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

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20 acoustic analysis. We also thank one anonymous reviewer for commenting on the manuscript
21 and Richard Iodice for the English proofreading.

22

23 **Abstract**

24 Context.

25 Collisions with wind turbines threaten bat populations worldwide. Previous studies tried to
26 assess the effects of landscape on mortalities. Yet, the count of carcasses found per species is
27 low, leading to a low statistical power. Acoustic surveys collect large datasets (proxy for bat
28 density); however, if bat vertical distribution is not accounted for, a key mechanism in
29 collisions is missed.

30 Objectives.

31 Our goal was to disentangle the effects of landscape on bat density and vertical distribution to
32 produce recommendations for wind farm siting.

33 Methods.

34 With a vertical array of two microphones, we monitored the acoustic activity and located the
35 vertical distribution of more than 16 bat species on 48 wind masts in France and Belgium (>
36 8,000 nights). We modelled bat density and vertical distribution for six species in function of
37 distance to water, woodland and buildings, and in function of the topography at three different
38 scales (200 m, 1,000 m and 5,000 m).

39 Results.

40 The proportion of flights at heights with collision risk was maximum in spring and autumn
41 and minimum in summer for three species. This effect was often antagonistic to the effect of
42 bat density. The landscape had a stronger effect on bat density than on bat vertical
43 distribution.

44 Conclusions.

45 Positioning wind farms away from woodland should reduce the density and therefore the
46 collision risks of low-flying species but should be inefficient for high-flying species. The
47 effect of topography was stronger at large scales and complex, thus studying situations such
48 as coastlines or mountain passes would provide more insight.

49

50 **Keywords**

51 bat collisions; distance to woodland; topography; per capita collision risks; acoustic location;
52 vertical flight distribution.

53

54 **Introduction**

55 International projections predict a global increase in solar and wind energy installations for
56 the next decades (AIE, 2017). Despite their benefits for climate, wind turbines (WT) can have
57 strong negative impacts on birds and bats through deaths by collision and barotrauma
58 (Laranjeiro et al., 2018; Loss et al., 2015; Rydell et al., 2010), or because of habitat loss
59 (Barré et al., 2018; Millon et al., 2018; Minderman et al., 2017, 2012). This has been a rising
60 cause of concern, especially for bats because of their poor conservation status and their low
61 reproductive rate, making them highly vulnerable to additional sources of mortality (Barclay

62 and Harder, 2003; Voigt and Kingston, 2016). Some projections identified WT as a possible
63 cause of extinction for certain bat species (Frick et al., 2017).

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

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

80 Several studies have tried to identify landscape predictors of bat fatalities at wind turbines.
81 Santos et al. (2013) found that mortality probabilities decreased with the distance to
82 eucalyptus forests. Other studies showed that open habitats such as prairies, pastures and
83 croplands triggered fewer collisions than closed habitats such as forests (Bolívar-Cimé et al.,
84 2016; Piorkowski and O'Connell, 2010; Thompson et al., 2017). Piorkowski and O'Connell

85 (2010) found more fatalities in ravine topography than in low topography relief and Santos et
86 al. (2013) found that distance to the slope was negatively correlated with mortality risks.

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

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

109

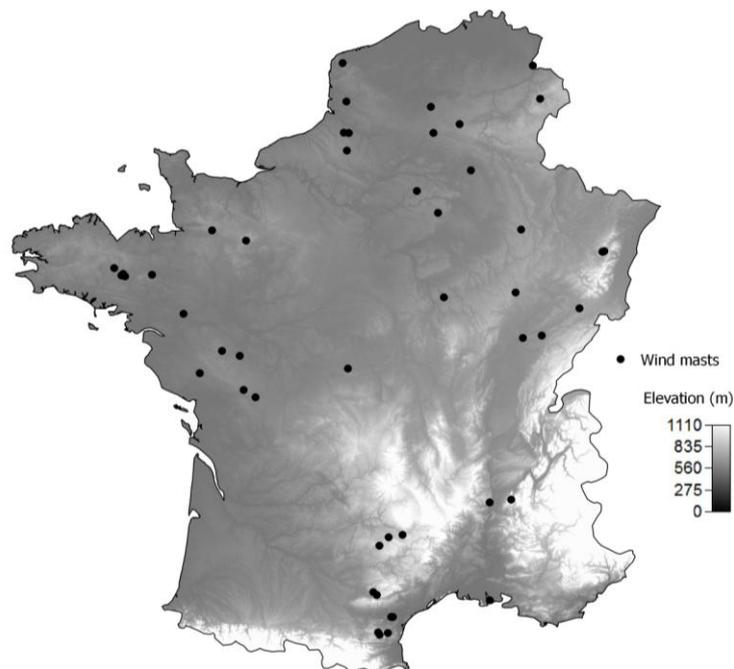
110 **Material and Methods**

111 *Acoustic recordings*

112 48 sites were surveyed in France and Belgium between 2011 and 2018 during a total of 8,435
113 nights (mean = 175.7, standard deviation = 76.1, min = 19, max = 352 nights per site) (Fig. 1).

