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RESEARCH ARTICLE

Influence of landscape and time of year on bat-wind turbines collision risks

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Abstract
Context Collisions with wind turbines threaten bat populations worldwide. Previous studies tried to assess the effects of landscape on mortalities. Yet, the count of carcasses found per species is low, leading to a low statistical power. Acoustic surveys collect large datasets (proxy for bat density); however, if bat vertical distribution is not accounted for, a key mechanism in collisions is missed.
Objectives Our goal was to disentangle the effects of landscape on bat density and vertical distribution to produce recommendations for wind farm siting.
Methods With a vertical array of two microphones, we monitored the acoustic activity and located the vertical distribution of more than 16 bat species on 48 wind masts in France and Belgium (> 8000 nights). We modelled bat density and vertical distribution for six species in function of distance to water, woodland and buildings, and in function of the topography at three different scales (200 m, 1000 m and 5000 m).
Results The proportion of flights at heights with collision risk was maximum in spring and autumn and minimum in summer for three species. This effect was often antagonistic to the effect of bat density. The landscape had a stronger effect on bat density than on bat vertical distribution.
Conclusions Positioning wind farms away from woodland should reduce the density and therefore the collision risks of low-flying species but should be inefficient for high-flying species. The effect of topography was stronger at large scales and complex, thus studying situations such as coastlines or mountain passes would provide more insight.

Keywords Bat collisions · Distance to woodland · Topography · Per capita collision risks · Acoustic location · Vertical flight distribution

Introduction

International projections predict a global increase in solar and wind energy installations for the next decades (AIE 2017). Despite their benefits for climate,

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wind turbines (WT) can have strong negative impacts on birds and bats through deaths by collision and barotrauma (Rydell et al. 2010; Loss et al. 2015; Laranjeiro et al. 2018), or because of habitat loss (Minderman et al. 2012, 2017; Barré et al. 2018; Millon et al. 2018). This has been a rising cause of concern, especially for bats because of their poor conservation status and their low reproductive rate, making them highly vulnerable to additional sources of mortality (Barclay and Harder 2003; Voigt and Kingston 2016). Some projections identified WT as a possible cause of extinction for certain bat species (Frick et al. 2017).

Currently, the most efficient way of mitigating bat fatalities is raising the WT cut-in speed (wind speed above which electrical power is produced) at a threshold above which bats avoid flying (Arnett 2016). Nonetheless, even if mortalities are greatly reduced with this method, they still occur (Arnett et al. 2016). Some evidence shows that not all bats respond similarly to wind speed, high-flying species being apparently more tolerant to strong winds than low flying species (Wellig et al. 2018), and WT operational mitigation may selectively affect them (Voigt et al. 2015).

The most efficient strategy to obtain no biodiversity net-loss is the avoidance of the impact (Bigard et al. 2017). In this process, landscape planning can be a very efficient tool for species conservation. Indeed, the level of impact of a wind farm may be highly influenced by the type of landscape surrounding it. If wind farm siting is carefully selected to avoid co-occurrence of high-flying species, WT operational mitigation should be more efficient both to avoid bat mortality and to maximise electrical power production. However, even if some initiatives exist at the regional level, we are aware of no national scheme for the strategy of wind energy planning that considers high-risk areas for birds or bats susceptible to WT collisions (Voigt et al. 2018; Sordello et al. 2019).

Several studies have tried to identify landscape predictors of bat fatalities at wind turbines. Santos et al. (2013) found that mortality probabilities decreased with the distance to eucalyptus forests. Other studies showed that open habitats such as prairies, pastures and croplands triggered fewer collisions than closed habitats such as forests (Piorkowski and O'Connell 2010; Bolívar-Cimé et al. 2016; Thompson et al. 2017). Piorkowski and O'Connell (2010) found more fatalities in ravine topography than in low topography relief and Santos et al. (2013) found that distance to the slope was negatively correlated with mortality risks.

Studies using the count of carcasses to infer the effect of landscape on anthropogenic mortalities have a debatable predictive power at large scale because of small datasets and because different species are often pooled. Indeed, species perceive landscape heterogeneity differently in function of their ecological needs (Peixoto et al. 2018) and the influence of the landscape should be studied for each of them. Furthermore, animal carcasses are a response variable that is, in fact, the product of two different components i.e., species local density and species behaviour (Zimmermann Teixeira et al. 2017). Consequently, if a landscape variable has antagonistic effects on animal density and per capita mortality, it will have no effect on the total count of carcasses, and key mechanisms will be missed. Moreover, the use of fatality data is subject to several methodological biases (i.e. carcass persistence time, observer efficiency, land cover, prospection area …) and the scarcity of data often prevents an efficient control of these biases (Huso et al. 2015).

