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1 **Bat flight height monitored from wind masts predicts mortality risk at wind farms**

2

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15

16 **Abstract**

17 Bat fatalities by collision or barotrauma at wind farms currently raise high conservation concerns. In  
18 many countries, pre-installation acoustic surveys are mandatory in order to assess the impacts of wind  
19 farm projects. In this purpose, the use of wind masts to estimate bat activity and hence predict  
20 collision risk is highly recommended by conservation committees worldwide. Yet, the degree to which  
21 collisions may be predicted from acoustic monitoring at wind masts has been strongly debated.

22

23 To assess this relationship, microphone arrays were installed on 23 wind masts in order to record and  
24 locate bat activity on the vertical axis during 3,260 nights. For each species, we also calculated a  
25 collision susceptibility index, based on fatality data gathered in the literature and corrected for species  
26 abundance. We demonstrate that the collision susceptibility index is correlated with the percentage of  
27 bat passes at blade height.

28

29 The acoustic recordings allowed us to establish a reference for the ratios of flight activity above  
30 heights of 20-45 m high for more than 16 European bat species. The correlation we demonstrate here  
31 between the percentage of bat passes at height – recorded from acoustic surveys on wind masts - and  
32 bat fatalities strongly supports that activity estimates from wind masts are appropriate for wind turbine  
33 impact assessments.

34

### 35 *Highlights*

- 36 • The most complete dataset of bat flight height distribution is presented
- 37 • A bat collision susceptibility index to wind turbine collisions was calculated
- 38 • The collision susceptibility index is correlated with time spent at blade height
- 39 • Results support the relevance of using wind masts for impact assessment studies

40

41

### 42 **Key words**

43 bat, wind turbine, carcass, impact assessment study, wind mast, actichiro

44

45

### 46 **Introduction**

47 Green energy development is today one of the top priorities of European governments. To answer this  
48 requirement, wind farm implantations have increased tremendously over the last years (Leung and  
49 Yang, 2012). Meanwhile, their impact has been proven lethal for numerous bird and bat species  
50 (Rydell *et al.*, 2010a; Drewit and Langston, 2006; Frick *et al.*, 2017; Hammerson *et al.*, 2017). In  
51 Europe, cases of fatalities by collision or barotrauma around wind turbines (WT) have been reported in  
52 27 bat species over the 51 extant European species for a total amount of circa 7,000 individuals and  
53 France alone has an impact on at least 17 species (Rodrigues *et al.*, 2015). Since a very small  
54 proportion of wind farms were surveyed and for a limited period of time, this number is only the tip of  
55 the iceberg. Estimates show that in Germany alone, wind turbines may account for more than two

56 million bats killed over the past 10 years, if mitigation measures were not practiced (Voigt *et al.*,  
57 2015).

58

59 All European bat species are under strict protection (Habitat Directive, Annex IV - Council Directive  
60 92/43/EEC, 1992), hence the necessity to develop proper tools to assess as accurately as possible the  
61 impacts of human activities before their occurrence on bat populations. Today, European impact  
62 assessment studies monitor bat activity with methods ranging from evening transects with ultrasound  
63 detectors or autonomous overnight recordings from the ground to long-term recordings with  
64 microphones at height (Rodrigues *et al.*, 2015).

65

66 To explain bat fatalities at WT and in the hope of predicting them, numerous hypotheses have  
67 emerged concerning the ultimate causes of collisions (Cryan and Barclay, 2009). The simplest  
68 explanation would be that mortality is directly linked to specific activity rates on site, independently  
69 from altitudinal distributions. However, uncommon species are sometimes more impacted than others  
70 (e.g. Georgiakakis *et al.*, 2012). Some hypotheses suggest that species mostly impacted are annual  
71 migrants that might be seasonally manoeuvring at heights with collision risks, or that they are tree  
72 roosting species that might mistake wind towers for trees (Cryan and Barclay, 2009; Cryan *et al.*, 2014;  
73 Jameson and Willis, 2014). Rydell *et al.* (2010b and 2016) doubt that migration is the only explanation  
74 for collisions because resident species are very often the most impacted species, and because insects  
75 resting on WT were identified in the stomach contents of bat carcasses found at wind farms. They  
76 conclude that there might not be a single explanation to the complex phenomenon of bat collisions at  
77 wind farms.

