla et al., 2022), but it also negatively impacts biodiversity (Gibson et al., 2017; Pörtner et al., 2021). In particular, renewable energies can generate direct or indirect habitat losses (i.e., functional losses). While all infrastructures for energy production inevitably impact the habitat on which they are installed, wind energy has the particularity to also impact the surrounding aerosphere, that is used by most flying taxa. Indeed, wind turbines (WT) generate massive

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airflow disturbances (i.e., increased turbulences and decreased wind speed) up to a few kilometers on the leeward side (downwind) when blades are spinning (so-called wake effect) (Porté-Agel et al., 2019), as well as antagonist behavioral responses within and between species (Dai et al., 2015; Gibson et al., 2017).

Specifically, WT can alter habitat use by birds and bats, either by generating attraction (Richardson et al., 2021; Shaffer and Buhl, 2015) or avoidance (Barré et al., 2018; Gómez-Catasús et al., 2018) responses. Attraction may increase fatality risk at turbines (Cryan and Barclay, 2009) which can threaten populations viability of various species (e.g., Duriez et al., 2022; Frick et al., 2017), while WT avoidance can include disturbance of migrating and commuting routes as well as functional losses of foraging habitats and roosts at a landscape scale (Roscioni et al., 2014). To limit collision risks, WTs can be curtailed when bats are the most active (i.e., at favorable weather conditions and time). Another way to limit both collision risks and habitat losses is to avoid siting WTs too close to optimal habitats for airborne biodiversity, such as migration routes, breeding, foraging, and wintering habitats (Rodrigues et al., 2015). However, in most situations none of these measures led to completely satisfying results: (i) most current WT curtailment schemes have incomplete effectiveness (Adams et al., 2021; Whitby et al., 2021), and (ii) scarce available guidelines for siting WTs far from optimal habitats, such as EUROBATS/UNEP guidelines for bats (Rodrigues et al., 2015), are little considered in WT planning (Barré et al., 2022). In addition, these guidelines only focused on fatality risks at the turbine scale and do not explicitly consider impacts at larger scales such as avoidance and resulting functional losses of foraging and commuting habitat.

These observations underline the need to establish new and complementary mitigation measures to limit impacts. For these measures to be effective, it is crucial to better understand which mechanisms underly avoidance and attraction responses of airborne biodiversity to WTs. Yet, these mechanisms are still poorly known especially for bats for which evidences of non-consensual responses to WTs have been increasingly reported recently (Barré et al., 2018; Ellerbrok et al., 2022; Richardson et al., 2021). This lack of consensus could be explained by context-dependent responses and sampling design differences between studies making the disentanglement of mechanisms nearly impossible. Another obstacle is that some factors related to WT operation and size have been largely overlooked or unstudied. Only one study showed that bats avoided small WTs only when they were operating (Minderman et al., 2012), highlighting the importance to investigate blade rotation related mechanisms. However, no study has so far assessed the effect of airflow disturbances on bat activity due to the wake effect generated by spinning blades, even though bats seem to approach the nacelle preferentially from the side sheltered from the wind (Cryan et al., 2014). Furthermore, there is little evidence for the role of WT size on bat habitat use. Larger rotors seem to increase avoidance by narrow-space foragers (*Myotis* and *Plecotus* spp.) (Ellerbrok et al., 2022), and to foster open-space foragers presence (*Nyctalus noctula*) (Reusch et al., 2022), while ground clearance remains unstudied. Finally, all these parameters have never been studied simultaneously.

In this study, we aim to disentangle the effects of WT size (rotor diameter and ground clearance), operation (blade rotation speed and wake effect), and configuration (WT density and distance) on the activity of eight bat species and groups and on the vertical distribution of the community which informs on collision susceptibility (Roemer et al., 2017). To do that we recorded bat activity using an extensive passive acoustic monitoring on one habitat (hedgerows) and on a short period (June) to avoid variability in bat responses due to the habitat (Leroux et al., 2022) or season (Ellerbrok et al., 2022), at 154 independent sites selected along a gradient of distance to WTs. We expected bat responses to WT features to be species-specific and especially related to their specific use of the aerosphere (Table 1). Firstly, we expected that the more species have a flight height overlapping the rotor swept area (e.g., *Pipistrellus* spp. and *Nyctalus* spp.), the more likely they are to be exposed

Table 1

Definition of explanatory variables included in the study and expected bat responses from scientific literature and/or expert opinion.

Explanatory variables	Definition	Expected bat responses based on available literature or expert opinion	References
Configurational variables			
Wind turbine density	Number of wind turbines in a 1500m buffer.	Negative, especially in windy conditions and for high-flying species.	/
Wind turbine distance	Distance to the nearest wind turbine in meters.	Positive (avoidance) for: <i>Myotis</i> spp. ⁽¹⁻³⁾ , <i>B. barbastellus</i> ⁽²⁾ , <i>Plecotus</i> spp. ^(2,4) and <i>E. nilssonii</i> ⁽³⁾ Negative (attraction) or positive (avoidance) for: <i>Nyctalus</i> spp. ^(1,2,4-6) and <i>P. pipistrellus</i> ^(2,4,7,8) .	⁽¹⁾ Ellerbrok et al. (2022); ⁽²⁾ Barré et al. (2018); ⁽³⁾ Gauthier et al. (2023); ⁽⁴⁾ Leroux et al. (2022); ⁽⁵⁾ Reusch et al. (2022); ⁽⁶⁾ Roeleke et al. (2016); ⁽⁷⁾ Richardson et al. (2021); ⁽⁸⁾ Minderman et al. (2016)
Operation variables			
Wind incidence angle	Angle between the line from the sampling site to the nearest wind turbine and the prevailing wind direction on the sampled night ([0–180°]).	Negative, especially in windy conditions and for medium- and high-flying species.	/
Wind incidence angle: Wind turbine distance	Interaction between the distance to the nearest wind turbine and the wind incidence angle.	Negative: avoidance of the stronger wake near the turbine.	/
Average blade rotation speed	Average blade rotation speed per night in km/h.	Negative ⁽⁹⁾ .	⁽⁹⁾ Minderman et al. (2012)
Size variables			
Ground clearance	Minimal height between the ground and the tip of a blade of the nearest wind turbine in meters.	Positive, especially for medium-flying species.	/
Rotor diameter	Rotor diameter of the nearest wind turbine in meters.	Negative for <i>Myotis</i> spp. ⁽¹⁾ and positive for <i>N. noctula</i> ⁽⁵⁾ .	⁽¹⁾ Ellerbrok et al. (2022); ⁽⁵⁾ Reusch et al. (2022)