In this study, we used an alternative approach to assess the influence of landscape features on bat collision risks at WT, disentangling their separate effects on bat species local density and on bat vertical distribution. To do so, we used unattended stereo acoustic monitoring, which provides information on species use of sites all-year-round, species density, and species vertical distribution thanks to multiple synchronous microphones (Jensen and Miller 1999). We assessed the effect of several landscape variables on bat species local density on one hand and on bat vertical distribution on the other hand. We performed those analyses at several spatial scales to identify the most influential on bat mortality risks at WT. We also controlled for the effect of time of the year, which is known to explain the temporal distribution of WT collisions (Arnett et al. 2016).

Materials and methods

Acoustic recordings

48 sites were surveyed in France and Belgium between 2011 and 2018 during a total of 8435 nights (mean =

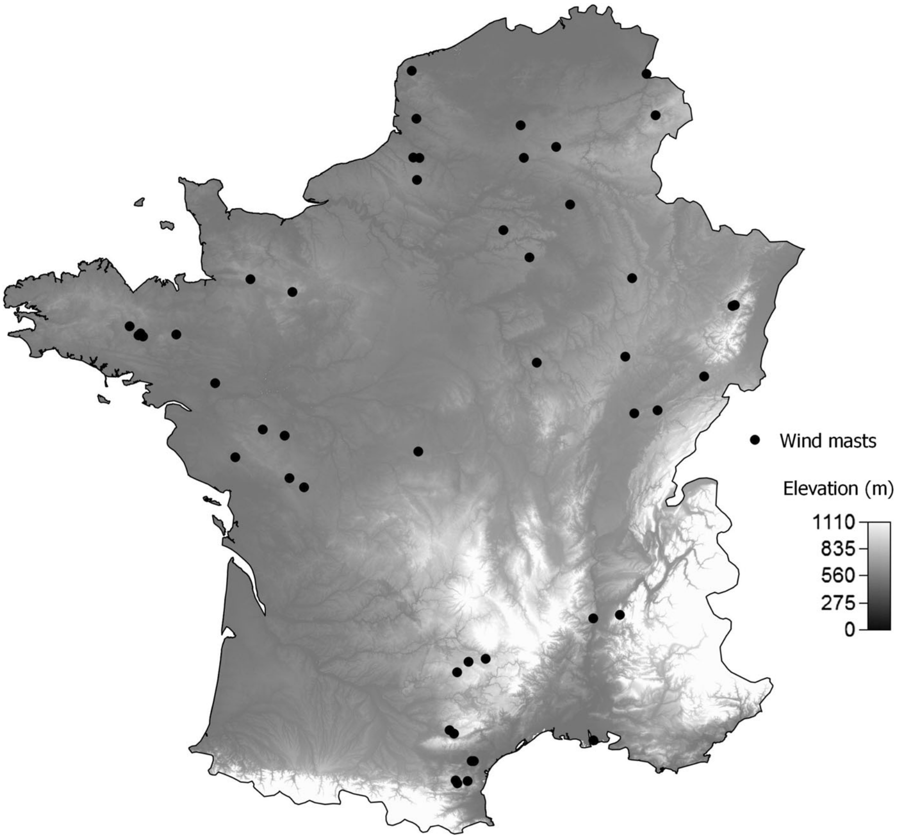

Fig. 1 Location of French and Belgian study sites and representation of the elevational gradient

175.7, standard deviation = 76.1, min = 19, max = 352 nights per site) (Fig. 1). Surveys targeted bat annual periods of activity (Fig. A1 in Electronic Supplementary Material 1). Lattice or monopole wind masts of 50–100 m high were equipped with two ultrasound microphones (SMX-US, SMX-U1 or SMM-U1, Wildlife acoustics, USA, or BMX-US, Biotope, France) plugged to an SM2BAT or SM3BAT recorder (Wildlife Acoustics, USA). One microphone was installed near ground level and a second at height (Fig. A2 in Electronic Supplementary Material 1). In forests, wind masts were installed in clearings of 10–30 m radius.

Recorders were programmed to start each day 30 min before sunset and stop 30 min after sunrise. Between 2013 and 2016 (38 sites), whole night recordings were performed. Before 2013 (10 sites), samplings were collected for 10 min every 20 min. The gain was set at 36 dB for SMX-US and BMX-US microphones or 0 dB for SMX-U1 and SMM-U1 microphones because they have a pre-integrated gain. Sampling rate was set at 192 kHz, trigger at 6 dB for SM2BAT and 12 dB for SM3BAT (for equivalent sensitivity) and trigger window at 2.5 s. A 1 kHz high pass filter was used.