114 Surveys targeted bat annual periods of activity (Fig. A1 in Electronic supplementary material
115 1). Lattice or monopole wind masts of 50-100 m high were equipped with two ultrasound
116 microphones (SMX-US, SMX-U1 or SMM-U1, Wildlife acoustics, USA, or BMX-US,
117 Biotope, France) plugged to an SM2BAT or SM3BAT recorder (Wildlife Acoustics, USA).
118 One microphone was installed near ground level and a second at height (Fig. A2 in Electronic
119 supplementary material 1). In forests, wind masts were installed in clearings of 10-30 m
120 radius.

121



122

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

124

125 Recorders were programmed to start each day 30 min before sunset and stop 30 min after
126 sunrise. Between 2013 and 2016 (38 sites), whole night recordings were performed. Before
127 2013 (10 sites), samplings were collected for 10 min every 20 min. The gain was set at 36 dB
128 for SMX-US and BMX-US microphones or 0 dB for SMX-U1 and SMM-U1 microphones
129 because they have a pre-integrated gain. Sampling rate was set at 192 kHz, trigger at 6 dB for
130 SM2BAT and 12 dB for SM3BAT (for equivalent sensitivity) and trigger window at 2.5 s. A
131 1 kHz high pass filter was used.

132 *Species identification and flight height classification*

133 Species identification was performed based on acoustic features as stated in Roemer et al.
134 (2017) using SonoChiro (Biotope/MNHN, France) and a manual check. Bat passes (defined
135 as one or more bat calls within 5 s) that belonged to the genera *Pipistrellus*, *Nyctalus*,
136 *Eptesicus* or *Vespertilio* and that could not be identified at the species level were marked as
137 unidentified bats. The latter sequences, as well as all other unidentified bat passes, represented
138 8.4 % of our dataset and were not used for further analyses. Concerning the group of species
139 *Pipistrellus kuhlii/nathusii*, acoustic knowledge is presently too scarce to differentiate both
140 species with certain confidence. Identifications were achieved using acoustic cues described
141 as “typical” for these species at the time of analysis (Barataud, 2015) and with the knowledge
142 that *Pipistrellus kuhlii* is very rare or absent in Northern France and Belgium (Arthur and
143 Lemaire, 2015). However, readers must be aware of potential biases in the results presented
144 here for *P. kuhlii* and *P. nathusii*. Bat passes with no typical feature of either species were not
145 identified (37.5 % of this group).

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

151 *Landscape variables*

152 To cover the variability of home ranges of European species (Arthur and Lemaire, 2015), we
153 described the landscape within buffers of 200 m, 1,000 m and 5,000 m radius around wind
154 masts (Fig. A3 in Electronic supplementary material 1).

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

167 Altitudinal variables were retrieved from the ASTER digital elevation model (DEM) version
168 2 (NASA JPL, 2009). This model represents the elevation of the terrain including buildings or
169 woodland and has a precision of approximately 30 m at the equator. We chose to use this

170 model instead of a classical topographical map (describing bare ground elevation) because we
171 were interested in the influence of all main three-dimensional structures on bat flight height.
172 We noted the altitude of wind masts at their foot, and for the three different buffers, we
173 calculated their altitudinal amplitude (difference between maximum and minimum elevations
174 within the buffers) and the position of the wind mast on the elevational gradient (difference
175 between mast elevation and minimum elevation multiplied by 100 and divided by the
176 altitudinal amplitude).

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

182 *Statistical analyses*

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

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

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

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

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

226 For some species, there were common variables in the two models (bat density and bat
227 vertical distribution). To interpret the effect of these variables on the resulting bat collision
228 risks, we also directly modelled the number of bat passes per night located at height in
229 function of all the variables that were selected in either model. This response was modelled
230 with a negative binomial distribution (nbinom2) using the package glmmTMB (Brooks et al.,
231 2017) of the R program (R Core Team, 2014). As in the previous models, study sites nested
232 within groups were introduced as a random variable.

