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Is bat activity a reliable predictor of mortality at onshore wind turbines? Evidence from a standardized multi-site monitoring in Europe

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ABSTRACT

Reducing bat mortality at wind turbines has become an urgent conservation priority. However, operators often fail to identify and avoid areas of high bat activity when planning wind facilities, despite recommendations from environmental authorities, and existing curtailment strategies still require optimization. Although acoustic monitoring has been suggested as a practical way of assessing collision risk, the relationship between bat activity and fatalities remains poorly understood and lacks scientific consensus. In this study, we analyze a unique long-term regulatory dataset from France, combining standardized nacelle-height acoustic monitoring and systematic carcass searches conducted at 51 onshore wind turbines over five years. We investigated whether 'exposed' bat activity, which is defined as acoustic activity recorded at nacelle height during turbine operation, could reliably predict bat fatalities while accounting for turbine characteristics. We also examined how this relationship varies among functional guilds and across biologically relevant seasons. We found a positive association between exposed activity and estimated fatalities. The relationship was stronger in late summer/early autumn than in spring/early summer. However, exposed activity contributed little to overall model performance. We suggest that the low explained variance reflects the substantial spatial and temporal heterogeneity of our dataset, as well as the limited resolution of mortality estimates. Improving mortality monitoring is therefore essential to better characterize activity–fatality relationships and enhance predictive capacity. While acoustic activity alone may be insufficient to predict bat fatalities across broad scales, it remains a valuable indicator for wind facility planning and an important tool for optimizing curtailment strategies.

1. Introduction

Although the global transition to renewable energy is crucial for mitigating climate change, this must not be at the expense of biodiversity. The rapid growth of the wind energy sector (IRENA, 2025) illustrates this issue, as wind turbines have emerged as a major source of mortality for flying fauna, such as bats (O'Shea et al., 2016). Indeed, collisions with rotating wind turbines likely cause millions of bat fatalities worldwide each year. For instance, current estimates suggest that over 800,000 bats are killed annually at wind energy facilities in the US, Canada, and Germany alone (Frick et al., 2020). Due to their longevity and low reproductive rates (Barclay and Harder, 2003), bat populations are particularly vulnerable to the impacts of wind energy facilities. Research has already documented severe population-level impacts, with existing fatality rates sufficiently high to drive rapid population declines and increase the risk of extinction for some migratory bat species (Frick et al., 2017; Friedenberg and Frick, 2021). Identifying effective strategies to promote energy production while reducing bat fatalities at wind turbines has therefore become an urgent conservation priority.

In Europe, Environmental Impact Assessments (EIAs) are legally mandated prior to the authorization of wind energy facilities to systematically evaluate and mitigate potential biodiversity impacts

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(Directive 2011/92/EU). The EIA process integrates a multi-step approach, beginning with the pre-selection of sites to avoid ecologically sensitive areas, followed by field-based ecological surveys to assess protected and threatened species (e.g., bat acoustic surveys) and habitats, and concluding with a comprehensive impact analysis. Central to this framework is the mitigation hierarchy, which prioritizes avoiding impacts, minimizing unavoidable impacts, and offsetting of residual effects (Bull et al., 2016; Business and Biodiversity Offsets Programme, 2012). In the context of wind energy, the avoidance phase typically involves avoiding locations with high bat diversity, such as forests and hedgerows (Kelm et al., 2014; Reusch et al., 2022) and areas of priority for conservation, such as migration or commuting corridors (Bach et al., 2022; Merlet et al., 2025; Reusch et al., 2022), in line with recommendations from the convention on the conservation of migratory species of wild animals EUROBAT (Rodrigues et al., 2015).

Unfortunately, this approach has significant limitations. EIAs often fail to prioritize sensitive natural areas (Froidevaux et al., 2025; Newson et al., 2017; Roscioni et al., 2013) to the same extent as other regulatory constraints, such as aviation, distance to houses or electrical grid connection. They also struggle to reliably predict the risk of bat casualties (Lintott et al., 2016). For instance, a recent study found that more than 90% of wind turbines in two French regions were installed in areas classified as having high or extremely high bat activity (Froidevaux et al., 2025). In addition, although the UNEP/EUROBATS agreement, ratified by 37 countries, has recommended since 2008 that wind turbines be sited at least 200 m away from woody edges to reduce bat fatality risk (Rodrigues et al., 2008), the majority of turbines in France, Germany and the UK are still installed within 200 m of forest edges (Barré et al., 2022).

In circumstances where avoidance is not possible, curtailment strategies—defined as the shutdown of wind turbines under contextual (e.g., seasonal) and meteorological conditions favorable to bat activity (e.g., foraging and migration)—are increasingly being implemented as mitigation measures. Conventional approaches, which are usually based on fixed thresholds such as wind speed or temperature, have been widely adopted, and are well documented as effective. For instance, Arnett et al. (2011) reported reductions in bat mortality ranging from 44% to 93%, while a meta-analysis of 29 North American studies found that fatalities decreased by 33% for each 1.0 m/s increase in the cut-in wind speed threshold (Whitby et al., 2024). In France, another study has reported a reduction in mortality of up to 84% (Ravache et al., 2026b). More recently, algorithmic approaches have been developed to model collision exposure risk based on temporal and environmental drivers (e.g., time of the night and year, precipitations, wind speed, temperature, blade rotation speed), and their interactions (Barré et al., 2023, 2026; Behr et al., 2017). These trained algorithms typically use nacelle-level acoustic activity at fine temporal resolution as a proxy for exposure risk to inform curtailment decision-making by predicting the risk at specific times based on the actual combination of these drivers. Compared to conventional approaches, these tools can substantially reduce bat exposure while maintaining the same level of energy production. This highlights their potential to reconcile renewable energy production with biodiversity conservation.

Nevertheless, predicting site-specific bat mortality at the pre-construction stage and defining highly effective curtailment measures remain challenging (Lintott et al., 2016), largely because the relationship between bat activity at nacelle height and actual collision risk is complex. It is commonly assumed that bat activity in the immediate vicinity of turbine blades reflects collision risk. Accordingly, EIAs widely use acoustic recordings collected at nacelle height as a proxy for site-specific bat presence and, by extension, potential collision risk. However, there is currently no empirical evidence supporting a consistent and predictive relationship between such activity measures and observed fatalities. While some studies report a strong association (Behr et al., 2023; Korner-Nievergelt et al., 2013; Peterson et al., 2025), others find weak or no evidence of such a relationship (Bach et al., 2020; Solick et al., 2020). Voigt et al. (2021) provide a comprehensive assessment of the methodological difficulties inherent in modelling this relationship. Numerous technical (e.g., recorder type) and biological factors (e.g., species-specific detectability and the spatial distribution of bats) influence acoustic detection at wind turbines, introducing substantial variability (i.e., statistical noise) and potential bias. The spatial distribution of bats within the rotor-swept zone is particularly relevant as it can affect the ability of nacelle-mounted acoustic detectors to predict bat fatalities (Voigt et al., 2022). Additionally, fatality estimates are strongly dependent on monitoring quality and heterogeneity, including survey effort, as well as on the estimation and integration of biases such as carcass persistence and observer efficiency (Korner-Nievergelt et al., 2013; Ravache et al., 2024). Therefore, a robust analytical framework must address both sources of uncertainty associated with mortality estimation and acoustic recording. To date, only one study has demonstrated such a relationship on a large scale using standardized nacelle-level bat recordings spanning more than one sampling season (i.e., 43 turbines monitored over four years) and modelling approaches adapted to turbine characteristics (Behr et al., 2023).