Species identification and flight height classification

Species identification was performed based on acoustic features as stated in Roemer et al. (2017) using SonoChiro (Biotope/MNHN, France) and a manual check. Bat passes (defined as one or more bat calls within 5 s) that belonged to the genera *Pipistrellus*, *Nyctalus*, *Eptesicus* or *Vespertilio* and that could not be identified at the species level were marked as unidentified bats. The latter sequences, as well as all other unidentified bat passes, represented 8.4% of our dataset and were not used for further analyses. Concerning the group of species *Pipistrellus kuhlii*/*nathusii*, acoustic knowledge is presently too scarce to differentiate both species with certain confidence. Identifications were achieved using acoustic cues described as “typical” for these species at the time of analysis (Barataud 2015) and with the knowledge that *Pipistrellus kuhlii* is very rare or absent in Northern France and Belgium (Arthur and Lemaire 2015). However, readers must be aware of potential biases in the results presented here for *P. kuhlii* and *P. nathusii*. Bat passes with no typical feature of either species were not identified (37.5% of this group).

To obtain species vertical distribution profiles, we calculated the Time of Arrival Difference (TOAD) of each call to both microphones (Koblitz 2018). According to the value of TOAD; it was then possible to deduce if the bat was above (i.e. at height) or below (i.e. at ground level) the median height of both microphones (see Roemer et al. (2017) for details about the method).

Landscape variables

To cover the variability of home ranges of European species (Arthur and Lemaire 2015), we described the landscape within buffers of 200 m, 1000 m and 5000 m radius around wind masts (Fig. A3 in Electronic Supplementary Material 1).

We estimated distance to trees, to buildings likely to provide roosts for bats (i.e. with hard roofs and walls), and to water bodies accessible for drinking for bats. Landscape data were retrieved from the BD TOPO 2.2 (Institut National de l’Information Géographique et Forestière 2017) for French study sites or measured visually on Google satellite pictures for Belgian study sites. To assess the effect of landscape structure, we also calculated for French study sites (46 out of 48) the percentage of woodland and woodland contagion index. The contagion index is an aggregation index implemented in the FRAGSTATS 4.2 software (McGarigal et al. 2012) which provides information about the balance of patch distribution in a defined landscape. It was considered in our study as a basic metric of the presence of landmarks that could be used for species during commuting. A high contagion score means that the landscape was either filled with one patch or empty of the type of patches considered. A low contagion score means that the different patches were evenly distributed.

Altitudinal variables were retrieved from the ASTER digital elevation model (DEM) version 2 (NASA JPL 2009). This model represents the elevation of the terrain including buildings or woodland and has a precision of approximately 30 m at the equator. We chose to use this model instead of a classical topographical map (describing bare ground elevation) because we were interested in the influence of all main three-dimensional structures on bat flight height. We noted the altitude of wind masts at their foot, and for the three different buffers, we calculated their altitudinal amplitude (difference between maximum and minimum elevations within the buffers) and the position of the wind mast on the elevational gradient (difference between mast elevation and minimum elevation multiplied by 100 and divided by the altitudinal amplitude).

The installation of wind masts in forests is preceded by clear-cuts that are generally not considered in the BD TOPO and the DEM. In this case, we manually modified the measured distance to trees using Google satellite pictures or our knowledge of the field. We did not modify the elevation of woodland retrieved from the ASTER digital elevation model to correct for this bias because grid size precision (30 m) exceeds distance to trees in forests.

Statistical analyses

All predictor variables were normalised if necessary and scaled to allow a comparison of effect magnitude. We first tested for any correlation between landscape variables using the corrplot function of the stats package in the R program (R Core Team 2014). Percentage of the woodland cover was positively correlated with altitude (r = 0.36–0.64 depending on buffer size) and altitudinal amplitude (r = 0.12–0.73 depending on buffer size) and contagion was positively correlated with distance to trees (r = 0.23–0.65 depending on buffer size) (Table A1 in Electronic Supplementary Material 1). We, therefore, removed percentage of woodland cover and contagion from our analyses to only retain variables that were retrievable with more direct calculations. We removed altitude to keep altitudinal amplitude because it integrated a proxy for slope.

We next separated our analysis in two steps: first the modelling of species density (number of bat passes per night) and second the modelling of species proportion of flight at height (number of bat passes at height divided by the total number of bat passes), both in function of landscape and topography variables. To model species density, the number of bat passes belonging to sites from before 2013 were multiplied by two because samplings were collected for 10 min every 20 min.

The package glmmTMB (Brooks et al. 2017) of the R program (R Core Team 2014) was used for both models. Bat density was modelled with a negative binomial distribution (nbinom2) while bat proportion of flight at height was modelled with a binomial distribution. Each species was modelled separately with the study site as a random effect, and an additional model concerned all species with the study site and species as crossed random effects. To ensure model robustness of species-specific models, we only kept the species for which we had enough bat passes at height in our dataset (> 1000) and that occurred on enough study sites (> 25) (Table A2 in Electronic Supplementary Material 1). Because some study sites were very close to each other (< 10 km), we avoided spatial autocorrelation of observations by creating a 'Group' variable that gave a common identity to study sites separated by less than 10 km. This variable was used in all models as a random effect. Study sites were nested within groups (i.e. (1|Group/Site)).