78

79 Before investigating complex hypotheses, it is important to focus on straightforward relationships. In  
80 all simplicity, bats spending most of their time foraging and commuting at similar heights as blade  
81 heights should be more susceptible to collisions. This assumption of coincidental collisions (Cryan and  
82 Barclay, 2009) has never been thoroughly investigated because of the lack of appropriate tools, i.e.  
83 tools that would not produce any attraction phenomenon.

84

85 Yet, in order to estimate impacts before the setting up of wind farms, the more the setting resembles a  
86 WT, the easier it will be to estimate future impacts and draw conclusions. Hence it is not necessarily  
87 desirable to free the survey material from any effect on bat behaviour. Korner-Nievergelt *et al.* (2013)  
88 demonstrated that bat activity at WT nacelles is correlated with the number of carcasses found at their  
89 foot. But it has never been formally proven that this correlation is also valid for pre-construction  
90 acoustic surveys from wind masts, which are recommended for impact assessment studies (Rodrigues  
91 *et al.*, 2015). An attempt by Hein *et al.* (2013) was not conclusive because of the variability in the  
92 methods of the studies that were available. Yet, this relationship most probably exists, notably because  
93 there is evidence that tall anthropogenic structures engender an attraction phenomenon toward tree  
94 roosting/migratory bats at the same time of the year where mortality peaks at WT are found (Jameson  
95 and Willis, 2014). Those bats are not the only species affected by WT collisions and others such as  
96 exclusive cave roosting species are also implicated although at much lower rates (e.g. *Miniopterus*  
97 *schreibersii*, Rodrigues *et al.*, 2015). It might be that specific differences in flight behaviour play an  
98 important role in explaining differences in collision susceptibility among tree roosting/migratory  
99 species but more generally among all bats, and this concomitantly to an attraction phenomenon.  
100 Müller *et al.* (2013) showed that wind turbine fatality counts are numerous for most species flying  
101 more often around tree canopy than close to the ground. But a clear identification of the role played by  
102 bat flight height distribution in species susceptibilities to collisions, independently of species relative  
103 densities, is still missing. This distinction is for instance essential in order to rank species  
104 susceptibility. To perform this distinction between species behaviour and density, the latter must be  
105 corrected by using a reference scale for species activity levels (see Haquart, 2013).

106

107 Our study aims at testing the relevance of using activity data from wind masts in wind farm impact  
108 assessment studies. Our hypotheses are that (1) WT collision susceptibility is strongly linked to the  
109 preference of species flying at altitudes similar to those of WT blades, and that (2) this correlation can  
110 be established from observations at wind masts, as they act as a similar stimulus as WT toward bats.

111

112

## 113 **Material and Methods**

### 114 *Acoustic recordings*

115 Recordings were conducted at 23 sites in France and Belgium (see Figure 1) between 2011 and 2016.  
116 Habitats consisted in pine, spruce and mixed forest clearings (11 sites), bocage (3 sites) wetlands (1  
117 site) and cultivated fields (8 sites). Sites in Southern and Eastern France were either located in  
118 mountainous areas or in plains while the remaining sites were in plains only. Months between April  
119 and October cumulated the maximum number of sites surveyed per night (Figure 2). In total, bat  
120 activity was monitored on 3,260 nights ( $\mu = 142$ ,  $\sigma = 72$  nights per site). The recording period at each  
121 site did not exceed one year.