233

234 **Results**

235 *Bat activity recorded*

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

239 *Vespertilio*, *Nyctalus* and *Tadarida* species prevailed at height (20-90 % of the time at height).
240 They were followed by *Hypsugo*, *Pipistrellus* and *Eptesicus* species (5-35% of the time at

241 height). *Myotis*, *Miniopterus* and *Barbastella* species were rarely recorded at height (< 5 % of
242 the time at height). *Rhinolophus* species were never recorded at height (Table A2 and Fig. A4
243 in Electronic supplementary material 1).

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

251 *Scale*

252 Larger scales were more effective to explain bat density and flight behaviour than smaller
253 scales (Table 1 and Table 2). Most species responded to buffers of 5,000 m (altitudinal
254 amplitude and position of a mast in elevational gradient), while only *P. pipistrellus* responded
255 to a scale of 1,000 m (altitudinal amplitude). The scale of 200 m for both response variables
256 was never selected in models.

257 *Control variables*

258 The density of species decreased to the North, except for *P. pipistrellus* and *P. nathusii*, and
259 increased to the East, except for *P. kuhli原因ii* (Table 1). We found a gradual increase in density
260 from spring to summer, followed by a decline in autumn. Patterns were similar for all species;
261 an example is displayed for *N. leisleri* (Fig. 3a). The proportion of bat passes at height was
262 near minimum at the time when bat density peaked for several species (e.g. *N. leisleri* (Table
263 2, Fig. 3b)), however, there was no significant pattern for *E. serotinus*, *P. nathusii* and *N.*

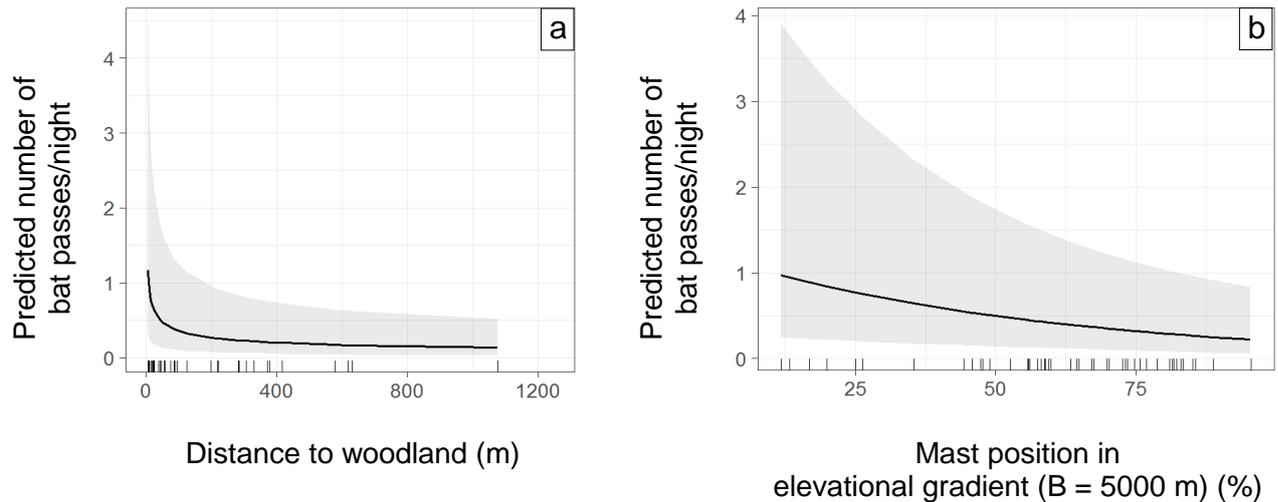
264 *noctula* (Fig. A6 in Electronic supplementary material 1). Density at height displayed similar
265 patterns as density (ground level and height included), with a peak in summer (Fig. 3c and
266 Fig. A6 in Electronic supplementary material 1). Microphone height influenced measured
267 species density when modelling all species at once but did not influence the measured
268 proportion of flight at height (Table 1 and Table 2). Nonetheless, for *P. kuhlii* and *E.*
269 *serotinus*, higher microphone median heights were associated with a lower density at height
270 (Table A3 in Electronic supplementary material 1).

271 *Landscape*

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

275 Altitudinal amplitude negatively affected the density of most species, but this variable was not
276 selected in the model where all species are grouped. Bat density for all grouped species was
277 lower near hill or mountain tops than near to valleys (Fig. 2b). For *P. nathusii*, in lowlands,
278 density (ground level and height included) decreased when the mast was closer to hilltops,
279 while in mountainous areas, few bats were recorded regardless of the mast position (Fig. A5a
280 in Electronic supplementary material 1). The same pattern was observed for the density of *P.*
281 *nathusii* at height (Fig. A5b in Electronic supplementary material 1).