to the wake effect and thus to be affected by both wind angle and blade rotation speed. Secondly, we expected high flying species (e.g., *Nyctalus* spp.) to be more likely to fly above wind farms and thus to be more sensitive to WT density than more local measures of WT effect such as the distance to the closest turbine. Besides, we expected that wind conditions would mediate the effects of WTs on bat activity. More specifically, we expected bat activity to be negatively affected by WTs features in windy conditions while attraction responses would be more likely to occur for braked or low rotating blades.

2. Material and methods

The objective of the study was to assess which wind turbine (WT) parameters affected bat activity in order to find relevant action levers to

mitigate WT impacts depending on the species. We assessed through Generalized Linear Mixed Models (GLMMs) bat responses to WT size (ground clearance and rotor diameter), configuration (density and distance), and operation (blade rotation speed and wake effect through the wind incidence angle) by analyzing variations in bat activity, while accounting for landscape and weather covariates and avoiding any collinearity issues. Bat activity was recorded using passive acoustic monitoring along gradients of distance to wind turbines and circular azimuth of wind incidence angle used as a proxy for the proximity to the wake area (Fig. 1). We ensured sufficient variations in all studied WT parameters, while minimizing landscape (i.e. distance to water bodies and forests) and weather (i.e. temperature and rain) covariate gradients as far as possible to limit their influence on the WT parameters results. These method points are developed in the sections below.

2.1. Study site and experimental design

We sampled bat activity at 154 independent sites in Western France, across five counties (Finistère, Côtes-d'Armor, Morbihan, Loire-Atlantique and Maine-et-Loire) that represented around 2145 MW of electricity production in 2022, i.e. 11% of the national wind energy production. Six to 16 sites were sampled per night (12.0 ± 4.0), at 20 wind farms (Fig. S1). Each farm included four to 11 WTs, among which we sampled one to six ones at each wind farm (3 ± 3). All sampled sites related to one wind farm were sampled the same night, during one to four consecutive nights (2.3 ± 1.0), resulting in 361 sites-nights. In total, 67 independent WTs were sampled. The sampling was conducted from 27 May to June 30, 2020, during the reproduction period, when adult bats are active but not or very few juveniles, thus avoiding to mix potentially different behaviors. The study area was dominated by farmland and high hedgerow density. Given that habitat can be a great source of variation in bat response to WTs (Leroux et al., 2022), we only sampled bat activity at hedgerows defined as linear landscape features of at least 2 m height including shrubs and/or trees. Hedgerows are a commuting and foraging habitat of major importance for bats (Boughhey et al., 2011; Lacoeuilhe et al., 2016).

To test the influence of WT density and distance on bat activity, we selected the sampling sites along a gradient of WT number in a 1500m buffer (4 ± 2 ; min: 1; max: 11) and a gradient of distance to WTs (604.1 ± 427.0 m; min: 23.2; max: 1484.0). The distance gradient range was chosen in line with a previous study which detected WT avoidance by bats up to at least 1000m (Barré et al., 2018).

To test the effect of WT operation, we sampled each site on several consecutive nights to obtain variation in wind speed and wind direction. Additionally, sampled sites were located on a circular azimuth gradient

of wind incidence angle, defined as the angle between the line from the sampling site to the nearest WT and the prevailing wind direction on the sampled night (Fig. 1). This angle ranges from 0° for a site located windward – upwind – the turbine, to 180° for a site located leeward – downwind – the turbine. This design resulted in wide gradients of average wind speed (5.57 ± 4.19 km/h; min: 0.20; max: 15.40; Fig. S2) and wind gusts (12.99 ± 7.42 km/h; min: 1.7; max: 30.4; Fig. S3), average blade rotation speed (162.46 ± 57.55 km/h; min: 0; max: 267.71; Fig. S4) and prevailing wind incidence angle ($84.16 \pm 54.50^\circ$; min: 0.16; max: 179.24) during the night. Importantly, these gradients were not correlated allowing to test them simultaneously in the modelling (Table S1; Fig. S5).

Finally, wind farms also varied in turbine size: the sampled WTs were on average 92 m in hub height (± 12 m; min: 66 m; max: 113 m), 86 m in rotor diameter (± 11 m; min: 70 m; max: 114 m) and 50 m in ground clearance (± 11 m; min: 30 m; max: 72 m) which is the minimum distance between the tip of the blade and the ground (i.e. when the blade is in a vertical position and below the rotor; Fig. 1).