122

123 In order to establish a link between bat behaviour before the presence of WT and the collision risk  
124 after their activation, a proper manner to assess bat flight height distribution had to be chosen. Collins  
125 and Jones (2009) obtained differences between bat activity at ground level and at height by mounting  
126 one microphone at ground level and one at 30 m on a mast. With two unsynchronised microphones  
127 however, the most detectable species might be counted twice (i.e. at both microphones). Some species  
128 can indeed be acoustically detected at more than 90 m (Holderied and von Helversen, 2003; Barataud,  
129 2015). Here, we performed a binary location of the bat position (i.e. near the nacelle height or near the  
130 ground), without any double count, while at the same time enabling a specific identification through  
131 the echolocation calls.

132

133 We installed microphones on lattice or monopole wind masts of 50-100 m high that all had aviation  
134 lighting at night. Arrays with two microphones were achieved with two SMX-US microphones  
135 plugged to an SM2BAT (all models, Wildlife Acoustics, Massachusetts, USA). Microphones were  
136 inserted into aluminium tubes, facing downward, in protection from weather alterations. The  
137 omnidirectionality of the setting was ensured by a custom-made round shaped 6 cm diameter  
138 aluminium reflector placed below the microphone with a 45° angle. Microphones were respectively

139 installed at heights ranging from 4 to 85 m (see Figure 3). Recorders were programmed to start each  
140 day 30 min before sunset and stop 30 min after sunrise. For study sites between 2013 and 2016 (13  
141 sites), whole night recordings were performed. On study sites from before 2013 (10 sites), samplings  
142 were collected during 10 minutes every 20 minutes. Gain was set at 36 dB, sampling rate at 192 kHz,  
143 trigger at 6 dB above background noise and trigger window at 2.5 sec. A 1 kHz high pass filter was  
144 used. Files were compressed in WAC4 format and analysed in WAV format.

145

#### 146 *Species identification and flight height classification*

147 Files were decompressed using the WAC2WAV (Wildlife Acoustics, Massachusetts, USA) software.  
148 When longer, files were automatically cut in 5 second bouts after each triggered recording to be used  
149 as a proxy for a bat pass, according to Barataud's method (2015). Species identifications were  
150 performed on SonoChiro (Biotope, France) (Newson *et al.* 2015). The verification of acoustic  
151 sequences was done on Syrinx (John Burt, USA) or BatSound (Pettersson Elektronik AB, Sweden)  
152 with spectrogram representations, allowing to measure acoustical parameters. Identification criteria are  
153 based on the association between acoustic call type, call shapes and measurable parameters (initial  
154 frequency, terminal frequency, signal length, maximum energy and its repartition ...), their rhythms  
155 (interval duration between calls) and the environment (distance to obstacles). With the knowledge  
156 accumulated today, this method born from Barataud's work (2015) allows the identification, in good  
157 recording conditions, of 29 species from the 33 extant in France and Belgium. Yet, sonar calls of  
158 certain species are sometimes very close, even identical in certain flight circumstances. Hence, they  
159 are assembled in species groups. In the present case, *Myotis* were grouped in two categories: *Myotis*  
160 *myotis* and *M. blythii* in a "large *Myotis*" group and all others in a "small *Myotis*" group, and all  
161 *Plecotus* individuals in the *Plecotus sp.* group. Within those two groups, species present flight heights  
162 comparable to the other species of their group (Rodrigues *et al.*, 2015). It was however not acceptable  
163 to group unidentified species from *Pipistrellus* or *Nyctalus/Eptesicus/Vespertilio* genera, because they  
164 display very different flight heights within their group. These unidentified bat passes (2.95 % of all bat  
165 passes) were not used for further analyses.

166

167 In order to classify flight heights, SonoChiro was used to automatically determine the time at which  
168 each call starts on each microphone. Then, using the find.matches function of Hmisc package (Harrell,  
169 2014) from R (R Core Team, 2014), we obtained the time differences of arrival for each call detected.