Julian day (as a quadratic effect) and microphone median height were introduced as obligatory fixed effects in all models to control for undesired variability in the results. Latitude and longitude as well as all other landscape and topographical variables were proposed as optional fixed effects and submitted to model selection. Topological and landscape parameters were tested in simple interactions with each other. This was not the case for Julian day, longitude and latitude, that we did not expect to play a role in interaction with other predictors.

A stepwise forward model selection was then performed using Akaike's information criterion (AIC) (Burnham and Anderson 2003; Bolker et al. 2009). At each step of model selection, the VIF (Variance inflation factor), which quantifies the degree of multicollinearity in least squares regression analyses, was calculated. If any of the selected variables had a VIF > 3 (Heiberger and Holland 2004; Zuur et al. 2010), the model was not considered as a candidate. At each step of model selection, the model with the smallest AIC was considered. This model was retained and the selection was allowed to continue as long as its AIC was at least inferior by two points to the AIC of the best model of the previous step (Arnold 2010).

For some species, there were common variables in the two models (bat density and bat vertical distribution). To interpret the effect of these variables on the resulting bat collision risks, we also directly modelled the number of bat passes per night located at height in function of all the variables that were selected in either model. This response was modelled with a negative binomial distribution (nbinom2) using the package glmmTMB (Brooks et al. 2017) of the R program (R Core Team 2014). As in the previous models, study sites nested within groups were introduced as a random variable.

Results

Bat activity recorded

In total, 634,000 bat passes were recorded. 17 species were identified with certainty, as well as the groups of *Plecotus* sp., *Myotis blythii*/*myotis* (large *Myotis*) and the other *Myotis* (small *Myotis*) (Table A2 in Electronic Supplementary Material 1).

Vespertilio, *Nyctalus* and *Tadarida* species prevailed at height (20–90% of the time at height). They were followed by *Hypsugo*, *Pipistrellus* and *Eptesicus* species (5–35% of the time at height). *Myotis*, *Miniopterus* and *Barbastella* species were rarely recorded at height (< 5% of the time at height). *Rhinolophus* species were never recorded at height (Table A2 and Fig. A4 in Electronic Supplementary Material 1).

From April to November, the mean number of bat passes at height per night and per month overall study sites varied between 3 and 18 (standard deviation varied between 24 and 62). This high variability was due to one study site that was monitored in October only and that was the only one in wetlands (32 m from a canal, near the Mediterranean coast). It showed an extremely high bat density at height (mean = 256.4 bat passes per night, mostly represented by *P.kuhlii*/*nathusii*) compared to all other sites monitored in October (mean = 10.9, standard deviation = 15.8 bat passes per night).

Scale

Larger scales were more effective to explain bat density and flight behaviour than smaller scales (Tables 1, 2). Most species responded to buffers of 5000 m (altitudinal amplitude and position of a mast

Table 1 Summarised statistical results of the negative binomial distributed generalised linear mixed effect models (GLMM) for the density of each species

Variables	All species			Pipkuh			Pippip			Eptser			Pipnat			Nyclei			Nycnoc		
	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P
Intercept	−0.72	0.63		0.03	0.33		4.21	0.13	***	0.45	0.24	.	−0.63	0.16	***	0.63	0.20	**	−2.50	0.40	***
Mic. Med. H.	−0.31	0.12	**	−0.34	0.31		−0.19	0.13		−0.26	0.24		−0.05	0.15		0.36	0.19	.	0.43	0.37	
Julian Day	0.09	0.01	***	−0.08	0.04	*	0.05	0.02	*	−0.46	0.05	***	0.39	0.04	***	0.27	0.04	***	0.30	0.06	***
Julian Day^2	−0.80	0.01	***	−0.87	0.04	***	−0.94	0.02	***	−1.75	0.06	***	−0.46	0.05	***	−0.75	0.04	***	−0.96	0.07	***
Latitude	−0.65	0.15	***	−2.40	0.39	***	0.29	0.13	*				1.05	0.19	***	−0.92	0.20	***			
Longitude				−1.13	0.37	**	0.29	0.13	*				0.48	0.17	**	1.18	0.21	***			
Dist. water													−0.31	0.18	.						
Dist. woodland	−0.60	0.15	***	−1.23	0.36	***	−0.59	0.14	***	−0.64	0.25	**									
Δ Alt. (B = 1000 m)							−0.39	0.14	**												
Δ Alt. (B = 5000 m)				−0.88	0.39	*				−1.04	0.25	***	−0.55	0.19	**				−1.07	0.39	**
Pos. elev. (B = 5000 m)	−0.37	0.13	**										−0.47	0.16	**						
Δ Alt. (B = 5000 m): Pos. elev. (B = 5000 m)													0.77	0.19	***						