2.2. Acoustic sampling, species identification and metrics

We recorded bat activity from 30 min before sunset until 30 min after sunrise with SM4BAT-FS bat detectors (Wildlife Acoustics Inc., Concord, MA, USA) coupled with one SMM-U2 ultrasonic microphone. Microphones were placed at hedgerows 1.70 m above the ground, inclined at 45° and oriented towards the open habitat. Recording was triggered by all sound events with a minimum of 6 dB Signal Noise Ratio between eight and 192 kHz, and set to continue recording until 2 s after last trigger event.

We defined bat activity as the number of bat passes per species during a full night. A bat pass was defined as one or more echolocation calls within a 5-s interval (Kerbiou et al., 2019). We used TADARIDA software (Bas et al., 2017) to automatically assign a bat species to each bat pass. We conducted the analysis on sounds assigned with a tolerance threshold of error risk ≤ 0.5 , and we checked that the results did not change for a threshold ≤ 0.1 to ensure the robustness of the results. This last threshold would reduce false positives at the cost of discarding more true positives, compared to the 0.5 threshold which discards less false positives (Barré et al., 2019). We conducted the analysis on the activity of three species groups difficult to acoustically distinguish from each other (*Nyctalus* spp., *Myotis* spp., *Plecotus* spp.) and five species (*Pipistrellus pipistrellus*, *Pipistrellus nathusii*, *Pipistrellus kuhlii*, *Eptesicus serotinus* and *Barbastella barbastellus*). We defined three classes of species or species groups depending on the ratio of time spent at blade height: the low-flying species as the group of *B. barbastellus*, *Myotis* spp. and *Plecotus*

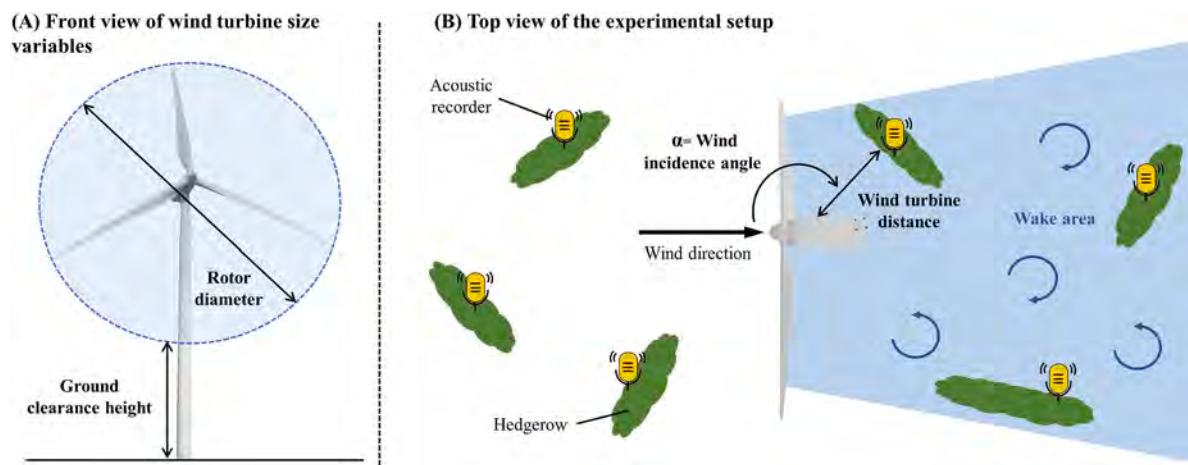


Fig. 1. Definition of wind turbine size variables (A), and a schematic top view of the experimental setup showing bat recorders placement during a night and theoretical spatial extent of the wake effect downwind the turbine (B).

spp. (ratio <0.01), the medium-flying species as the group of *P. pipistrellus*, *P. nathusii*, *P. kuhlii* and *E. serotinus* (0.01 < ratio <0.4) and the high-flying species as the *Nyctalus* spp. (ratio >0.4) (Table S2; Roemer et al., 2017).

Since bat responses to WT features may vary depending on whether they are flying at blade height (Table 1), we also built a mean community trait index based on the time spent at blade height (i.e. above the ground clearance). This index of Community Sensitivity to WT (CSWT) built as follows (1):

$$CSWT_j = \frac{\sum_{i=1}^n \alpha_{ij} (T_i)}{\sum_{i=1}^n \alpha_{ij}} \quad (1)$$

where n is the number of species, α_{ij} the corrected abundance of the species i for a sampled night-site j (i.e. the abundance of the species i for a sampled night-site j divided by the maximum abundance of the species i in all sampled night-site), and T_i the ratio of time spent at blade height for the species i extracted from Roemer et al. (2017) (i.e. ratios of flight activity computed above heights of 20–45 m high). The higher the index, the higher the relative abundance of high-flying species in the community.

2.3. Wind turbines and environmental variables

Maps of the WTs were extracted from the Geobretagne and sigloire catalogs (2020) and WT density was computed for a 1500 m buffer to be consistent with the sampled gradient of distance to WT. The blade rotation speed was provided by wind farm operators and averaged on each night scale. WT size was also provided by wind farm operators.

We collected environmental variables (i.e. weather and landscape variables) known to strongly influence bat activity: (i) mean wind speed and temperature of the night (Erickson and West, 2002; Wellig et al., 2018), from meteociel database (www.meteociel.fr) at a 1-h temporal resolution, (ii) distance to the nearest forest (Froidevaux et al., 2021) from the CES OSO (<http://osr-cesbio.ups-tlse.fr/oso/>, 2019, 10 m resolution), (iii) and distance to the nearest water body (Walsh and Harris, 1996) from the French hydrographic reference map BD Topage (<https://geo.data.gouv.fr/fr/datasets/237d2617f3377a6b74187a17adc83ee948619b9e>, 2019).