170

171 For each site, a height threshold was defined as the median height between the two microphones (see  
172 figure 3). This threshold corresponds for each site to the lowest height at which the planned WT blade  
173 would operate and therefore the altitude above which collisions can occur. This means that in forests  
174 also, the median height represents the height above which bats would be at collision risk. This  
175 threshold was used to assign bat calls to two classes: “at height” if the source of the signal is above the  
176 threshold and “at ground level” if it is below the threshold. If a bat call is detected by the highest or the  
177 lowest microphone only, the call is considered to be respectively located at height or at ground level.  
178 If several calls of the same bat pass give different location results (both at ground level and at height),  
179 location is determined by a majority vote among the calls (e.g. if 12 calls are at ground level and three  
180 calls are at height, the bat pass is assigned to “at ground level”). We then calculated a ratio of the time  
181 spent at height for each species. This method has also the advantage of freeing the comparison of  
182 several study sites from detectability bias linked to the type or the quality of the recording equipment.  
183 The count of the number of bat passes at height would be itself more prone to such bias.

184

#### 185 *Calculation of collision susceptibility index*

186 Mortality data (total amount of bat carcasses found at WT) were transmitted by the agreement on the  
187 conservation of populations of European bats EUROBATS (2015 update). The identity of the sites  
188 surveyed and the months during which carcass searching was performed were not available for data  
189 after 2014. Before 2014, the surveyed months were not available for half of the sites. From the  
190 information we could obtain, the seasonal distribution of fatality searches during the year was very  
191 similar to the distribution of our acoustic samplings (see figure A1 in suppl. Material). The spatial  
192 distribution of the mortality survey sites was very similar to the one of wind masts (see figure A2 in  
193 suppl. material), except for Northern and Eastern France, where we had more wind masts. Fatality data  
194 were collected from 2008 to 2012. From the information available, the zone swept by the rotor blades



195 was then above 32 (+/- 8) meters high. We defined species susceptibility to collisions as the mortality  
196 rate relative to species density. To calculate this latter value, we used acoustic data and accounted for  
197 variations in acoustic detectability between species. For each species, for the whole French territory,  
198 the density index was calculated as follows:

199

200 eqn 1  $Density\ index = \frac{Mean\ activity}{Detection\ distance}$ ,

201

202 where detection distance is the approximate maximal distance from which an individual of a species  
203 can be acoustically detected (Barataud, 2015) and where mean activity was taken from the French  
204 reference scale of activity levels “Actichiro” (Haquart, 2013). The latter was built from acoustic  
205 recordings on more than 2,757 nights between 2007 and 2011 and orders species on a scale from the  
206 least to the most commonly recorded. This reference scale used recordings from microphones installed  
207 at ground level only. However, in our dataset, species relative activity recorded from ground is similar  
208 to species relative total activity (sum of ground level and height activity) (Pearson’s  $r = 0.98$ ; see table  
209 A1 in suppl. material). The recordings in Actichiro oversampled the Mediterranean region (see table  
210 A2 in supplementary material) while our sampling was more balanced (see table A5 in supplementary  
211 material). Thus, we used a mean activity weighted by the areas of the four biogeographical regions to  
212 get more accurate measures of species relative density all over the country. To do this, we multiplied  
213 the mean activities for each of the four biogeographical regions by a regional area ratio (i.e. region  
214 area divided by the area of the whole French territory). We then summed all weighted mean activities  
215 to obtain a French mean activity. Since no activity data was available for Belgium, our collision  
216 susceptibility index relied only on data from France. It was calculated as follows for each species:

217

218 eqn 2  $Collision\ susceptibility\ index = \frac{Number\ of\ carcasses + 1}{Density\ index}$ ,

219

220 where number of carcasses is the total amount of bat carcasses found at French wind farms. We added  
221 one to the number of carcasses for each species to avoid a multiplication by zero. The limit of this  
222 method lies in the overcorrection of the susceptibility of rare species.