282

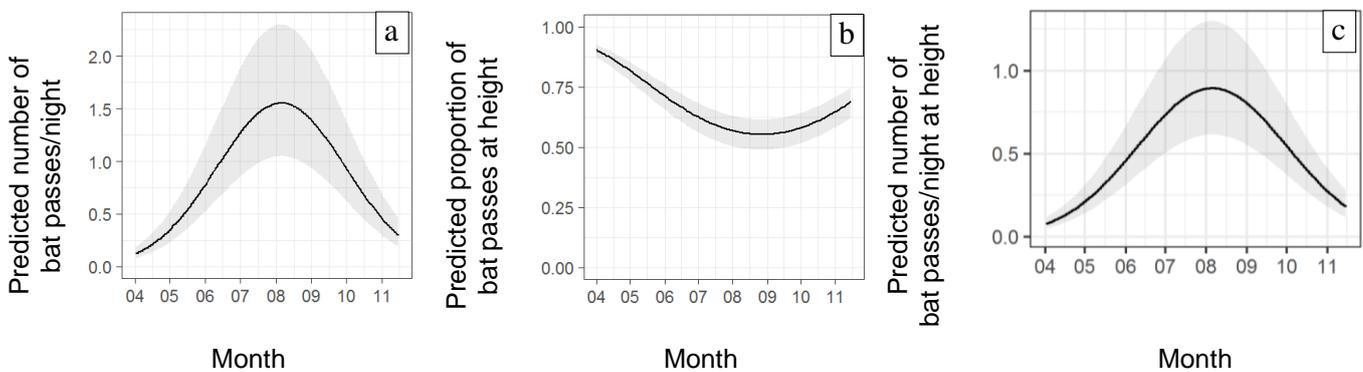


283 **Fig. 2** Influence of distance to trees (a) and mast position in elevational gradient (b) on bat density for all species (high values mean a closer mast position from hill or mountain tops). B = Buffer size. 95%
 284 confidence intervals are shown. Ticks on the x axis represent the sampled values.
 285

286

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

294



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

298 **Table 1** Summarised statistical results of the negative binomial distributed generalised linear mixed effect models (GLMM) for the density of each species.
 299 $\hat{\beta}$ = 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
 300 noted with a colon. B = buffer size. Mic. Med. Height = Microphone median height; Dist. = Distance; Δ Alt. = altitudinal amplitude; Pos. elev. = Position of
 301 wind mast in elevational gradient.

302

<i>Variables</i>	<i>All species</i>			<i>Pipkuh</i>			<i>Pippip</i>			<i>Eptser</i>			<i>Pipnat</i>			<i>Nyclei</i>			<i>Nycnoc</i>		
	$\hat{\beta}$	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
<i>Intercept</i>	-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	***
<i>Mic. Med. H.</i>	-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	
<i>Julian Day</i>	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	***
<i>Julian Day²</i>	-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	***
<i>Latitude</i>	-0.65	0.15	***	-2.40	0.39	***	0.29	0.13	*				1.05	0.19	***	-0.92	0.20	***			
<i>Longitude</i>				-1.13	0.37	**	0.29	0.13	*				0.48	0.17	**	1.18	0.21	***			
<i>Dist. water</i>													-0.31	0.18	.						
<i>Dist. woodland</i>	-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	**
<i>Pos. elev. (B = 5000 m)</i>	-0.37	0.13	**										-0.47	0.16	**						
Δ Alt. (B = 5000 m) : Pos. elev. (B = 5000 m)													0.77	0.19	***						

$p < 0.1 = .$

$p < 0.05 = *$

$p < 0.01 = **$

$p < 0.001 = ***$

303

304

305 **Table 2** Summarised statistical results of the binomial distributed generalised linear mixed effect models (GLMM) for the proportion of flight at height of
 306 each species. $\hat{\beta}$ = estimate; SE = standard error; P = significance of P value. Species names are given with the first three letters of the species and genera.
 307 Interactions are noted with a colon. B = buffer size. Mic. Med. Height = Microphone median height; Dist. = Distance; Pos. elev. = Position of wind mast in
 308 elevational gradient.