Acoustic monitoring was carried out under weather conditions favorable to bats: the average temperature of the night was 14.4 ± 2.7 °C and 90% of sampled sites-nights had no or negligible rain (i.e. less than 1 mm in average over the night). Distance between sites to the nearest forest and water body was in average 336.8 ± 228.5 m and 287.0 ± 189.3 m, respectively.

2.4. Statistical analysis

As our aim was to assess whether a count variable (bat activity) varied depending on various explanatory variables while accounting for the nested structure of the sampling design, we modeled the relative effects of WT features (Table 1) on bat activity using Generalized Linear Mixed Models (GLMMs; R package glmmTMB). For each species or species groups, we used either a quasipoisson (nbinom1) or a negative binomial distribution (nbinom2), applying a zero-inflation correction when necessary (Table S3). We checked the model assumptions on residuals using the package DHARMA (Table S3). Regarding the CSWT, we used a gaussian distribution after applying an Ordered Quantile transformation using the R bestNormalize function.

For each response variable (eight species or species groups and the CSWT), we constructed a full model containing the WT distance and density, the rotor diameter, the ground clearance height, the wind incidence angle and the mean blade rotation speed, as well as weather and landscape variables known to influence bat activity mentioned in

the “Wind turbines and environmental variables” section. We also added an interaction between the distance to WT and the wind incidence angle as we expected the wake effect to affect differently bat activity near and far from the turbine. Finally, we included two random effects on the night and the site to control for inter-nights and inter-site variations. All distance variables (distance to WT, forest, and water body) were log-transformed as we expect bat activity to vary in a logarithmic way with these distances (Barré et al., 2018; Kelm et al., 2014; Santos et al., 2013). All variables were centered and scaled to improve model convergence. Although not strictly correlated (Spearman's Rank correlation coefficient < |0.7|), WT distance and density as well as rotor diameter and ground clearance height are likely to provide redundant information. We therefore constructed four different models for each response variable to avoid including redundant variables: (2, 3) two including WT distance and either rotor diameter or ground clearance, and (4, 5) two including WT density and either rotor diameter or ground clearance, as follows.

- (2) Response variable ~ WT distance*wind incidence angle + Rotor diameter + blade rotation speed + mean wind speed + mean temperature + distance to the nearest forest + distance to the nearest water body + (1|night) + (1|site).
- (3) Response variable ~ WT distance*wind incidence angle + Ground clearance + blade rotation speed + mean wind speed + mean temperature + distance to the nearest forest + distance to the nearest water body + (1|night) + (1|site).
- (4) Response variable ~ WT density + wind incidence angle + Rotor diameter + blade rotation speed + mean wind speed + mean temperature + distance to the nearest forest + distance to the nearest water body + (1|night) + (1|site).
- (5) Response variable ~ WT density + wind incidence angle + Ground clearance + blade rotation speed + mean wind speed + mean temperature + distance to the nearest forest + distance to the nearest water body + (1|night) + (1|site).

As we expected wind speed to drive bat activity and to trigger WT effects on bats, we split our dataset based on the median of average wind speed (4.7 km/h) to obtain two balanced sub-datasets (see Table S4 for more details), hereafter named “low wind speed dataset” and “high wind speed dataset”, on which models presented above were performed. In total, we thus ran four full models for low wind conditions and four full models for windy conditions for each response variable, ensured that all variables included in a model were not correlated (Table S1) and that the variance inflation factor (VIF) of the variables included in the models was always <2 (*check_collinearity* function, r package performance; Table S3), showing no collinearity issues (Zuur et al., 2010).

3. Results

3.1. Bat survey

In total, we detected 455,487 bat passes. Most bat passes were assigned to *P. pipistrellus* and *P. kuhlii* (65% and 30%, respectively) which were detected in 100% and 95% of the sampled site-night, respectively (Table S4). Other species represented less than 2% of the total number of bat passes. All studied bat species (*P. pipistrellus*, *P. nathusii*, *P. kuhlii*, *E. serotinus* and *B. barbastellus*) or groups (*Nyctalus* spp., *Myotis* spp., *Plecotus* spp.) were detected in at least 40% of the sampled nights-sites (Table S4).

3.2. Effects of wind turbine density and distance

We found that increasing wind turbine (WT) density negatively affected the index of Community Sensitivity to WT (CSWT). Regardless of the model (i.e., including either rotor diameter or ground clearance covariate) and the wind conditions, *Nyctalus* spp. activity (i.e., species

spending the most time at height among the studied species) was negatively affected by WT density in a 1500 m buffer. In contrast, *B. barbastellus* and *P. nathusii* activity tended to be or was positively affected, respectively, by higher WT density for low wind conditions, while no significant effect was detected for other species (Fig. 2; Tables S5–S8).

WT distance affected the activity of species belonging to the low-flying species (*B. barbastellus* and *Plecotus* spp.) and medium-flying species (pipistrelle species). *P. kuhlii* was significantly more active near WTs regardless of the model and the wind conditions. We found a trend towards a similar pattern for *B. barbastellus*, although with only nearly significant p-values. In contrast, the nearly significant effect we found for *Plecotus* spp. in windy conditions show an avoidance of WTs (Fig. 2; Tables S5–S8).