Consequently, a more comprehensive effort to test the relationship between recorded activity and mortality remains necessary, as it could (i) improve EIA assessments by strengthening mortality risk predictions at wind facilities and (ii) optimize curtailment strategies to achieve greater and more consistent reductions in bat fatalities. In France, the EIA process goes further than just project approval, as it also includes mandatory post-construction monitoring of the impact of wind facilities. Since 2018, this monitoring has followed a standardized protocol combining nacelle-height acoustic surveys with systematic carcass searches (MTES, 2018), which has substantially reduced methodological heterogeneity and improved data quality. This regulatory framework has generated a uniquely large, standardized dataset on bat activity and turbine-related fatalities, providing a rare opportunity to investigate the drivers of bat mortality with a level of consistency and statistical power seldom achievable elsewhere. Thus, using these data from regulatory environmental monitoring of 51 onshore turbines monitored over five years, we aimed to assess whether bat activity recorded at nacelle height can serve as a reliable predictor of mortality. Overall, we expect bat activity during turbine operation to be positively associated with bat fatality rates, as greater activity near turbines may increase exposure to the risks posed by rotating blades. However, we expect the strength of this relationship to vary among functional guilds due to substantial differences in flight height and acoustic detectability. Additionally, we anticipate stronger correlations at finer temporal scales, as finer temporal resolution may better capture variation in bat activity and mortality rates. We also expect the strength of the relationship to vary between seasons, particularly when distinguishing between spring/early summer (associated with gestation and juvenile rearing), and late summer/mid-autumn (associated with post-reproductive and migratory periods), the latter being characterized by elevated activity.

2. Methods

2.1. Selection of the wind energy facilities

As there is currently no centralised national database for acoustic data, we compiled a dataset from 99 onshore wind turbines across France, based on data provided by the consultancies Ouest Am' and Exen. Between 2019 and 2023, we selected wind energy facilities with at least one turbine where bat acoustic activity was continuously monitored using a single type of recorder between weeks 20 and 43 (i.e., mid-May to mid-October). During the same period, carcass searches were conducted weekly at each turbine, complemented by a series of carcass persistence and search efficiency tests to allow accurate estimation of bat fatalities. To ensure the turbines were operational and to identify periods of risk of bat collisions, we restricted our analysis to turbines with available 10-minute average rotation speed data and excluded

those with more than 5% missing data during intervals with detected bat activity. The final dataset comprised 51 turbines distributed across 45 wind facilities, including 12 turbines monitored over two consecutive years (Fig. 1).

2.2. Turbine characteristics

To account for variability in turbine characteristics, we compiled turbine-specific data from a national database (www.georisques.gouv.fr). We collected turbine height (m), nacelle height (m), power rating (MW), and rotor diameter (m), and calculated rotor-swept area (m^2) and ground clearance (m). Within a given wind facility, all turbines had identical characteristics. The selected turbines represented a wide range of turbine configurations, with nacelle heights ranging from 44 to 117 m, total turbine heights from 70 to 180 m, rotor diameters from 52 to 150 m, ground clearance from 18 to 63 m, rotor-swept areas from 2,123 to 17,671 m^2, and installed power from 0.8 to 3.9 MW. In total, these turbines were made up of 17 different machine models from six different manufacturers.

2.3. Estimated bat fatalities

According to the French national post-construction monitoring protocol (MTES, 2018), a minimum of 20 carcass searches were conducted at each turbine between weeks 20 and 43, within either a 100 × 100 m square (or twice the blade length for blades >50 m) or a circle with a radius equal to the blade length (with a minimum radius of 50 m), complemented by semi-annual carcass persistence tests and searcher efficiency tests (see Supplementary Material S1 for details). Raw data including carcass search schedule, carcass observation, search area coverage as well as carcass persistence and observer efficiency tests, were compiled from the regulatory environmental monitoring reports. We estimated bat fatalities using a homogeneous workflow based on the GenEst (Dalthorp et al., 2018) and Evidence of Absence (EOA3; Dalthorp, 2023) packages in R (version 4.4.0; R Core Team, 2024a). GenEst adjusts detected carcass counts for observer detection, carcass persistence, search area coverage and search timing. EOA3 uses a Bayesian approach with similar parameters to estimate plausible mortality intervals even when zero carcasses are observed. Accordingly, GenEst was used when surveys yielded two or more carcasses, while EOA3 was used in cases where zero or one carcass was found (Fig. 2A). This dual approach is particularly useful when carcass counts are very low, as GenEst does not generate estimates when no carcasses are observed.

Uncertainty in mortality estimates was quantified using parametric bootstrapping. For each iteration, the following parameter values were randomly drawn from their estimated distributions: carcass persistence, detection effectiveness and probability of falling within the search area (Supplement S1). A total of 5,000 fatality estimates were generated for each wind facility, forming a distribution from which the 95% confidence interval (excluding the lowest and highest 2.5%) was derived. These distributions were then used in subsequent models to compare mortality rates across monitoring periods while accounting for uncertainty. More frequent surveys, higher search effectiveness and longer carcass persistence produced narrower confidence intervals and more consistent estimates across iterations. Fatality estimates were calculated at the wind facility level and standardized per turbine by dividing the total estimated mortality by the number of monitored turbines, thereby enabling comparisons among wind facilities independently of their size.

Fatality estimates were first generated for the entire regulatory monitoring period (weeks 20–43) and separately for functional guilds (Supplement S1). To assess potential seasonal patterns that may be obscured by aggregating data over the entire season, we also estimated fatalities for two sub-periods (weeks 20–31 and 32–43). The subperiods corresponded to spring/early summer (gestation and juvenile rearing) and late summer/mid-autumn (post-reproductive and migratory

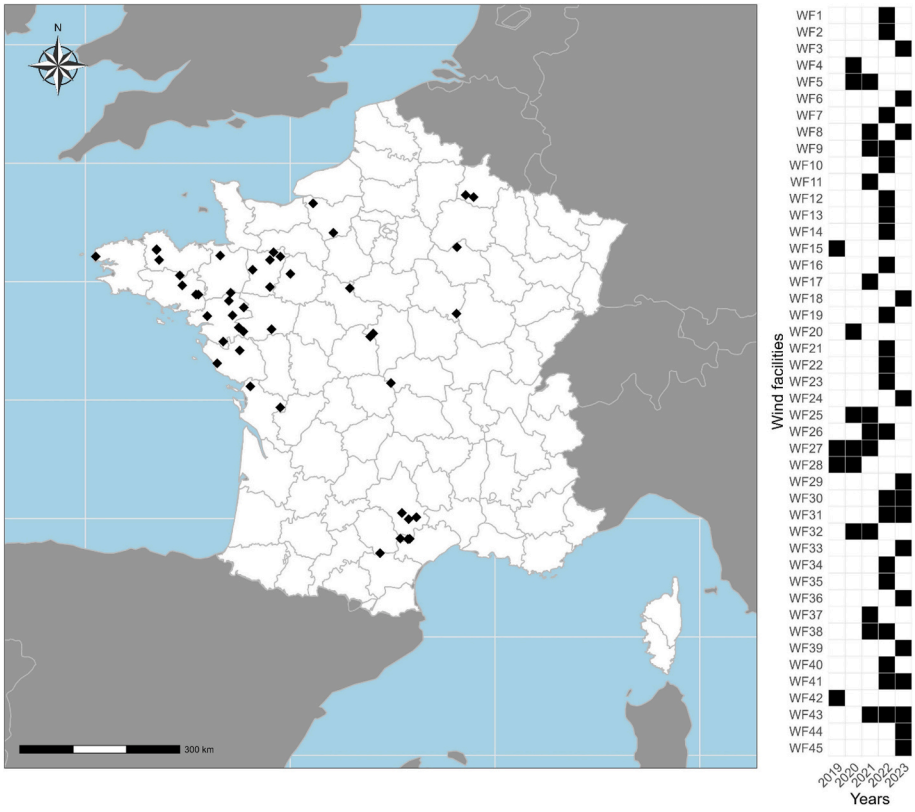


Fig. 1. Map of the locations of the selected wind facilities (left), and overview of the recording periods for each of them (right). The study only included recordings from weeks 20 to 43.