$\hat{\beta}$ = estimate; SE = standard error; P = significance of P value. Species names are given with the first three letters of the species and genera. Interactions are noted with a colon. B = buffer size. Mic. Med. Height = microphone median height; Dist. = distance; Δ Alt. = altitudinal amplitude; Pos. elev. = position of wind mast in elevational gradient

.$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

Table 2 Summarised statistical results of the binomial distributed generalised linear mixed effect models (GLMM) for the proportion of flight at height of each species

Variables	All species			Pipkuh			Pippip			Eptser			Pipnat			Nyclei			Nycnoc		
	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P	$\hat{\beta}$	SE	P
Intercept	−2.49	0.60	***	−3.50	0.22	***	−2.10	0.16	***	−2.12	0.19	***	−0.22	0.16		0.34	0.13	*	0.53	0.20	**
Mic. Med. H.	0.10	0.13		0.11	0.21		0.19	0.15		−0.16	0.19		−0.09	0.16		−0.13	0.12		−0.22	0.18	
Julian Day	0.12	0.00	***	0.34	0.02	***	0.17	0.01	***	0.02	0.05		0.02	0.02		−0.27	0.02	***	0.06	0.04	
Julian Day2	0.23	0.00	***	0.82	0.02	***	0.16	0.01	***	0.09	0.04	*	−0.05	0.02	*	0.22	0.01	***	0.00	0.04	
Dist. water																0.27	0.12	*			
Pos. elev. (B = 5000 m)													0.55	0.16	***						

$\hat{\beta}$ = estimate; SE = standard error; P = significance of P value. Species names are given with the first three letters of the species and genera. Interactions are noted with a colon. B = buffer size. Mic. Med. Height = microphone median height; Dist. = distance; Pos. elev. = position of wind mast in elevational gradient

.$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

in elevational gradient), while only *P. pipistrellus* responded to a scale of 1000 m (altitudinal amplitude). The scale of 200 m for both response variables was never selected in models.

Control variables

The density of species decreased to the North, except for *P. pipistrellus* and *P. nathusii,* and increased to the East, except for *P. kuhlii* (Table 1). We found a gradual increase in density from spring to summer, followed by a decline in autumn. Patterns were similar for all species; an example is displayed for *N. leisleri* (Fig. 3a). The proportion of bat passes at height was near minimum at the time when bat density peaked for several species (e.g. *N. leisleri* (Table 2; Fig. 3b)), however, there was no significant pattern for *E. serotinus*, *P. nathusii* and *N. noctula* (Fig. A6 in Electronic Supplementary Material 1). Density at height displayed similar patterns as density (ground level and height included), with a peak in summer (Figs. 3c and A6 in Electronic Supplementary Material 1). Microphone height influenced measured species density when modelling all species at once but did not influence the measured proportion of flight at height (Tables 1, 2). Nonetheless, for *P. kuhlii* and *E. serotinus*, higher microphone median heights were associated with a lower density at height (Table A3 in Electronic Supplementary Material 1).

Landscape

Distance to woodland negatively affected density for species of low or medium flight height (i.e. *P. pipistrellus*, *P. kuhlii* and *E. serotinus*), and more generally on the density of all species (Table 1; Fig. 2a). Distance to water had a negative effect on *P. nathusii* density.

Altitudinal amplitude negatively affected the density of most species, but this variable was not selected in the model where all species are grouped. Bat density for all grouped species was lower near hill or mountain tops than near to valleys (Fig. 2b). For *P. nathusii*, in lowlands, density (ground level and height included) decreased when the mast was closer to hilltops, while in mountainous areas, few bats were recorded regardless of the mast position (Fig. A5a in Electronic Supplementary Material 1). The same pattern was

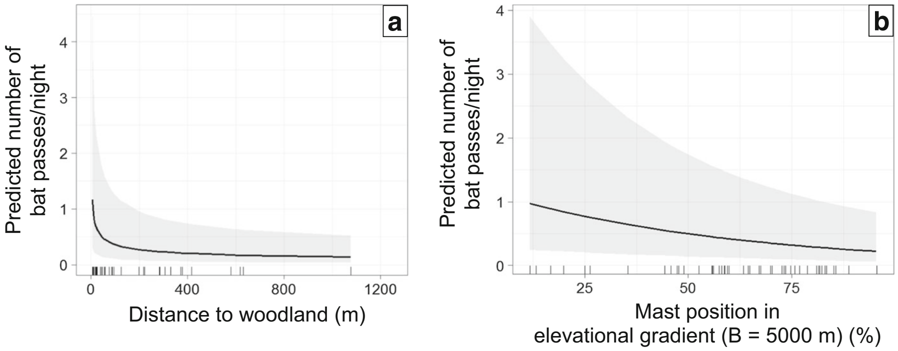

Fig. 2 Influence of distance to trees (**a**) and mast position in elevational gradient (**b**) on bat density for all species (high values mean a closer mast position from hill or mountain tops). B = Buffer size. 95% confidence intervals are shown. Ticks on the x axis represent the sampled values

observed for the density of *P. nathusii* at height (Fig. A5b in Electronic Supplementary Material 1).