3.3. Effects of wind turbine operation

Wind incidence angle affected all pipistrelle species and *B. barbastellus* activity. It always had a negative effect with less bat activity downwind the turbine. This effect was found in the low wind speed conditions (<4.7 km/h in average per night) for *P. nathusii* and *B. barbastellus* and in windy conditions (≥4.7 km/h in average per night) for *P. pipistrellus*. When considering the interaction between the wind incidence angle and the distance to WT, we found a significant negative effect on all *Pipistrellus* species in windy conditions. Specifically, bats showed an avoidance response with the distance to WTs upwind, while the opposite response was observed downwind (Figs. 2 and 3; Tables S5–S8). We found a similar trend for *B. barbastellus* with a nearly significant interaction.

In relatively windy conditions, the activity of *P. pipistrellus* and *P. kuhlii* increased with increasing average blade rotation speed. The positive effect on *P. kuhlii* was also significant in relatively low wind speed conditions, along with a nearly significant negative effect on

E. serotinus. However, we also detected some negative effect of average blade rotation speed in low wind conditions: the activity of *Nyctalus* spp. and *B. barbastellus* was significantly lower for higher blade rotation speed. Finally, average blade rotation speed did not seem to affect *Myotis* and *Plecotus* spp activity (Fig. 2; Tables S5–S8).

3.4. Effects of wind turbine size

In windy conditions, we found that increasing ground clearance height positively affected the ISWT, as well as *Nyctalus* spp. activity. This means that the higher the ground clearance, the higher the activity of high-flying species in the community. At the contrary, it affected negatively *P. nathusii* and *B. barbastellus* activity. In low wind conditions, increasing ground clearance height also had contrasted effects depending on the species: it significantly decreased the activity of *Myotis* spp. and increased the activity of *P. nathusii* and *Plecotus* spp. It also nearly significantly decreased and increased the activity of *P. nathusii* and *Nyctalus* spp., respectively. Ground clearance did not affect *P. pipistrellus*, *P. kuhlii* and *E. serotinus* activity (Fig. 2; Tables S5–S8).

Finally, rotor diameter had a significant negative effect on *P. pipistrellus*, *E. serotinus* and *Plecotus* spp. activity for low wind speed, and a nearly significant negative effect on *P. kuhlii*. In windy conditions, rotor diameter also negatively affected the activity of *P. pipistrellus*. Rotor diameter did not affect *B. barbastellus*, *Nyctalus* spp. and *Myotis* spp. activity (Fig. 2; Tables S5–S8).

When conducting the analysis using a highly conservative threshold of maximum error risk (0.1), results did not qualitatively change (Tables S9–S12).

3.5. Effects of landscape and weather covariates

First, the distance to water bodies had overall a positive effect on all species in relatively low wind speed conditions, except for *E. serotinus*,