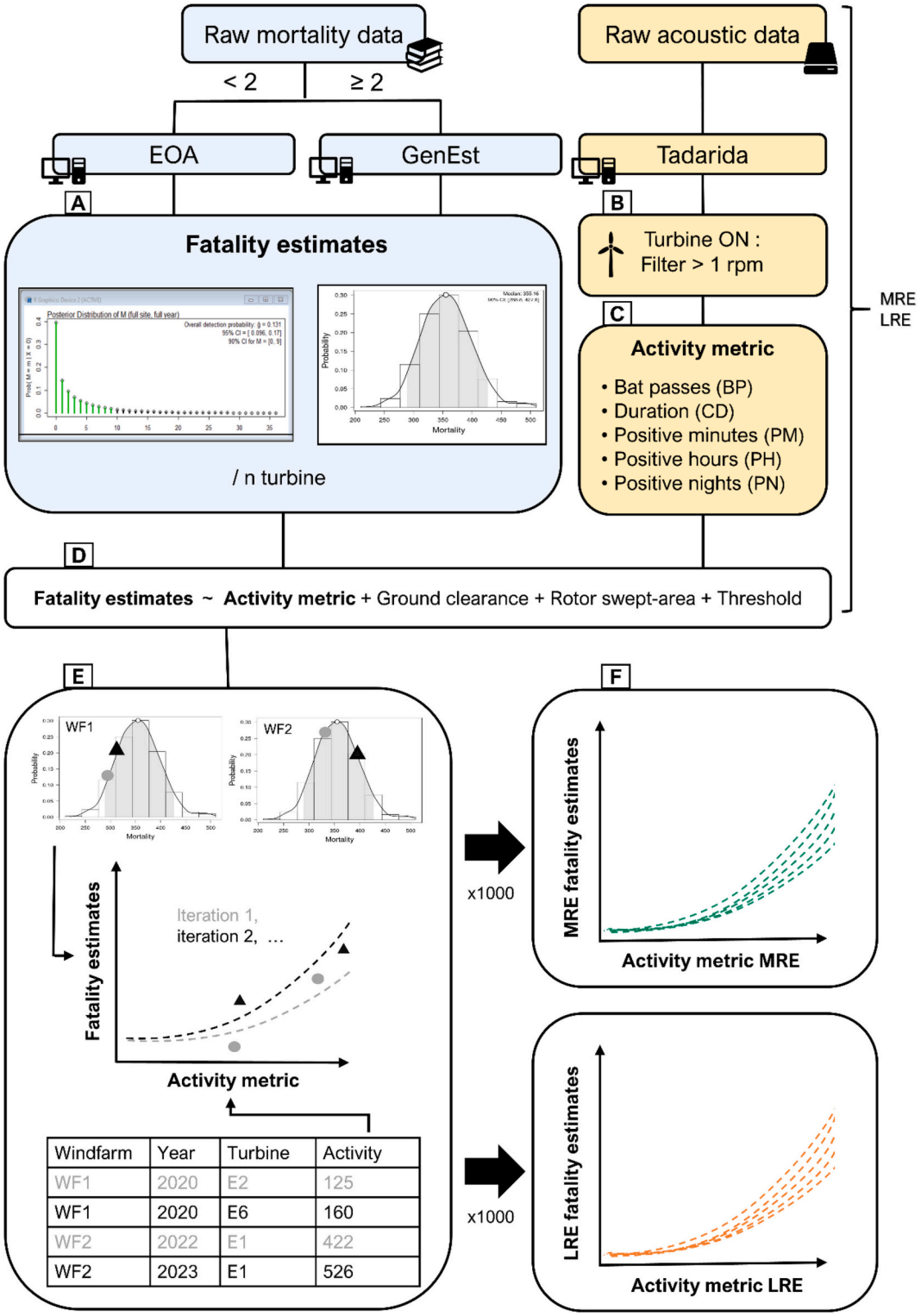


Fig. 2. Workflow illustrating the construction of the dataset, the modelling approach, and the two-level bootstrap procedure used to obtain the results. Note that panel E illustrates an example of the two-level bootstrap procedure, with the upper section showing the selection of fatality estimates from distributions generated by GenEst, and the lower section showing the selection of activity values among turbines and years available for each wind facility. Grey circles represent values selected during the first iteration, whereas black triangles represent values selected during the second iteration for two wind facilities (WF1: wind facility 1; WF2: wind facility 2).

periods), respectively. This subdivision halved the number of carcass searches available for each monitoring period. As the protocol requires only one carcass search per week and mortality rates were low (i.e., 222 carcasses were observed across all turbines and years), further subdivision would result in overly wide confidence intervals and reduce the reliability of the estimates.

2.4. Monitored and exposed bat activity

Following the French national post-construction monitoring protocol (MTES, 2018), bat acoustic activity was monitored at nacelle height from sunset to sunrise. All acoustic surveys were conducted using a single detector type (GSM-batcorders; ecoObs, Nuremberg, Germany), mounted on the nacelle and oriented downward. This standardized setup substantially reduced a major source of heterogeneity in bat acoustic monitoring data (Barré et al., 2023). Each device was programmed to trigger a recording when an acoustic event exceeded a threshold of 60 or 69 dB SPL within a frequency range of 14–150 kHz, with a post-trigger duration of 800 ms. Continuous monitoring (i.e., no recorder failure from weeks 20 to 43) was verified by confirming that a test file automatically generated by the recorder was produced each day.

Recorded sound files were segmented into 5 s intervals, thus ensuring sufficient coverage of the average duration of a bat pass (Kerbiriou et al., 2019). Each 5 s file was then automatically classified to the closest taxonomic level using Tadarida software (Bas et al., 2017). Then, bat species were grouped into three functional guilds, based on similarities in echolocation call structure and species-specific detectability, as previously described by Frey-Ehrenbold et al. (2013): long-range echolocators (LRE, *Cnephaeus* and *Nyctalus* genus), mid-range echolocators (MRE, *Pipistrellus genus*, *Hypsugo savii* and *Miniopterus schreibersii*), and short-range echolocators (SRE, *Myotis*, *Rhinolophus* and *Plecotus* genus and *Barbastellus barbastella*). This approach substantially reduces errors associated with automated species identification. Furthermore, the defined guilds reflect distinct levels of collision risk based on aerial ecology. Long-range echolocators are the most exposed, spending most of their activity within the rotor-swept area, followed by mid-range echolocators, while short-range echolocators rarely reach such heights (Roemer et al., 2019). In line with Barré et al. (2019), we implemented procedures to account for the risk of misclassification associated with automated identification by assessing the sensitivity of the results to variation in identification error rates. We therefore created two distinct datasets using the confidence index: (i) one including only bat passes with a confidence score of at least 0.90 (allowing for an error rate of up to 10%), and (ii) one including passes with a score of at least 0.50 (allowing for an error rate of up to 50% while retaining substantially more data). All statistical analyses were carried out on the dataset of bat passes with a confidence index greater than or equal to 0.5, and the reliability of the results was verified using the other dataset.

To investigate bat activity in terms of exposure to turbine operation and associated collision risk, we retained only bat passes recorded at rotor speeds ≥ 1 rotation per minute (rpm), following previous studies (Peterson et al., 2021, 2025; Fig. 2B). This threshold reflects the low likelihood of collisions when turbine blades are stationary or rotating at very low speeds (Horn et al., 2008). Using these "exposed bat passes" we derived several acoustic activity metrics to assess the level of temporal resolution (fine-scale vs. broad-scale) required to accurately predict fatality estimates (Fig. 2C). The activity metrics were: (a) the total number of bat passes (BP); (b) the total number of positive minutes (i.e., minutes with at least one bat pass; PM); (c) the total number of positive hours (i.e., hours with at least one bat pass; PH), (d) the total number of positive nights (i.e., nights with at least one bat pass; PN); and (d) the cumulative duration of bat passes (CD). The cumulative duration was calculated as the sum of durations, each defined as the time elapsed between the first and last calls of a given species within a 5 s recording. For all bat activity metrics, activity was summarized over the full study period (weeks 20–43) and two subperiods (weeks 20–31 and 32–43), consistent with fatality estimates.