For *N. leisleri*, increasing distance to water increased flight height, and for *P. nathusii*, the closer to hill or mountain tops, the more elevated the bat passes (Table 2, Fig. A7b in Electronic Supplementary Material 1). The effects of the relative position of wind masts in the slope on the density (ground level and height included) and on the proportion of flights at height were antagonistic for *P. nathusii* (Fig. A7a in Electronic Supplementary Material 1). There was no significant effect of this variable on density at height (Table A3 and Fig. A7c in Electronic Supplementary Material 1).

Discussion

To our knowledge, this is the first case where the influence of landscape on bat collision risks with WT is studied while differentiating between bat density and bat proportion of flights at collision risk. Our results show that generally, collision risks are proportional to bat density. In some cases, the effect of the relative position of wind masts in the slope had antagonistic effects on the collision risks (e.g. *P. nathusii*). As a result, it was necessary to disentangle the conditioning events of collisions to unravel fine mechanisms leading to bat collisions at WT.

Effect of geographic coordinates

Our models of species density show that bats are less abundant in Northern France and Belgium than in Southern France, except for *P. nathusii*, more abundant in the North. The density of *E. serotinus* and *N. noctula* did not respond to latitude or longitude. This confirms what is known from the literature (Arthur and Lemaire 2015). Reers et al. (2017) also found a high influence of longitude and latitude on bat density at WT nacelle height, and Arnett and Baerwald (2013) suggest that fatalities might decrease with increasing latitudes on the North American territory. However, these studies did not investigate bat vertical flight distribution. In the present study, latitude and longitude were never selected in the models for vertical flight distribution, although it is still possible that flight height varies locally, for example in areas where bat migration is concentrated.

Effect of distance to woodland, water and buildings

Distance to trees had a significant effect on the density of species of low or medium flight heights (i.e. *P. pipistrellus*, *P. kuhlii* and *E. serotinus*) but high-flying species (i.e. *P. nathusii*, *N. leisleri* and *N. noctula*) did not respond to this variable, or the effect could be too weak compared to the other variables. Reers et al. (2017) also found that an increasing percentage of forest in a 500 m buffer enhanced the density of *P. pipistrellus* at WT nacelle height but not of *P. nathusii* and the group of *Vespertilio*/*Nyctalus*/*Eptesicus* species. However, these authors did not study bat vertical flight distribution. In our study, distance to trees was never selected to explain vertical flight distribution. This shows that distance to woodland is a factor of WT collision risks with species of low or medium flight heights because it acts on their local density, but not on their flight height. This contradicts a common hypothesis that assumes that bats fly higher over forests than over open landscapes (Menzel et al. 2005). It could still be the case at a very small scale (i.e. a few meters above tree canopy), which would be insufficient to bring low-flying species in the zone at collision risk (> 25 m above ground).

A minimum distance to trees of 200 m is currently a strong recommendation regarding the placement of European WT (Rodrigues et al. 2015). This recommendation emerged from one bat fatality study (Dürr and Bach 2002), in which the authors state that their sample size per species was relatively small. Heist (2014), Kelm et al. (2014) and Heim et al. (2015) provided additional elements that show that bat density at ground level decreases with increasing distance to woodland, but it is not known whether these results obtained at ground level can be generalised at height. Our model for all species predicted a decrease of bat density of 77% for masts located at 200 m from trees compared to masts positioned a few meters from trees, but our density models for high flying species (*Nyctalus* bats), most susceptible to WT collisions, showed no effect of distance to woodland.

Distance to water was only important in explaining *P. nathusii* density, which is concurring with the literature that shows that this species selects habitats close to water (Dietz et al. 2009). Besides, *N. leisleri* was more likely to fly at height when distance to water increased. It is possible that when commuting away from wetlands, *N. leisleri* flies higher—and faster—compared to when it is foraging or drinking at wetlands, as suggested by some pieces of evidences in *N. noctula* (Roeleke et al. 2016).