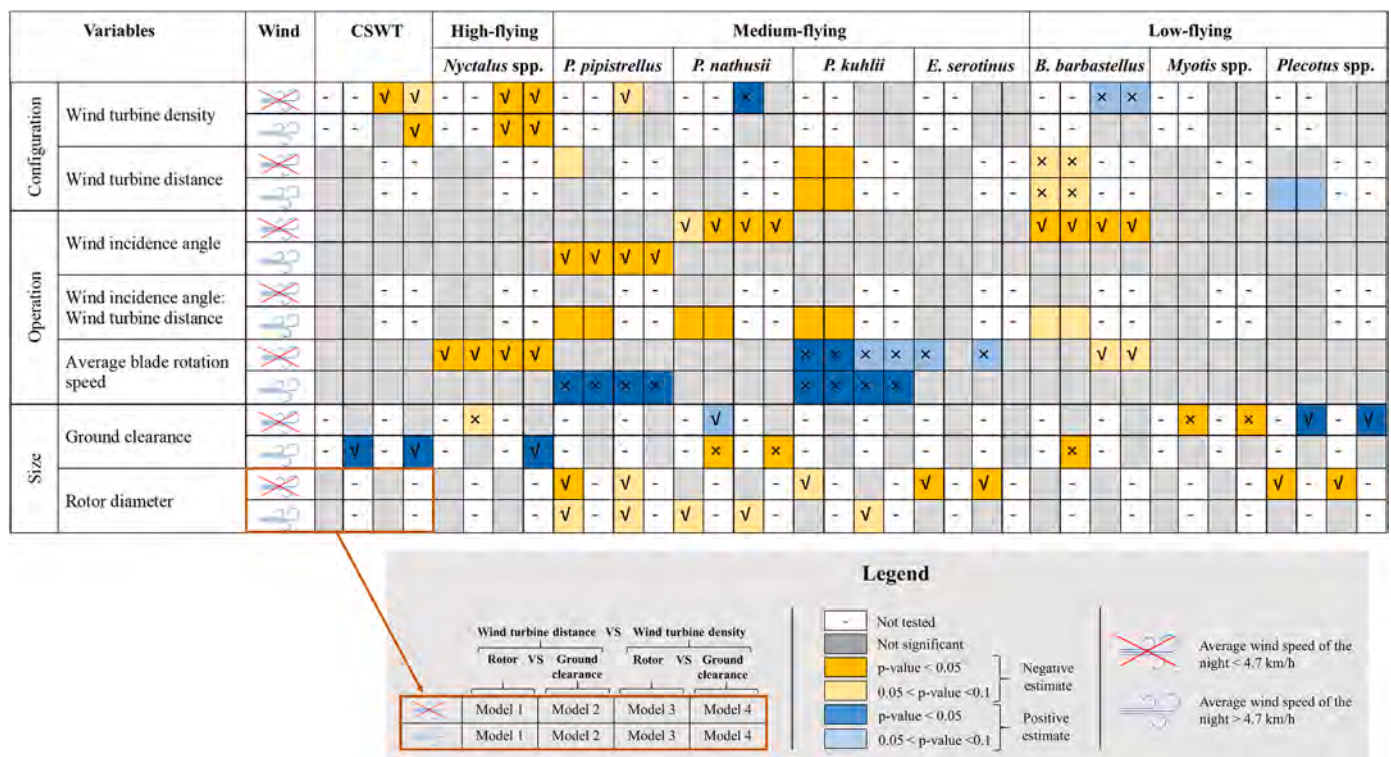


Fig. 2. Summary of the effects of wind turbine variables on bat activity from GLMMs for a maximum error risk threshold in automated acoustic identification of 0.5. Dashes show variables not tested, grey cases non-significant effects, yellow cases significant negative estimate and blue cases significant positive estimate, light yellow cases almost significant negative estimate and light blue cases almost positive estimate. Crosses indicate results opposed to the initial hypothesis and ✓ indicate results in line with the initial hypothesis.

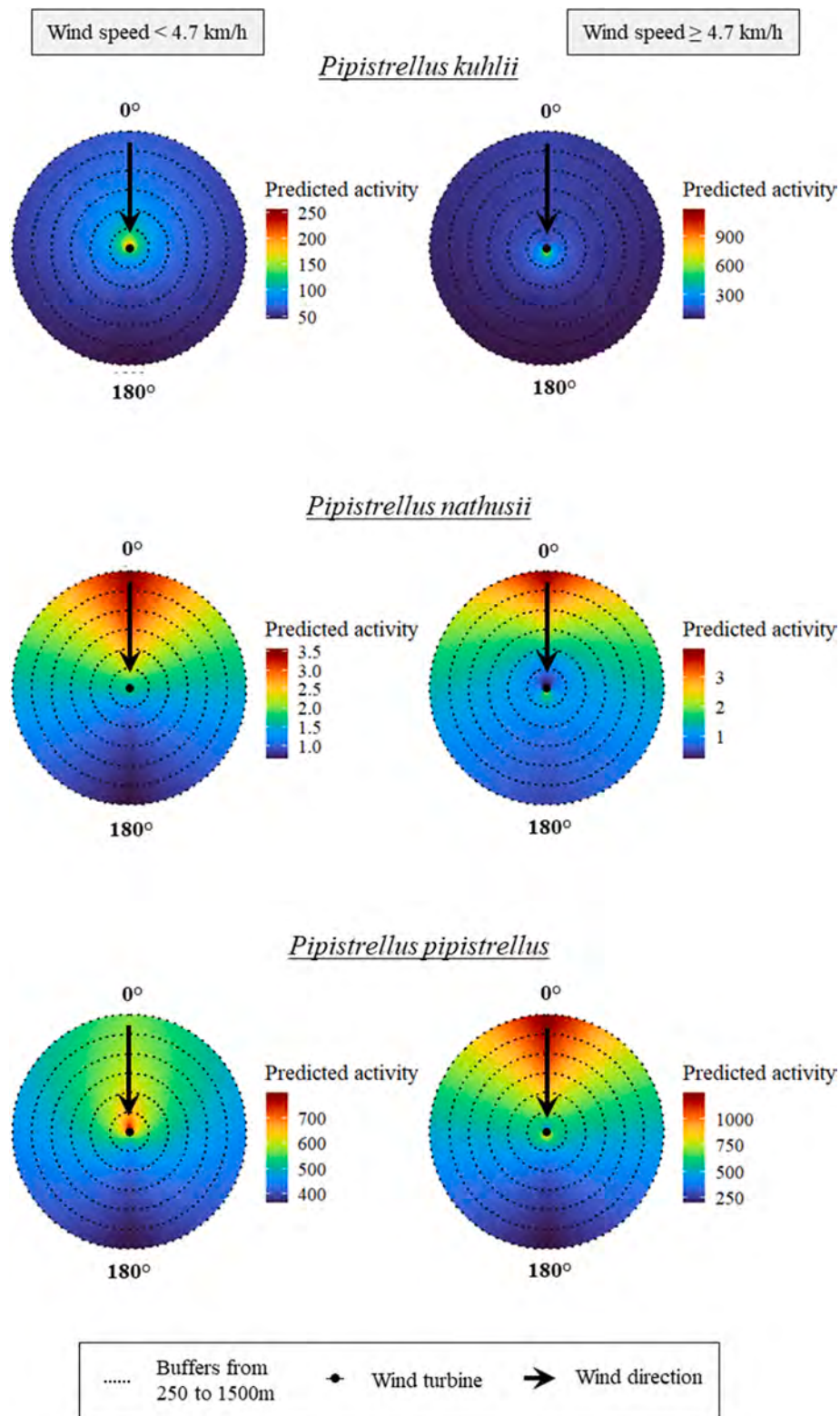


Fig. 3. Predicted activity of *Pipistrellus* species per night around and up to 1500 m from the wind turbine for each wind speed-based dataset from GLMMs. As the two models including the wind turbine distance/wind incidence angle interaction (i.e. models 2 and 3) presented similar estimates and p-values, we conducted the predictions only on the model 2.

while it was rarely significant in windy conditions. Conversely, the effect of the distance to forest was almost never significant, except for a weakly significant and positive effect on *Myotis* spp. in only one model out of four in low wind conditions. Second, regarding weather variables, average temperature positively affected the activity of *E. serotinus*,

P. nathusii and *P. kuhlii* while the average wind speed only significantly and negatively affected *E. serotinus* and *Myotis* spp. activity.