309

<i>Variables</i>	<i>All species</i>			<i>Pipkuh</i>			<i>Pippip</i>			<i>Eptser</i>			<i>Pipnat</i>			<i>Nyclei</i>			<i>Nycnoc</i>		
	$\hat{\beta}$	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	***						

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

310

311

312 **Discussion**

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

319 *Effect of geographic coordinates*

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

330 *Effect of distance to woodland, water and buildings*

331 Distance to trees had a significant effect on the density of species of low or medium flight
332 heights (i.e. *P. pipistrellus*, *P. kuhlii* and *E. serotinus*) but high-flying species (i.e. *P. nathusii*,
333 *N. leisleri* and *N. noctula*) did not respond to this variable, or the effect could be too weak
334 compared to the other variables. Reers et al. (2017) also found that an increasing percentage

335 of forest in a 500 m buffer enhanced the density of *P. pipistrellus* at WT nacelle height but not
336 of *P. nathusii* and the group of *Vespertilio/Nyctalus/Eptesicus* species. However, these
337 authors did not study bat vertical flight distribution. In our study, distance to trees was never
338 selected to explain vertical flight distribution. This shows that distance to woodland is a factor
339 of WT collision risks with species of low or medium flight heights because it acts on their
340 local density, but not on their flight height. This contradicts a common hypothesis that
341 assumes that bats fly higher over forests than over open landscapes (Menzel et al., 2005). It
342 could still be the case at a very small scale (i.e. a few meters above tree canopy), which would
343 be insufficient to bring low-flying species in the zone at collision risk (> 25 m above ground).

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

354 Distance to water was only important in explaining *P. nathusii* density, which is concurring
355 with the literature that shows that this species selects habitats close to water (Dietz et al.,
356 2009). Besides, *N. leisleri* was more likely to fly at height when distance to water increased. It
357 is possible that when commuting away from wetlands, *N. leisleri* flies higher – and faster –
358 compared to when it is foraging or drinking at wetlands, as suggested by some pieces of
359 evidences in *N. noctula* (Roeleke et al., 2016).

360 *Effect of topography*

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

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

380 *Effect of time of the year*

381 The effect of the Julian day on bat vertical flight distribution had never been investigated to
382 our knowledge and was, contrary to our expectations, the most influential factor of bat
383 proportion of flight at height. Its effect on bat density was antagonistic to its effect on bat

384 vertical flight behaviour for several species (Fig. 3, Table A3 in Electronic supplementary
385 material 1). Indeed, bat density peaked in summer/autumn, while the proportion of flights at
386 height peaked in spring and autumn for most bats. Higher bat activity in late summer/autumn
387 is linked to increasing energy demands during migration and in preparation of hibernation,
388 and to the presence of juveniles that temporarily raises population density (Dietz et al., 2009).
389 Two highly plausible and non-exclusive phenomena could explain higher proportions of flight
390 at height in spring and autumn: (1) they are due to migrating bats that would benefit from
391 exploiting high altitude strong winds during long-distance flights (Hedenström, 2009) (2) they
392 are due to an increase in prey (i.e. insects) presence at height during favourable conditions for
393 insect migration (high altitude winds blowing to the north in spring, and to the south in
394 autumn) (Reynolds et al., 2017). Bat density located at height was maximal in summer and
395 autumn for all focus species. It is the first time to our knowledge that this phenomenon is
396 clearly demonstrated using acoustic tracking, and it explains WT fatality peaks in late summer
397 and autumn found in numerous studies (Arnett et al., 2016; Rydell et al., 2010).

398 *Effect of microphone height*

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

408 *Limits*

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

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

431 *Consideration of guilds in the study of bat landscape ecology*

432 Contrary to the other focus species, the density of *Nyctalus* species did not respond or
433 responded very little to the landscape variables that we tested. They might respond to more
434 detailed categories of habitat (e.g. for open habitats, differentiation between pastures and
435 arable lands) (Mackie and Racey, 2007). However, the perception of landscape heterogeneity
436 varies according to the ecological requirements of each bat species (Peixoto et al., 2018).
437 Thus, high-flyers, which travel greater distances and which perceive background further away
438 than other species thanks to their use of low frequencies (Dietz et al., 2009; Roemer et al.,
439 2019), might respond more to landscape described at even greater scales than at a radius of
440 5,000 m. Alternatively, high-flying bats, which forage on high-flying insects, could also select
441 their foraging grounds in a highly opportunistic way depending on nightly wind or lunar
442 conditions that will impact the presence of insects in elevated air layers (Reynolds et al.,
443 2017; Roeleke et al., 2018).

444 *Recommendations for wind turbine siting in France and Belgium*

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

457 features (Newson et al., 2017). Indeed, contrary to the French national scale where latitude
458 had the greatest influence on bat density, we expect landscape to play a more important role at
459 the regional scale.

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

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

477

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482

483 **Conflict of interest**

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

488

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