Effect of topography

Topography had a strong influence on bat density. Indeed, increasing altitudinal amplitude, positively correlated with altitude, significantly decreased the density of all focus species, except for *N. leisleri*, that did not respond significantly to this variable. This finding supports what is known in the literature (Arthur and Lemaire 2015). The siting of wind masts near hill or mountain tops also decreased the density in the model for all species. The effect of topography on *P. nathusii* density was more complex as density was higher in areas with small altitudinal amplitude, and in these areas, density was weaker if masts were installed on hilltops. Besides, our analysis shows that *P. nathusii* is more likely to fly at height when wind masts were positioned closer to hill or mountain tops than to valleys. This variable thus produced antagonistic effects which resulted in equivalent collision risks at valleys and hilltops for *P. nathusii*.

The most influential scale for topography description was 5 km, while the 1 km scale was only selected for the *P. pipistrellus* density model, and the 200 m scale was never selected. Steep slopes are suspected to generate ascending currents favourable for high altitude flight (Roeleke et al. 2018a, b) and to create thermal conditions favourable for insect aggregations and foraging bats (Arnett et al. 2016). However, the selected scale for topography description in our models is more likely to be a proxy for the presence of mountainous areas in the 5 km (1 km for *P. pipistrellus*) buffer, rather than the proxy of the presence of a steep slope near the mast.

Effect of time of the year

The effect of the Julian day on bat vertical flight distribution had never been investigated to our knowledge and was, contrary to our expectations, the most influential factor of bat proportion of flight at height. Its effect on bat density was antagonistic to its effect on bat vertical flight behaviour for several species (Fig. 3, Table A3 in Electronic Supplementary Material 1). Indeed, bat density peaked in summer/autumn, while the proportion of flights at height peaked in spring and autumn for most bats. Higher bat activity in late summer/autumn is linked to increasing energy demands during migration and in preparation of hibernation, and to the presence of juveniles that temporarily raises population density (Dietz et al. 2009). Two highly plausible and non-exclusive phenomena could explain higher proportions of flight at height in spring and autumn: (1) they are due to migrating bats that would benefit from exploiting high altitude strong winds during long-distance flights (Hedenström 2009) (2) they are due to an increase in prey (i.e. insects) presence at height during favourable

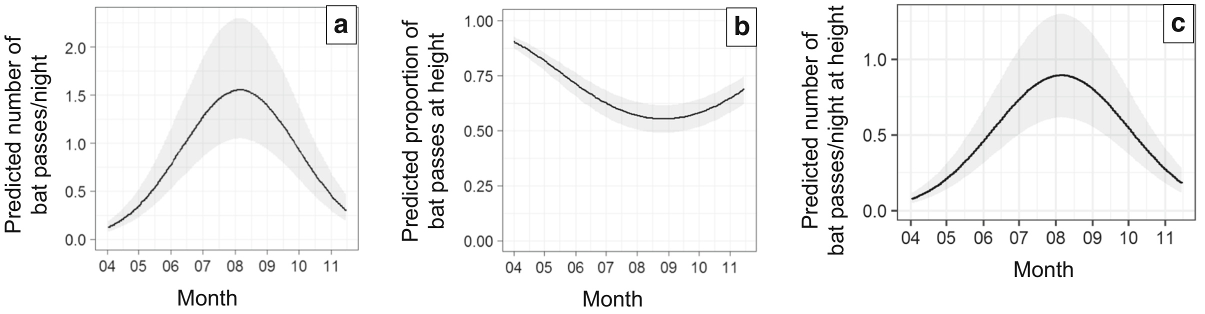

Fig. 3 Predicted bat density (ground level and height included) (**a**), proportion of flight at height (**b**), and bat density at height (**c**) in function of period of the year for *N. leisleri*. 95% confidence intervals are shown in light grey

conditions for insect migration (high altitude winds blowing to the north in spring, and to the south in autumn) (Reynolds et al. 2017). Bat density located at height was maximal in summer and autumn for all focus species. It is the first time to our knowledge that this phenomenon is clearly demonstrated using acoustic tracking, and it explains WT fatality peaks in late summer and autumn found in numerous studies (Arnett et al. 2016; Rydell et al. 2010).

Effect of microphone height

Microphone median height only influenced bat density (ground level and height included) in the model for all species. When microphone median height was more elevated, the lowest microphone was often installed at more than 20 m high (Fig. A2 in Electronic Supplementary Material 1) and fewer bat passes were recorded. Thus, short-range echolocating species flying near ground level (e.g. *Myotis*, *Plecotus*) were probably not recorded. On the contrary, species susceptible to WT collisions such as *Nyctalus* or *Pipistrellus* (Roemer et al. 2017) are middle- or long-range echolocators, and were never or rarely missed when microphone median height was elevated. Nonetheless, higher microphone median heights were associated with less density at height for *P. kuhlii* and *E. serotinus*.