4. Discussion

Our study shows that high wind turbine (WT) density and low ground clearance negatively affect the prevalence of bat species spending the more time at height. Pipistrelle species (medium-flying species) is the only species affected by WT distance and/or wake effect, along with *B. barbastellus*. Overall, the study reveals that WT size (rotor diameter or ground clearance), spatial configuration (WT density or distance), and operation (wind incidence angle or blade rotation speed) affect the activity of most bat species or groups. At a landscape scale, the study suggests that a specific attention should be paid to not over-densifying the turbines. At a local scale, the findings highlight the need to site turbines far from attractive habitats as recommended by EUROBATS guidelines (Rodrigues et al., 2015), and preferably not between bat habitats and the source of prevailing winds, to avoid exposing these habitats to the wake area. Our results also suggest to decrease rotor diameter as much as possible, to avoid exacerbating attraction and avoidance phenomena. Finally, bat responses can either occur in specific wind speed classes only, or independently, highlighting the importance for each WT features to consider the wind conditions at which responses will occur to build reduction schemes of impacts.

4.1. Bat responses to wind turbine configuration variables

The negative effect of WT density on the Index of Sensitivity to WT (ISWT) suggests that the more time species spend at height, the more likely they are to be negatively affected by WT density, as hypothesized. This negative effect of WT density is likely to be driven by *Nyctalus* spp. which are high flying species with a large home range size (Laforge et al., 2021). These results are consistent with previous studies showing a lower probability of *N. noctula* presence for higher WT densities, an effect detectable up to a few kilometers (Reusch et al., 2022). This suggests that the predicted future densification of WTs could cause large habitat losses for *Nyctalus* spp. Since these species have large home range and high interannual site fidelity, these results could result from a learning of the collision risk leading to a perceived landscape of fear (Bleicher, 2017; Bonnot et al., 2013).

Additionally, the WT distance alone only affected significantly and positively *P. kuhlii* activity, while in interaction with the wind incidence angle it affected all pipistrelle species (responses are discussed in section 4.2 below), highlighting the need to consider both factors in future studies.

4.2. Bat responses to wind turbine operation variables

In terms of vertical distribution, the bat community was not affected by WT operation. However, all pipistrelle species and *B. barbastellus* responded to the interaction between the WT distance and the wind incidence angle (i.e., the proximity to the wake effect area). Specifically, *P. pipistrellus*, *P. nathusii* and *B. barbastellus* simply avoided the wake area, while *P. kuhlii* was attracted to WTs from windward or leeward side in low and high wind speed condition, respectively. However, we call for caution regarding the response of *P. nathusii* that was no longer significant for a conservative threshold (0.1) of maximum error risk of automated identifications. Due to the time they spend at blade height, *Pipistrellus* spp. are likely to be exposed more often to the wake area than lower flying species such as *Plecotus* spp. and *Myotis* spp. In addition, *Pipistrellus* spp. resistance to challenging flight conditions (i.e. high wind speed or/and turbulences) may be lower than higher flying species such as *Nyctalus* spp. (Behr et al., 2017; Verboom and Huitema, 1997), making them especially vulnerable to the wake area. Yet, the negative effect of the wind incidence angle on *B. barbastellus* is surprising as this species spend less time at blade height (Roemer et al., 2017).

Then, *P. pipistrellus* and *P. kuhlii* activity increased with higher blade rotation speeds, while it decreased for *Nyctalus* spp. The higher pipistrelle activity recorded at ground could result from a vertical shift of bats

to lower heights due to stronger airflow disturbances at height resulting from increasing blade rotation speed (Wellig et al., 2018), while the lower activity of noctules having a much larger detection range probably reflects avoidance responses.

4.3. Bat responses to wind turbine size

In terms of vertical distribution, bat community was positively affected by a higher ground clearance in windy conditions, meaning that the relative abundance of high-flying species in the community was higher for higher ground clearance. Activity of *Nyctalus* spp., *Plecotus* spp., *P. nathusii*, *B. barbastellus* and *Myotis* spp. was globally (i.e. regardless of WT distance or operation) affected by ground clearance height. Additionally, activity of all medium-flying species and *Plecotus* spp. was globally lower for larger rotor diameter. The avoidance of larger rotors is consistent with recent findings about *Myotis* spp. and *Plecotus* spp. (Ellerbrok et al., 2022), which could be explained by noise or airflow disturbances.

4.4. Bat responses to landscape and weather covariates

The increasing bat activity with increasing distance to water bodies appears inconsistent with previous studies (e.g. Heim et al., 2017). Since water bodies are well-known to attract bats, one explanation could be that the presence of water bodies close to sampled hedgerows would drain bat activity from hedgerows to water bodies. Then, regarding the absence of effect of distance to forests for almost all species, this could be linked either to an insufficient gradient which was minimized when building the design to focus on WT parameters, to an attractiveness of forests no greater than the one of the habitat sampled here (i.e. hedgerows), or to a lack of statistical power. Finally, the positive effect of average temperature as well as the negative effect of wind speed are consistent with the literature (Behr et al., 2017). Finally, these four covariates did not cause any collinearity problems in the models and therefore did not influence the results relating to WT parameters.

4.5. Limitations, recommendations and perspectives

Firstly, *B. barbastellus* seemed to have responses more similar to *Pipistrellus* spp. than to the other low-flying species, while *E. serotinus* had rather different responses than the other medium-flying species. Also, *P. nathusii* presented some responses that other *Pipistrellus* spp. did not: a positive effect of WT density and a negative effect of ground clearance. Further studies could clarify why these species did not respond in the same way than others in the same flight-based guild.