2.5. Statistical analysis

To test the relationship between bat fatalities and activity, we fitted generalized linear models using the glmmTMB package (Magnusson et al., 2017) to assess the effects of different activity metrics (i.e., BP, CD, PM, PH, or PN) on fatality estimates (generated for weeks 20–43, 20–31, or 32–43, separately for MRE and LRE). We used exposed activity for all models. For comparison, however, we also examined the relationship using monitored activity (i.e., not filtered to retain only activity exposed to turbine operation) for the best models. As fatality values are continuous, resulting from division of estimates by the number of turbines within wind facilities, and include many values near zero as well as a long right tail (Figs. S2.1, S2.2 in Supplement S2), the response variable (fatality estimates) was $\log_{10}$-transformed (i.e., $\log_{10}(x + 0.01)$) to reach normality or near normality (Figs. S2.3, S2.4). We therefore assumed a Gaussian error distribution for all models. To account for variability in turbine characteristics and the spatial heterogeneity of bat activity, we included rotor-swept area and ground clearance as fixed effects (Fig. S2.5). These variables were selected because they were not strongly correlated (all pairwise correlations $r^2 < 0.5$; Fig. S2.6) and represent key turbine characteristics identified in the literature as influencing fatality estimates (Garvin et al., 2024; Labuzzetta et al., 2026). We also included a variable "Threshold", corresponding to the two microphone trigger thresholds (60 or 69 dB SPL), as a fixed factor to account for differences in microphone sensitivity that could influence bat species detectability (Fig. 2D). Prior to modelling, all continuous explanatory variables were standardized to zero mean and unit variance (z-score scaling) to allow comparison of effect sizes across variables with different units and ranges. Models were fitted for the full period (weeks 20–43), for the two subperiods (weeks 20–31 and 32–43), and by functional guild (LRE, MRE). SRE fatalities and activity were negligible (Fig. S2.1) and were therefore excluded from the analysis.

Nearly 5,000 fatality estimates were generated for each wind facility, and sometimes these spanned a relatively wide range of values, so relying solely on a median would not account for this uncertainty. In addition, our dataset included multiple turbines and multiple years for some wind facilities (Fig. 1B) and repeated measurements across years or turbines were too infrequent to be included as random effects. We therefore implemented a two-level bootstrap procedure for all models (Fig. 2E). In brief, at each iteration, one year and one turbine were randomly selected from each wind facility where multiple options were available, and one fatality estimate was randomly selected from the estimates available (Fig. 2E). This procedure enabled the propagation of uncertainty in both fatality estimates and acoustic activity metrics. To obtain robust results, we ran 1,000 iterations (Fig. 2F) and extracted model coefficients and *p*-values for each iteration. For each model, we recorded the proportion of iterations in which the acoustic metric had a significant *p*-value. The models' predicted fatality estimates were back-transformed to the original scale.

To compare the variance explained by the models, we calculated the R^2 of each model and the pseudo-R^2 of each predictor using the performance package (Lüdecke et al., 2021) for each iteration. We then reported the mean R^2 and pseudo-R^2 values, together with their 95% confidence intervals, across all iterations. Model diagnostics, including outlier detection, dispersion checks, Kolmogorov–Smirnov tests, and zero-inflation tests, were performed for each iteration using the DHARMa package (Hartig and Hartig, 2017), and the proportion of iterations passing all diagnostic tests was recorded. No spatial autocorrelation of model' residuals was detected based on Moran tests, and all variables showed variance inflation factors (VIF) < 2, indicating no evidence of multicollinearity. All analyses were conducted in R (version 4.4.2; R Core Team, 2024b).

3. Results

3.1. Exposed bat activity

Acoustic bat detectors recorded over 80,581 bat passes across more than 11,100 nights at 51 wind turbines. Of these passes, 60% were attributed to MRE species, 39% to LRE species, and approximately 1% to SRE species. Fatality estimates for SRE species were also negligible

(Fig. S2.1), we therefore excluded SRE species from the analyses.

Filtering bat passes to retain only those recorded during turbine operation (>1 rpm) considerably reduced activity rates (Fig. S3.1 in Supplement S3). During turbine operation, LRE passes showed a marked seasonal pattern, with most exposed activity occurring from early August to early September (weeks 31–37). An earlier peak was observed in June (week 23), although this was largely driven by a single wind facility (Fig. 3B). In contrast, MRE passes were more evenly distributed throughout the year, with the highest activity peak occurring in August (week 36). Additional peaks were recorded in October (weeks 40–41), but these were primarily driven by two wind facilities (Fig. 3A).

3.2. Exposed activity as predictor of mortality

Overall, the results suggest a positive relationship between estimated fatalities and exposed activity, when aggregated over weeks 20–43, for both MRE and LRE guilds (Fig. 4). Among tested activity metrics, positive Hours (PH) showed the highest level of significance across all iterations of the MRE and LRE models. Positive Nights (PN) performed similarly well in the MRE model, while Positive Minutes (PM) showed comparable performance in the LRE model (Tables S3.1 and S3.2). Similar patterns emerged when using a dataset in which MRE and LRE passes were identified with a confidence score of at least 0.90, although the slope of the activity-mortality relationship and the variance explained were lower (Fig. S3.2; Tables S3.3 and S3.4). Additionally, when acoustic activity was not filtered to retain only exposed activity, the relationship became much weaker (Fig. S3.3).

In the best MRE model (i.e., considering exposed PH as the activity metric), the model fit was moderate (mean R^2 = 0.22, mean R^2adj = 0.12). Exposed PH was identified as a significant predictor in only 17% of iterations (mean pseudo-R^2 = 0.03), showing low and unstable effect estimates (Fig. 4A). By contrast, turbine characteristics, particularly rotor swept area and ground clearance, exhibited more consistent associations with mortality: rotor swept area was a significant predictor in 91% of iterations (mean pseudo-R^2 = 0.12), and ground clearance was a significant predictor in 26% of iterations (mean pseudo-R^2 = 0.04). Estimates indicate that mortality increased with increasing swept area and decreasing ground clearance (Table S3.1).

In the LRE model using exposed PH as the activity metric, model fit was slightly higher than in the MRE model (mean R^2 = 0.27; mean R^2adj = 0.18). Exposed PH was identified as a significant predictor in 67% of iterations (mean pseudo-R^2 = 0.08), with almost all estimates being positive (Fig. 4B; Table S3.2). As in the MRE model, rotor swept area was the most consistent predictor (significant in 95% of iterations; mean pseudo-R^2 = 0.14).

The MRE model predicted that 150 h with at least one bat pass were associated with an estimated five fatalities per turbine per year (Fig. 4A), whereas the LRE model predicted one fatality per turbine per year for the same level of activity (Fig. 4B).

3.3. Seasonal variation in the mortality-activity relationship

Estimated LRE fatalities were substantially lower between weeks 20 and 31 than during weeks 32 to 43, whereas estimated MRE fatalities remained relatively high throughout both periods, reaching extreme values of up to 80 individuals per turbine (Fig. S2.2).

For MRE, positive nights (PN) showed the highest level of significance across iterations, followed closely by positive hours (PH) during weeks 20–31 (Table S3.5), whereas PH and positive minutes (PM) yielded similar results during weeks 32–43 (Table S3.6). Specifically, PH was identified as a significant predictor in 19% of MRE model iterations during weeks 20–31, compared to 66% during weeks 32–43 (Fig. 5A and B). By comparison, PN was identified as a significant predictor in 33% of model iterations during weeks 20–31 and 43% during weeks 32–43 (Fig. 5C and D). However, model performance remained relatively low for both models. Models including PH explained, on average, 24% of the variation in estimated fatalities during weeks 20–31 (mean R^2adj = 0.14) and 22% during weeks 32–43 (mean R^2adj = 0.12). Similarly, models including PN explained 25% of the variation during weeks 20–31 (mean R^2adj = 0.15) and 20% during weeks 32–43 (mean R^2adj = 0.09). During weeks 20–31, the contribution of PN and PH to model performance was only marginal (mean pseudo-R^2 = 0.04–0.05), whereas the rotor-swept area explained a substantially larger proportion of the variance (mean pseudo-R^2 = 0.18–0.19).