223

#### 224 *Correlation between the ratio of time spent at height and collision susceptibility index*

225 We used a generalised linear mixed model (GLMM) to estimate rates of flight at height for each  
226 species. Bat pass height was modelled as a binomial variable (at height or at ground level) according  
227 to species as a fixed effect. In order to take into account the local environment effect on flight  
228 behaviour, study sites were introduced as a random variable. The GLMM was built using the  
229 `glmmPQL` function of the MASS package (Venables and Ripley, 2002) of R (R Core Team, 2014).  
230 The estimated species rate of flight at height was then correlated to species collision susceptibility  
231 index. The first variable did not follow a normal distribution and for this reason a Spearman's rank  
232 correlation test was performed. The same method has been applied to test the correlation between the  
233 total amount of bat passes at height and the raw fatality counts.

234

## 235 **Results**

236 Flight heights of 340,797 bat passes have been recorded, among which 330,740 could be attributed to  
237 a species or a group of species and used for further analysis. At least 28 species have been determined.  
238 The most commonly recorded species was *P. pipistrellus*. On average, 10 % of its time was spent at  
239 height (Table A3: Ratio of time spent at height for each species. Figure 4). The small *Myotis* group  
240 contains data from at least *M. alcaethoe*, *M. bechsteinii*, *M. brandtii*, *M. capaccinii*, *M. emarginatus*, *M.*  
241 *nattereri*, *M. daubentonii*, *M. dasycneme* and *M. mystacinus* (see table A4 in suppl. material for  
242 details). The only bat passes at height that could be identified for this group were from *M. daubentonii*  
243 and for a probable *M. dasycneme*. The *Plecotus* group contains data from at least *P. auritus* and *P.*  
244 *austriacus* and both have been recorded at height. *Rhinolophus* bats are the only genus that was never  
245 recorded at height. All *Nyctalus* bats, *Tadarida teniotis* and *Vespertilio murinus* spent more than 40 %  
246 of their time at height.

247

248 The collision susceptibility index, which takes into account the abundance of species, classified *V.*  
249 *murinus*, *Nyctalus* bats and *P. nathusii* as most susceptible to WT collisions (**Erreur ! Source du**  
250 **renvoi introuvable.**) *P. pipistrellus* had a low level of susceptibility to collisions (**Erreur ! Source**  
251 **du renvoi introuvable.**) despite being the most common species found in mortality surveys  
252 (Rodrigues *et al.*, 2015). Small *Myotis*, *Plecotus*, *Barbastella* and *Rhinolophus* had a very low level of  
253 susceptibility (**Erreur ! Source du renvoi introuvable.**).

254  
255 A significant correlation ( $\rho = 0.94$ ;  $p = 4.57e-06$ ) could be demonstrated between species'  
256 susceptibility to WT collisions and their preference to fly at height (Figure 5). Low flying species  
257 (*Rhinolophus*, small *Myotis* and *Plecotus* bats) correspond to species with a low index and high flying  
258 species (*Nyctalus*, *Vespertilio* and *Tadarida* bats) to a high index. A significant correlation has also  
259 been found between the total amount of bat passes at height and the raw fatality counts (see figure A3  
260 in suppl. material).

261  
262 There was a high correlation between the number of bat passes recorded from the ground microphone  
263 and the number of bat passes recorded from the upper microphone for certain species (e.g. *N. noctula*  
264 and *N. leisleri*), however the activity at height of several species (e.g. Small *Myotis* or *P. pipistrellus*)  
265 could not be explained by the ground microphone only, or poorly (see Table A1 in suppl. Material).

266

## 267 **Discussion**

### 268 *Flight behaviour*

269 The dataset presented here is the first objective assessment of flight height distribution of European  
270 species, at similar environments to where wind blades operate. It extends the results found by Müller  
271 *et al.* (2013) by covering several landscape types with a very large sample size, ensuring a fair  
272 representativeness of the variability that may occur across several biogeographical regions.