Then, we could not account for the interactions between WT distance and WT size or operation because it would have added much more complexity to the study and required more statistical power. Thus, the results regarding these last factors should be interpreted carefully as their influence on bat activity could vary with the distance to WTs. However, despite not controlling for WT distance, WT variables tested in our study already show significant and interpretable effects which should be considered in wind energy planning and mitigation. In addition, WT size are even the only parameters affecting significantly *Myotis* spp. and *Plecotus* spp. activity. Given the ongoing increase of WT size (Serrano-González and Lacal-Arántegui, 2016) these results call for a great caution regarding future WT size that could definitely be a factor generating strong changes of habitat use for these species.

Our results about WT parameters are valid for the studied landscape, weather (i.e. mainly farmland and high hedgerow density under favorable weather conditions) and period (i.e. June). Importantly, it should be noted that reported WT parameters effects are robust against environmental covariates (i.e. landscape and weather) since we ensured through the sampling design and analyses that no collinearity occurred within the entire pool of modeled variables. Further studies could go further and assess the potential variation of WT parameters effects

according to variations in landscape, weather and time of the year, using larger environmental gradients than our study. Additionally, the potential role of WT obstruction lights could be assessed in further studies that would have access to a variation in lighting type and time, as artificial light is well known to influence bat activity. Finally, it would be relevant to further investigate WT parameters following different scenarios of wind energy development including either WT with larger rotors in lower density compared to WT with smaller rotors in higher density. It would allow to provide direct and concrete recommendations about the most biodiversity friendly strategy regarding wind energy planning.

Main recommendations resulting from this study are (1) to avoid high density of WTs in areas where high-flying species such as *Nyctalus* spp. are present, (2) to site WTs as far as possible from attractive habitats, especially woody edges, (3) to avoid sitting WTs between prevailing wind direction and attractive habitats to avoid exposing them to the wake area, especially for *Pipistrellus* spp. and *B. barbastellus*, and (4) to prefer smallest possible rotor diameters. Regarding ground clearance, we now know that it affects the activity of five species but further studies including a vertical sampling (i.e. at least two different heights) are needed to fully understand how to interpret these effects. Finally, the study key message is that environmental impact assessment studies should always consider the combination of all these parameters when assessing the suitability of a project.

5. Conclusions

This study shows that bat responses to WTs highly depend on the species and wind conditions, and that many WT parameters can affect bat activity. Specifically, bat response to WT proximity can vary depending on the wind incidence angle. This effect, along with bat response to features often overlooked in the literature such as WT size or blade rotation speed, most likely explains the non-consensus effects (attraction and avoidance) reported in the literature so far. These features should therefore be systematically considered. From an operational perspective, although increasing rotor diameter would allow to produce more electricity per turbine, it will also generate stronger and larger wake effect, impacting a larger part of the aerosphere and in turn more bat species. These impacts could be a loss of habitat as well as higher collision risks due to the larger area swept by the rotor. Nevertheless, installing smaller WTs but in higher density to reach the same production of electricity will still generate habitat losses for many species found to avoid WTs (Barré et al., 2018), as well as possibly increase overall collision risk (Thaxter et al., 2017). Comparing the cumulated impacts of collisions and functional habitat losses between less dense and larger WTs and denser and smaller WTs would constitute a promising way of future research to guide wind energy planning. Our results emphasize the importance of keeping WTs as far away as possible from important habitats for bats and to apply curtailment schemes, in order to minimize habitat losses and collision risks generated by avoidance and attraction phenomena, respectively. The wake effect should also be considered in the planning phase to avoid installing WTs between prevailing winds and attractive habitats. Finally, as the current wind energy development involves bigger and more WTs, the study calls to carefully consider all factors addressed in this study in future wind energy planning.

Credit author statement

Camille Leroux: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Visualization; Writing – original draft; Writing – review & editing. Kevin Barré: Conceptualization; Formal analysis; Methodology; Supervision; Visualization; Writing – original draft; Writing – review & editing. Nicolas Valet: Funding acquisition; Resources; Writing – review & editing. Isabelle Le Viol and Christian Kerbiriou: Conceptualization; Formal analysis; Funding acquisition;

Methodology; Resources; Supervision; 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. Camille Leroux reports equipment, drugs, or supplies was provided by France Energie Eolienne. Camille Leroux reports financial support was provided by Audicé biodiversité. Nicolas Valet reports financial support was provided by Audicé biodiversité. Kevin Barre reports a relationship with France Energie Eolienne that includes: funding grants.

Data availability

Data are available at <https://doi.org/10.5281/zenodo.8358475>.

Acknowledgments

We thank the Association Nationale de la Recherche et de la Technologie (Grant No. 2019/1566) and Audicé biodiversité for funding this research; IN2P3 Computing Centre and PCIA-MNHN for providing computing and storage facilities to process and archive in the long term all the bat recordings used in this study; Yves and Didier Bas for their help with the archiving; wind farm developers for funding part of the bat recorders; wind farm developers, operators and owners, for providing us with information on features of the wind turbines and blade rotation speeds for the nights on which we sampled; Nancy Jennings for the editing service; and Jérémy Prouff, Anne-Laure Brissard and Jean-Noël Caron for helping with the figures. Kevin Barré was funded by the Agence de la transition écologique (ADEME), Christian Kerbiriou by Sorbonne University, and Isabelle Le Viol by the french National Museum of Natural History (MNHN). We thank the two anonymous reviewers for their constructive comments improving this work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2023.118987>.

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