For LRE, positive hours (PH) showed the highest level of significance across iterations, followed closely by positive nights (PN) during weeks 20–31 (Table S3.7). In contrast, positive minutes (PM) showed the highest level of significance across iterations during weeks 32–43, followed closely by PH (Table S3.8). Specifically, PH was identified as a significant predictor in 68% of LRE model iterations during weeks 20–31, compared to 55% in weeks 32–43 (Fig. 6A, B). By comparison, PM was identified as a significant predictor in 45% of model iterations

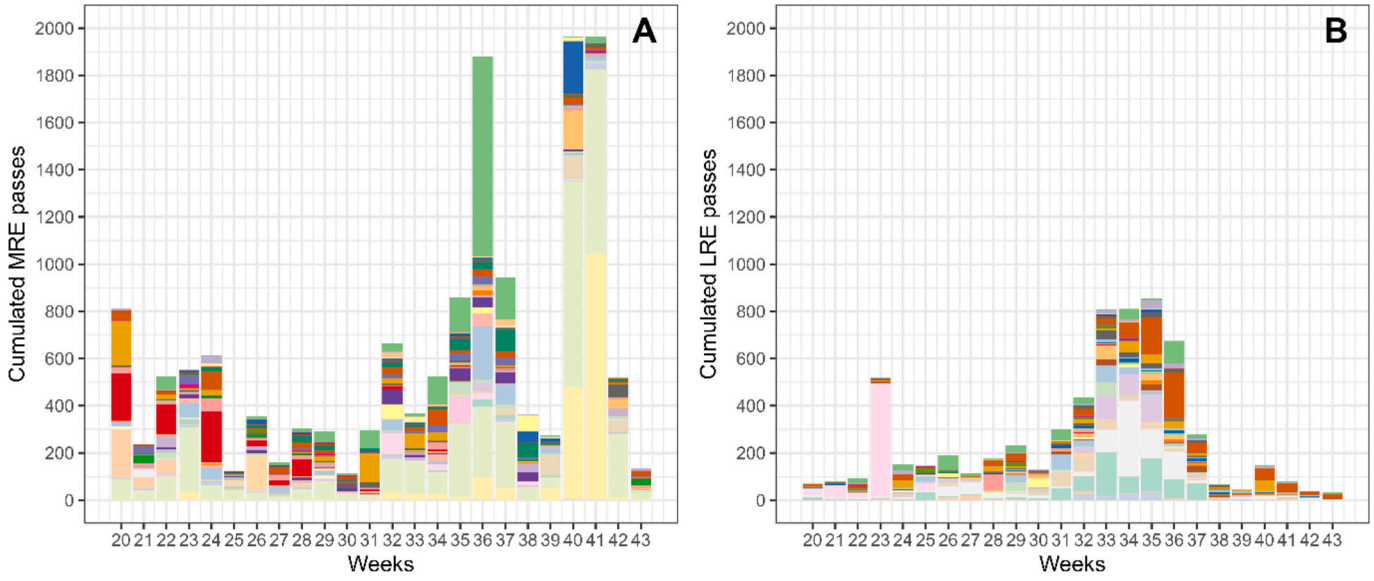


Fig. 3. Cumulative weekly MRE (A) and LRE (B) bat passes pooled across all monitored turbines and years. Only passes recorded during turbine operation (>1 rpm) are included. Colors represent different wind facilities (n = 45).

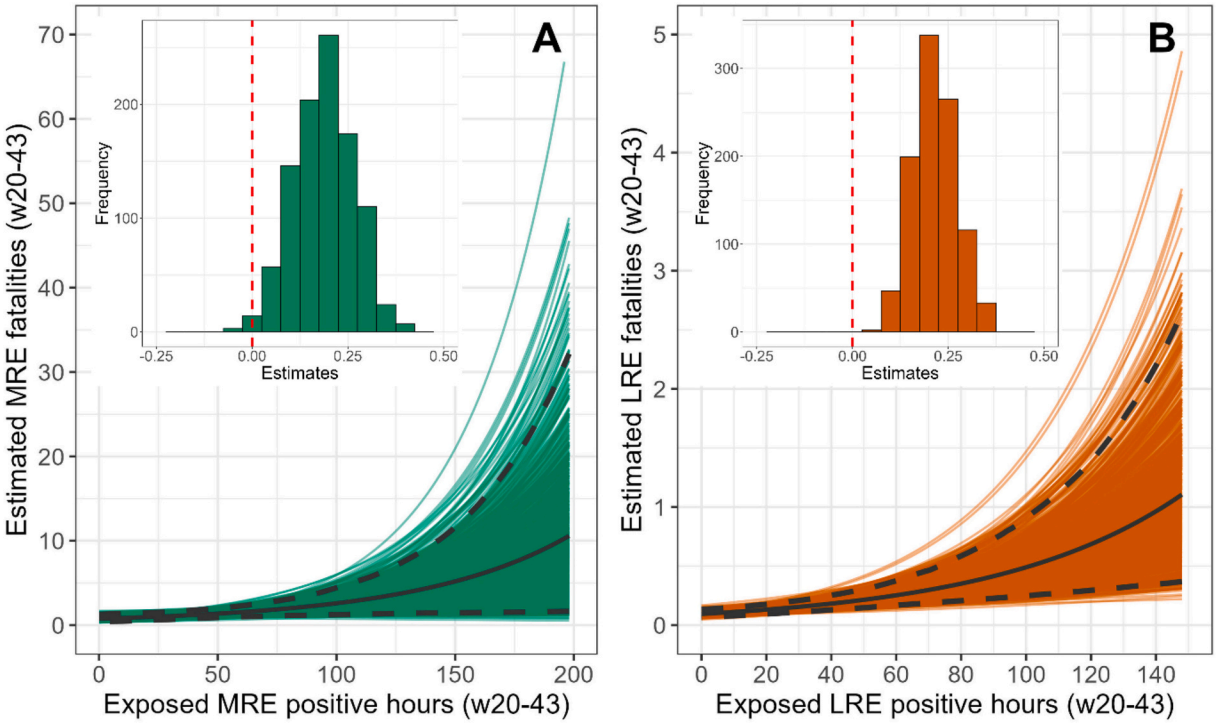


Fig. 4. Predicted number of MRE (A) and LRE (B) bat fatalities from bootstrapped generalized linear models, with 95% confidence intervals shown as dashed lines. These are plotted against exposed MRE (green) and LRE (orange) positive hours recorded during turbine operation (>1 rpm) and summarized for weeks 20–43. The solid black line represents the mean prediction curve. Each colored line corresponds to the prediction curve of one model iteration. The insets show the distribution of estimates across all iterations, with the red dashed line indicating zero. The y-axis has been back-transformed to the original scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

during weeks 20–31 and 66% during weeks 32–43 (Fig. 6C and D). LRE models that included either PH or PM as the activity metric performed slightly better than MRE models, particularly during weeks 20–31 (mean $R^2 = 0.31–0.33$, mean $R^2adj = 0.21–0.24$). However, both PH and PM contributed relatively little to model performance during this period (mean pseudo-R^2 = 0.06–0.08), compared to rotor-swept area (mean pseudo-R^2 = 0.17). Note that all model iterations presented in the Results section satisfied the model assumptions, as confirmed by standard residual diagnostic tests.

4. Discussion

Our study aimed to assess whether bat activity recorded at nacelle height could reliably predict mortality. To our knowledge, this study is based on one of the most comprehensive datasets assembled to date. It encompasses multiple regions and years, and explicitly accounts for key sources of bias affecting activity and fatality estimates. We also employed a dedicated analytical workflow to identify the temporal scale at which bat activity is most strongly associated with mortality. Even though fatality estimates bear a relatively high degree of uncertainty, our results indicated an overall positive relationship between estimated fatalities and exposed activity for both medium-range echolocators (MRE) and long-range echolocators (LRE). The relationship was stronger in late summer and early autumn, a period associated with peak activity and migratory movements. Although these results have several limitations and are restricted to onshore turbines in Western Europe, they provide further insight into the relationship between bat activity and mortality and highlight considerations that may improve its interpretation and application in wind facility planning and mitigation strategies.