273

274 Our results show that species flight behaviour can be organised into three different categories  
275 embracing Denzinger and Schnitzler (2013) guilds definitions. The first category includes four

276 different guilds, namely edge space trawling foragers and narrow space active gleaning foragers (i.e.  
277 small *Myotis*), narrow space flutter detecting foragers (i.e. *Rhinolophus*) and narrow space passive  
278 gleaning foragers (i.e. *Plecotus*, *Barbastella* and large *Myotis*). These species were always or almost  
279 exclusively located at ground level. The second category corresponds to the guild of edge space aerial  
280 foragers with species flying more often close to the ground or vegetation than at height (i.e.  
281 *Miniopterus*, *Pipistrellus*, *Eptesicus* and *Hypsugo* species). The third category corresponds to the guild  
282 of open space aerial foragers (i.e. *Nyctalus*, *Tadarida* and *Vespertilio* species), that spent a  
283 considerable proportion of time at high heights. These results underline the close relationship between  
284 bat sonar and flight behaviour. Indeed, the first group mainly uses very high-pitched frequencies  
285 and/or strongly modulated frequencies, with short duration (*Rhinolophus* excluded because of their use  
286 of a specific strategy to detect prey flutter (Schnitzler and Denzinger, 2011)), implying a short  
287 acoustical range. The third group on the other hand often uses quasi-constant frequencies with very  
288 short bandwidth and long duration calls, which carries a signal over long distances (Barataud, 2015).  
289 The first acoustical strategy is adequate to forage and commute close to the ground and vegetation  
290 whereas the second is on the contrary best suited for high flight. Between those two groups, one can  
291 clearly observe a progressive range of those acoustical strategies (e.g. *Eptesicus serotinus*, which  
292 displays low frequencies but large bandwidths). The specific distribution of flight heights found in our  
293 study is concordant with what is described in the literature (Arthur and Lemaire, 2015; Dietz *et al.*,  
294 2009; Rodrigues *et al.*, 2015).

295

### 296 *Correlation between fatalities and behaviour*

297 In order to establish a relationship between species distinctive flight height distribution and their  
298 susceptibility to WT collisions, a proper method for the assessment of this susceptibility had to be  
299 chosen. Since study sites with standardised methods in both pre-construction acoustic surveys and  
300 post-activation fatality surveys are very scarce, we chose to use publicly available mortality data from  
301 French wind farms. Here, to distinguish between the effect of behaviour and density, French carcass  
302 counts had to be corrected for species abundance. Relative densities for bat species are only available

303 in the literature for the French territory (Haquart, 2013). This approach is worth considering for other  
304 territories and opens novel possibilities for assessing correlations such as the one presented here.

305  
306 Our results demonstrate that species susceptibility to WT collision is highly correlated with their  
307 propensity to spend time at height (i.e. at collision risk) when monitored from wind masts. This novel  
308 finding disentangles the roles played by species densities on one hand, and by species flight height on  
309 the other hand, and brings new elements to the understanding of the ultimate causes of WT collisions  
310 (see Cryan and Barclay, 2009). Furthermore, the behavioural relevance of this relationship is that tall  
311 structures like wind masts or WT seem to act as similar auditory or visual stimuli to bats, as this was  
312 suggested by Jameson and Willis (2014) for North American species.

313  
314 *Limits and proposals for improvement*

315 The robustness of the correlation has to be enhanced with more observations for rare species. *T.*  
316 *teniotis* and *N. lasiopterus* populations for instance are suspected to be significantly impacted by WT,  
317 although few data have been reported in France – 1 and 6 carcasses respectively (Rodrigues *et al.*,  
318 2015). Spain and Portugal studies report the majority of mortality data for these two large European  
319 species. According to French population densities calculated by Haquart (2013), they are among the  
320 five rarest species in the French Mediterranean region (57 000 km<sup>2</sup>). The estimates are of about 16 000  
321 individuals for *T. teniotis* and about 600 individuals for *N. lasiopterus*. The impact of WT might be  
322 underestimated because of the low probability to find the carcasses of rare species.