Limits

The predictions of our models are dependent on the features present in our study sites (see Electronic Supplementary Material 2) and must be interpreted with this knowledge. Indeed, our sampling does not allow predictions for high mountains and we did not test for the influence of the positioning of a wind mast at a marked mountain pass, although it must be noted that Rodrigues et al. (2015) expect increased collisions in these passes and recommend avoiding them for WT siting. Distance to water was rarely retained in models, possibly because only one study site was closer than 100 m to water. Our study sites do not cover homogeneously the France and Belgium territory. Nonetheless, the locations of our wind masts match with the highest wind energetical density areas selected for the installation of wind farms (ADEME 2015) and thus adequately cover onshore areas with potential bat-WT conflicts.

At last, our observations were done on wind masts, and not on WT. Several phenomena could lead to differences in bat activity at operating wind turbines compared to lattice masts, and these differences should be tested in future large-scale studies, e.g. (1) blade rotation—which by mixing air layers warms surface temperatures, especially at night (Miller and Keith 2018)—could attract insects and in turn attract bats, or (2) the colour of wind turbine poles could attract insects (Long et al. 2011), and in turn attract bats. Besides, most bats seem to avoid wind turbines at larger scales (Minderman et al. 2012, 2017; Barré et al. 2018). Thus, in the absence of evidence that bat behaviour is not equivalent at both structures, and considering that bat acoustic activity recorded at wind masts was a predictor of the number of bat fatalities at independent wind turbine locations (Roemer et al. 2017), we assume that the differences in behaviour are negligible in regard to the questions addressed in our study.

Consideration of guilds in the study of bat landscape ecology

Contrary to the other focus species, the density of *Nyctalus* species did not respond or responded very little to the landscape variables that we tested. They might respond to more detailed categories of habitat (e.g. for open habitats, differentiation between pastures and arable lands) (Mackie and Racey 2007). However, the perception of landscape heterogeneity varies according to the ecological requirements of each bat species (Peixoto et al. 2018). Thus, high-flyers, which travel greater distances and which perceive background further away than other species thanks to their use of low frequencies (Dietz et al. 2009; Roemer et al. 2019), might respond more to landscape described at even greater scales than at a radius of 5000 m. Alternatively, high-flying bats, which forage on high-flying insects, could also select their foraging grounds in a highly opportunistic way depending on nightly wind or lunar conditions that will impact the presence of insects in elevated air layers (Reynolds et al. 2017; Roeleke et al. 2018a).

Recommendations for wind turbine siting in France and Belgium

WT operational mitigation (i.e. raising of WT cut-in speed) can be efficient to reduce the number of bat collisions while causing reductions in energy production often equivalent to an annual loss of $< 1\%$ (Arnett et al. 2011, 2016; Martin et al. 2017). However, it is not a sufficient solution to eliminate collisions, and impacts must be also prevented by avoiding high collision risk areas. Macro-siting can be done based on species occurrence and population densities at the national scale. Our models show that species density decreases to the North of France. If per capita collision probabilities are similar on the whole French territory, prioritising wind energy development in Northern France should lead to a smaller toll on bats, but our models also showed that Northern France is a region with a high *P. nathusii* density, and this species is among the most susceptible to WT collisions (Roemer et al. 2017). Prediction maps of bat occurrence and density on smaller (i.e. regional) scales are potentially a very efficient approach to do macro-siting based on landscape and habitat features (Newson et al. 2017). Indeed, contrary to the French national scale where latitude had the greatest influence on bat density, we expect landscape to play a more important role at the regional scale.

After macro-siting based on species distribution, micro-siting is then conceivable using local landscape information such as distance to woodland (including hedgerows). Our model for the density of all species is based on observations of species regardless of their susceptibility to WT collisions. Although, it can be used to mitigate both the impacts of collision and of habitat loss due to WT (Minderman et al. 2012, 2017; Barré et al. 2018; Millon et al. 2018). Our results support the recommendation that distance to woodland should be maximised to significantly decrease general bat density. However, it is very important to be aware that following this recommendation will not be effective in decreasing the density of high-flying species susceptible to WT collisions. Our results also suggest that placing WT near or at hilltops could be effective in decreasing bat mortalities through a lower local bat density, but it can also enhance the proportion of flights at collision risk for some species. Thus, we strongly recommend that the decision to place WT on hill or mountain tops should be based on bat density found in the zone at collision risk during pre-construction monitoring.

Landscape planning is thus one of the tools that can help species conservation in the context of growing impacts due to anthropogenic activities. We advocate using this tool in a scale-dependent process, as described above, especially in developing countries where land is still available for an ambitious wind energy development.

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Compliance with ethical standards

Conflict of interest Biotope is an environmental consultancy involved in wind turbine impact assessment studies. Two of the authors, Charlotte Roemer and Thierry Disca, were employees at Biotope at the time of submission. Authors thus declare a conflict of interest. However, authors take complete responsibility for the integrity of the data and the accuracy of their analysis.

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