4.1. Exposed activity as predictor of mortality

Overall, we observed a positive relationship between fatalities and nacelle-height activity for both MRE and LRE guilds, during all tested periods of the year. However, the strength of this relationship was only moderate, with R^2 values rarely exceeding 0.3. In most models, rotor-swept area contributed more to explaining fatality variation than exposed activity. This explanatory power is substantially lower than the values reported by Peterson et al. (2025) ($R^2 \approx 0.8$), who included exposed activity as the sole predictor in their models. A key difference between our study and that of Peterson et al. (2025) likely lies in temporal resolution. In our case, both activity and mortality were aggregated over relatively long periods (10 to 23 weeks) due to the low observed mortality rates (i.e., 222 carcasses observed across all 51 turbines and years combined) and the weekly frequency of carcass searches mandated by the French national protocol (MTES, 2018). In contrast, Peterson et al. used a biweekly resolution, enabled by carcass searches conducted every 2–3 days in a high-mortality region (i.e., 617 carcasses observed across all 69 turbines), which allowed for a finer characterization of short-term dynamics. Consistent with this difference, broad activity metrics (e.g., the number of positive hours or nights) performed better than other metrics in our models, likely because they are less sensitive to short-term fluctuations and are therefore better aligned with the coarse temporal structure of the fatality estimates. Our analyses were constrained by the limitations inherent in the fatality estimates derived from GenEst and EOA. Estimates based on a small number of carcass searches, particularly those spanning fewer than 10 weeks, were associated with significantly greater uncertainty. These constraints also limited the scope of our inferences. We had to aggregate estimates at wind facility and functional guild levels because search frequencies and observation biases prevented us from generating robust estimates of fatalities at the turbine or species level. This limitation is partly rooted in current monitoring protocols. Although the French national guidelines

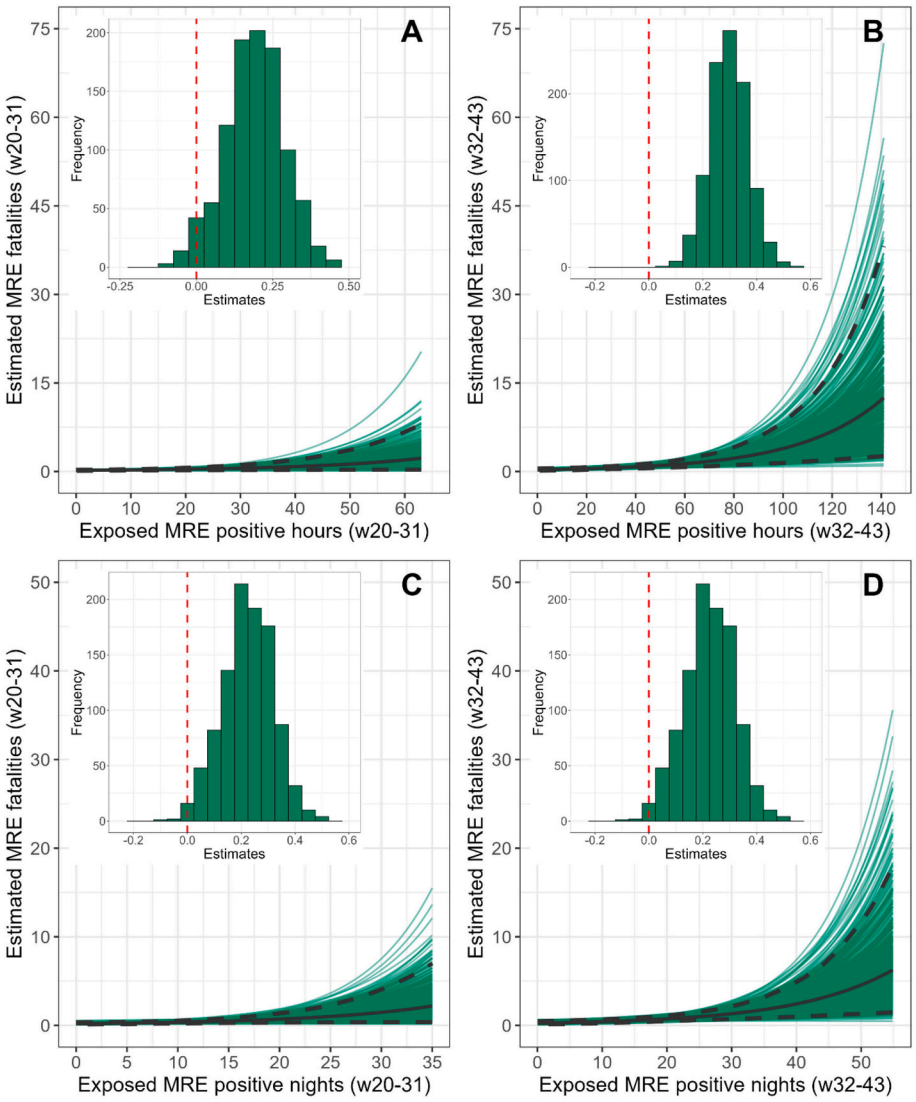


Fig. 5. Predicted number of MRE fatalities during weeks 20–31 (A, C) and weeks 32–43 (B, D) from bootstrapped generalized linear models. Dashed lines indicate 95% confidence intervals. Predictions are plotted against positive hours (A, B) and positive nights (C, D) recorded during turbine operation (>1 rpm), summarized for the corresponding weeks. The solid black line shows the mean prediction curve, while each colored line represents the prediction curve from a single model iteration. Insets display the distribution of parameter estimates across all iterations, with the red dashed line indicating zero. One wind facility was excluded from both datasets due to the absence of turbine operation data ($n = 44$ wind facilities). The y-axis has been back-transformed to the original scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recommend one carcass search per week, approximately 50% of bat carcasses in France disappear within two days (Ravache et al., 2026a), so such a sampling frequency is unlikely to accurately capture mortality data. Therefore, we strongly recommend increasing the frequency of carcass searches to improve the accuracy of mortality estimates. This may enhance our ability to predict collision risk from acoustic activity.

Although the explanatory power of our models was lower than that reported by Peterson et al. (2025), this comparison should be interpreted in light of important differences in study design. First, our microphones were oriented downwards, whereas those used by Peterson et al. were oriented horizontally. Future studies could therefore evaluate whether microphone position affects the strength of the activity–mortality relationship. In addition, Peterson et al. analyzed only two wind facilities under experimental conditions that minimized spatial and temporal heterogeneity and were restricted to a single turbine model. In contrast, our real-world dataset encompasses a much broader range of environmental contexts, years, and turbine characteristics, while relying on mortality estimates derived from large-scale monitoring programs rather than controlled experimental conditions. The lower explanatory power observed here is therefore an expected consequence of modelling a more heterogeneous system across a wider range of ecological and operational conditions. This trade-off is compensated by the greater generality and transferability of our findings, which are likely to be more representative of real-world variation among wind energy developments.

Another important point is the substantial difference in estimated fatalities between MRE and LRE functional guilds. Our models predict approximately five times more MRE than LRE fatalities for the same amount of activity. This difference should be interpreted while considering differences in acoustic detectability between MRE and LRE species (Frey-Ehrenbold et al., 2013). MRE species have shorter detection ranges than LRE species, meaning individuals are likely to be detected at different distances from the rotor-swept zone. Consequently, the same level of recorded activity may not represent an equivalent level of collision risk across functional guilds, since MRE activity may more frequently reflect individuals flying closer to the area of highest collision risk. Nevertheless, the higher mortality estimated for MRE species is consistent with observations across Europe, where MRE species such as

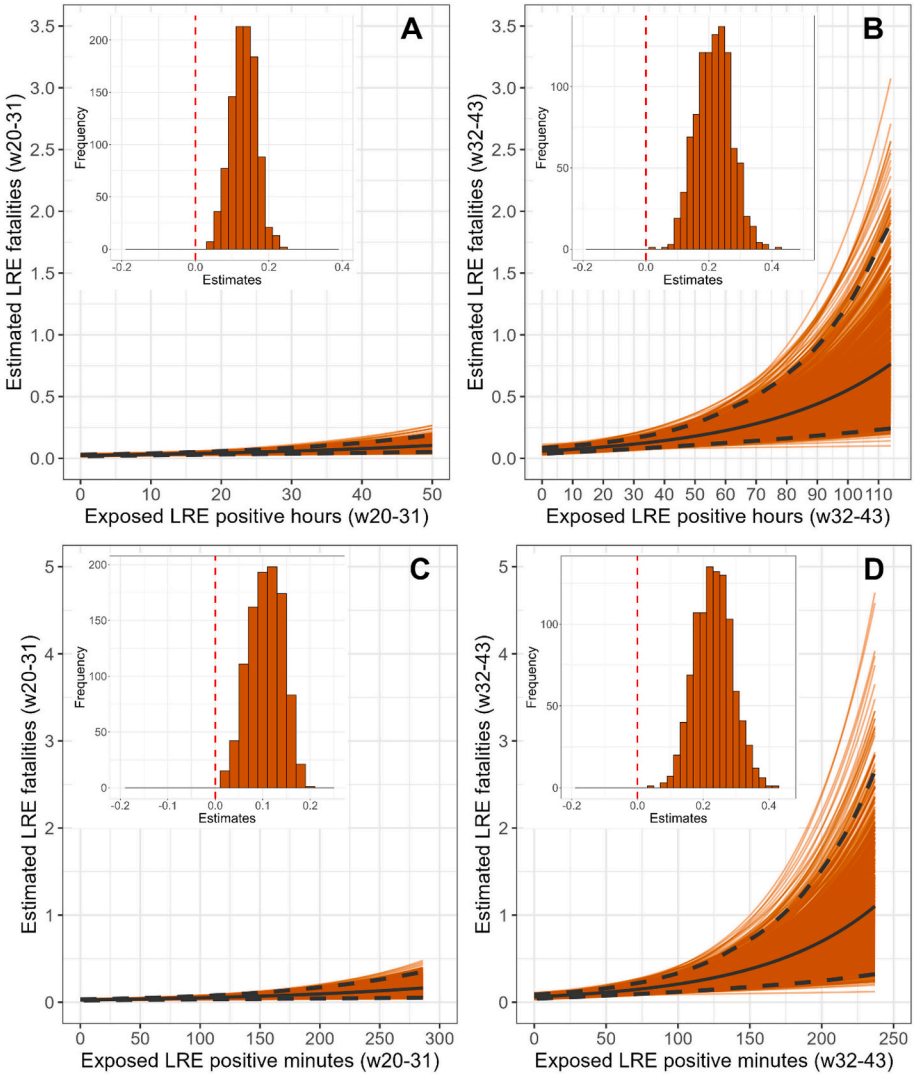


Fig. 6. Predicted number of LRE fatalities during weeks 20–31 (A, C) and weeks 32–43 (B, D) from bootstrapped generalized linear models. Dashed lines indicate 95% confidence intervals. Predictions are plotted against positive hours (A, B) and positive minutes (C, D) recorded during turbine operation (>1 rpm), summarized for the corresponding weeks. The solid black line shows the mean prediction curve, while each colored line represents the prediction curve from a single model iteration. Insets display the distribution of parameter estimates across all iterations, with the red dashed line indicating zero. Three wind facilities were excluded from both datasets due to the absence of turbine operation data ($N = 42$ wind facilities). The y-axis has been back-transformed to the original scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Pipistrellus spp. are among the most frequently recorded carcasses at wind turbines (Amorim et al., 2012; Rydell et al., 2010; Salguero et al., 2023). However, despite their higher recorded mortality, the population-level consequences are likely more pronounced for LRE species, as their populations are smaller (Kerbiriou et al., 2015) and declines have already been reported in central Europe, for example in the noctule bat *Nyctalus noctula* (Printz et al., 2021). In addition, a recent study in France that used stable isotope analysis of bat carcasses demonstrated that turbine-related mortality primarily affects local populations (Merlet et al., 2025). However, approximately 28% of common noctules originated from north-eastern Europe. As migratory bats can travel across large geographic areas, encountering numerous wind turbines along the way, mortality at individual wind facilities can have cumulative consequences at the population level.

4.2. Seasonal variation in the mortality-activity relationship

The activity recorded at turbine rotor speeds above 1 rpm followed patterns that aligned with the overall activity reported at other wind energy facilities in temperate regions of North America and Europe. Specifically, bat activity near wind turbines generally peaks in late summer and extends into autumn for most species (Barré et al., 2023; Goldenberg et al., 2021; Nagy et al., 2026; Peterson et al., 2025). This seasonal increase in activity is generally attributed to three non-mutually exclusive processes: (i) the passage of migratory individuals (Voigt et al., 2023); (ii) the elevated energy requirements associated with migration, mating and pre-hibernation fat accumulation; during this period, bats may be attracted to wind turbines by local insect aggregations (i.e. "attraction to insect aggregations" hypothesis; Cryan and Barclay, 2009) and (iii) the presence of juveniles following the breeding period, which may contribute to a temporary increase in local abundance (Dietz et al., 2009). More recently, evidence has emerged to suggest that some European species actively use the rotor-swept zone for mating behavior (Nagy et al., 2026), indicating that turbines may also serve as attractive structures for such activities at this time of year. In line with this, our study found steeper slopes (i.e., higher estimates) in the mortality–activity relationship during the period from late summer to mid-autumn (weeks 32–43) than in the earlier period, for both MRE

and LRE. This suggests an increased risk of collisions during this time of year. This seasonal pattern may be related to changes in bat population structure and behavior following the breeding season. A previous study investigating Nathusius' pipistrelles (*Pipistrellus nathusii*) killed at wind turbines identified age as a key factor in mortality, with juveniles appearing particularly vulnerable to collisions (Kruszynski et al., 2022). The stronger mortality–activity relationship observed during this period may therefore partly reflect the increased presence of recently fledged individuals with lower flight experience who are more susceptible to turbine collisions. Consequently, particular caution may be warranted when maternity colonies are located in close proximity to wind facilities. Further fine-scale studies conducted after the implementation of wind facilities would be valuable in assessing how colonies adjust their movements and whether displacement or altered habitat use occurs. Furthermore, seasonal changes in flight behavior should be considered. The late summer/autumn period coincides with increased migratory activity in some species (Rydell et al., 2014; Voigt et al., 2023). Migratory individuals may exhibit flight patterns that increase their exposure to turbines, such as "investigative behaviors," characterized by repeated approaches in close proximity to turbine surfaces (Cryan et al., 2014; Goldenberg et al., 2021). These behaviors may reflect attempts to assess potential resources or responses to unfamiliar structures in the environment. These findings emphasize the need to incorporate seasonal variations in bat vulnerability into mitigation strategies (i.e., curtailment schemes), since measures that are effective during one period may not provide the same level of protection throughout the year.

4.3. Caveats and recommendations

(a) *Uncertainty in the spatial representation of collision risk*

Despite the care taken in modelling the relationship between activity and mortality, including limiting material variation, filtering bat passes below 1 rpm to account for turbine operation and incorporating ground clearance and rotor-swept area to better represent the zone of collision risk, several key assumptions remain. First, our analyses did not account for the vertical distribution of LRE and MRE species within the rotor-swept zone, assuming a homogeneous one (Fig. 7A). Yet, collision risk depends not only on bat activity levels but also on how activity is distributed within the airspace intersecting turbine blades. Unmeasured variation in flight-height use among species, sites, or periods may therefore decouple acoustic activity from observed fatalities, potentially obscuring the true relationship between bat presence and mortality (Voigt et al., 2022). A key limitation is the current lack of detailed information on species-specific flight-height distributions, which prevents a more accurate characterization of the airspace actually exposed to collision risk and may contribute to unexplained variation in mortality patterns (Fig. 7B). Although several approaches are increasingly being developed to quantify bat flight heights, including GPS tracking (Roeleke et al., 2016) or acoustic monitoring at multiple heights (Wellig et al., 2018), such data remain available for only a limited number of species. Second, we assume that bats flying within the rotor area all have the same probability of collision. However, it is plausible that collisions occur more frequently near the fast-moving blade tips, where even low rotation speeds can result in lethal impacts. In this context, a concentration of bats near the nacelle (close to acoustic detectors), may not translate into higher fatality rates (Cryan et al., 2014; Goldenberg et al., 2021), and could even be associated with lower risk compared to activity concentrated near the outer edge of the rotor-swept area (Fig. 7B). We further highlight the urgent need for additional movement ecology studies, particularly employing 3D trajectory tracking approaches (Cryan et al., 2014), to more precisely characterize spatial use in relation to wind turbine components such as the nacelle and blades. Finally, the high spatial variation, previously reported, in bat activity at nacelle height (Barré et al., 2023) and mortality (Thompson et al., 2017) due to factors such as landscape composition, topography, and distance from the coast, could generate statistical noise and contribute to the low proportion of variance explained. Bach et al. (2020), for instance, reported a weak correlation between acoustic activity and bat fatalities at coastal sites, which could be due to differences in bat flight behavior during migration. Therefore, future studies covering sufficient landscape gradients could assess the activity-mortality relationship across different landscape contexts.

(b) *Acoustic activity as an indicator, not an accurate predictor, of bat mortality*

Our results demonstrate a positive relationship between bat fatalities and acoustic activity, although the strength of this relationship appeared variable among guilds and season. This variability does not negate the

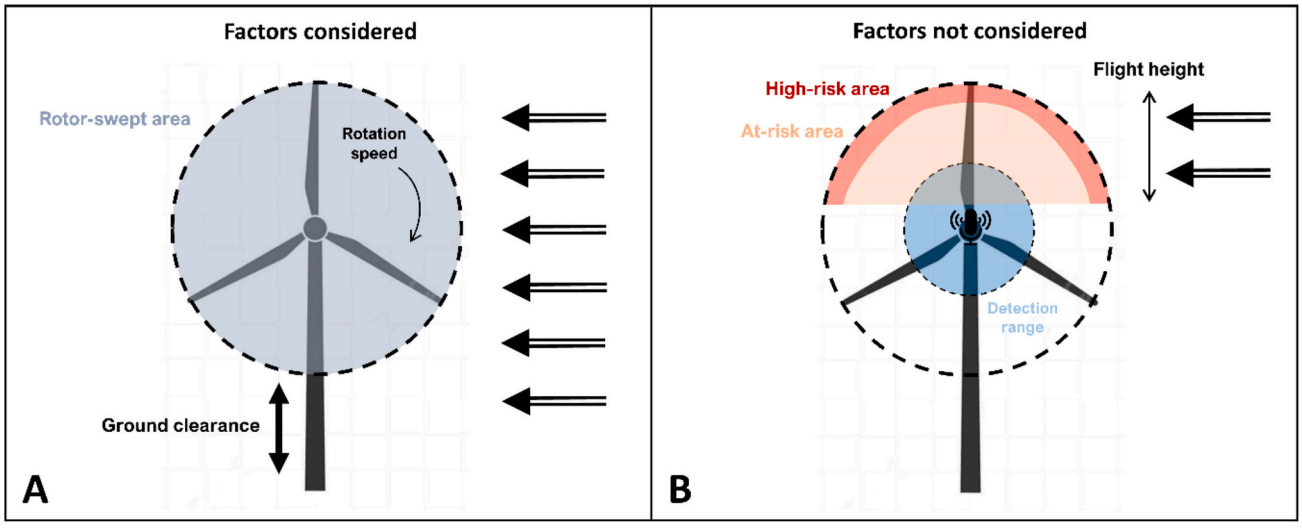


Fig. 7. Schematic representation of wind turbines illustrating (A) the parameters included in this study such as rotor-swept area (grey shading), turbine rotation speed, and ground clearance and (B) key missing information, notably species-specific flight heights, which are critical for accurately defining the at-risk area (pink shading) and the detection range of the batcorders (blue shading). The highest-risk zone is expected to occur at the blade tips (red shading). Thick arrows represent bat flux, assumed to be homogeneous in our study but likely species-specific in reality. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

operational relevance of acoustic recording to determine activity on one site. Acoustic activity has considerable potential to support environmental authorities in their decision-making regarding wind turbine approvals. However, as our models only explained a limited proportion of the observed variance, our findings do not support using acoustic activity as a reliable standalone predictor of bat fatalities before or after wind facility construction within the framework of an Environmental Impact Assessment (EIA). This limitation is further emphasized by evidence that bat activity can differ substantially between the pre- and post-construction phases (Hein et al., 2013; Lintott et al., 2016; Richardson et al., 2021; Solick et al., 2020). Several studies have shown that attraction behaviors follow the implementation of wind facilities (Cryan et al., 2014; Ellerbrok et al., 2023; Horn et al., 2008; Richardson et al., 2021), while others have demonstrated repulsive effects (Ellerbrok et al., 2022; Gaultier et al., 2023). Our results also emphasize the importance of considering turbine characteristics, particularly rotor-swept area and ground clearance, when planning wind facilities. MRE fatalities were negatively associated with ground clearance, whereas a strong positive association was observed between rotor-swept area and fatalities in both MRE and LRE species. Therefore, selecting turbine configurations adapted to local bat assemblages could help to reduce the risk of collisions and limit the need for curtailment, thereby minimizing associated energy losses.

(c) *Acoustic activity as a tool for designing effective curtailment strategies*

Our results do not contradict the use of acoustic activity data to inform effective curtailment strategies. The absence of a strong relationship between acoustic activity and recorded mortality is likely due, at least in part, to the limited temporal resolution of the mortality data, which was aggregated over several weeks. In contrast, acoustic monitoring provides continuous, high-resolution measurements of bat activity, enabling much finer characterization of temporal patterns in collision risk. Therefore, even when direct relationships with estimated fatalities are difficult to detect, acoustic activity remains a valuable tool for informing targeted curtailment strategies. This can be achieved by incorporating acoustic activity into predictive curtailment algorithms (e.g., Barré et al., 2023; Behr et al., 2017; Brinkmann et al., 2011), or by using it to define wind speed and temperature thresholds that are calibrated to local patterns of bat activity (Ravache et al., 2026b). The differences we observed between LRE and MRE functional guilds and across seasons suggest that mitigation strategies should adopt a precautionary, season- and guild-specific approach. Defining curtailment thresholds based on seasonal and guild-specific acoustic activity could improve mitigation efficiency while limiting unnecessary energy losses. Curtailment could be intensified during peak activity periods, particularly under low wind conditions favorable for bat activity, and relaxed during lower-risk periods to balance protection goals and energy production. Despite the growing body of evidence demonstrating the efficacy of such approaches (even when based on relatively simple thresholds, e.g., Arnett et al., 2011; Whitby et al., 2024), they are not systematically implemented or do not always operate effectively.

5. Conclusion

Our results confirmed a relationship between acoustic activity and estimated fatalities. However, they also highlight the limitations of using acoustic activity alone to accurately predict bat mortality levels since the strength of this relationship varies seasonally and is subject to substantial uncertainty. Additionally, our findings are specific to onshore wind facilities in Western Europe, and their applicability to other contexts is yet to be determined. Nevertheless, this study provides valuable insights into interpreting and applying acoustic activity data to assess collision risk, inform wind facility planning, and develop effective curtailment strategies. Ultimately, these contributions could help reconcile biodiversity conservation with wind energy development.

CRediT authorship contribution statement

Elise Sivault: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Andreas Ravache:** Writing – review & editing, Methodology, Conceptualization. **Nell Jousselin:** Writing – review & editing, Data curation. **Kevin Barré:** Writing – review & editing, Validation, Methodology. **Brice Normand:** Writing – review & editing, Supervision, Funding acquisition, Data curation, Conceptualization. **Christian Kerbiriou:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

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Declaration of competing interest

At the time of submission, co-author Brice Normand was employed by Ouest Am', and Nell Jousselin was employed by Calidris, both of which are environmental consultancies involved in wind turbine impact assessment studies. Authors thus declare a direct conflict of interest according to Biological conservation ethics. Authors take complete responsibility for the integrity of the data and the accuracy of their analysis.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.112182.

Data availability

Data used in this study are available at https://doi.org/10.5281/zenodo.23889623. Rotation speed data cannot be shared due to confidentiality agreements.

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