323  
324 The results presented here were obtained from data originating from relatively small WT (rotor blades  
325 above 32 (+/- 8) meters high) or wind masts compared to many WT that are currently being built.  
326 However, we can assume that flight height distribution of each species are simple gradients, thus  
327 species ordering along the susceptibility gradient should not change according to WT height.

328  
329 Bat fatalities at wind farms collected by EUROBATS are not corrected for predation rates, the  
330 efficiency of the observer and the surface prospected. It is one of the reasons why the correlation

331 established in our study is a relative correlation and cannot be used as such to predict the number of  
332 carcasses that would be found at a WT by an acoustic survey alone. To achieve this goal, a different  
333 method has to be used, where flight height monitoring and carcass searches would be performed at the  
334 same sites. Korner-Nievergelt *et al.* (2013) achieved this work in Germany with the formulation of an  
335 N-mixture model from acoustic surveys at WT nacelles. This allowed the prediction of bat fatalities  
336 from acoustic monitoring data at the WT nacelle. The same undertaking has to be done before and  
337 after the wind farm installation in order to predict bat fatalities from pre-construction acoustic surveys.  
338 This has been attempted by Hein *et al.* (2013) but the relationship between both variables was not  
339 conclusive. It will be greatly improved if the data collection methods are standardised and if precision  
340 in bat species identification is enhanced.

341

#### 342 *Applications of the collision susceptibility index*

343 Finally, the creation of an index for species susceptibility to WT collisions, independently of their  
344 abundance, is an important achievement for the objectivity of impact assessment studies. The latter  
345 need this index in order to assess a local susceptibility to collisions, using additional information such  
346 as local activity level recorded from the ground and site function (e.g. presence of roost, presence of  
347 foraging activity). Unless bat flight height distribution is significantly different from one geographical  
348 region to another – which remains to be studied – this index could potentially be used in studies from  
349 any European region where those species are extant. But this index neglects possible variations in  
350 flight behaviour across locations, that can be assessed with recordings from wind masts. Our results  
351 indeed support that studying bat acoustic activity on a wind mast is a powerful method to assess  
352 impacts prior to the settlement of wind farms.

353

#### 354 *Variability of flight height*

355 Abiotic and biotic factors, such as wind speed, insect concentrations, or vegetation height are known  
356 to influence bats flying heights (e.g. Menzel *et al.*, 2005; Arthur and Lemaire, 2015; Kunz *et al.*, 2007,  
357 Rydell *et al.*, 2010). In addition, knowledge about the precise distribution of migration flight routes is  
358 missing in the literature. The position of a study site on one of these routes might significantly alter

359 flight heights. While the response of bats to meteorological factors that fluctuate year-round at one  
360 study site are easily monitored, very little information exists about the precise influence operated by  
361 habitat variables on bat flight altitude. Some studies explored the link between, on one hand, bat  
362 mortality and activity, and on the other hand, bat mortality and habitat (e.g. Ferreira et al., 2015,  
363 Johnson et al., 2004, Arnett *et al.*, 2016). However, the question of how habitat alters flight height was  
364 to our knowledge only addressed by Menzel *et al.* (2005) on five bat species with one sampling per  
365 habitat. Throughout Europe, a multitude of small datasets with similar methodologies are collected  
366 each year for the purpose of WT impact assessment studies. Put together, they would offer an  
367 excellent opportunity to study this relationship more thoroughly.

368

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377 acoustic analysis.

378

### 379 **Conflict of interest**

380 Biotope is an environmental consultancy involved in wind turbine impact assessment studies. Two of  
381 the authors, Charlotte Roemer and Thierry Disca, were employees at Biotope at the time of  
382 submission. Yves Bas was an employee at Biotope until March 2014. Authors thus declare a direct  
383 conflict of interest according to Elsevier ethics. However, all data used to calculate bat susceptibility to  
384 wind turbines were taken from the literature and are completely independent from Biotope's activities  
385 and clients. Authors furthermore take complete responsibility for the integrity of the data related to  
386 flight behaviour and the accuracy of their analysis.

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477

478 **Tables and Figures**

479

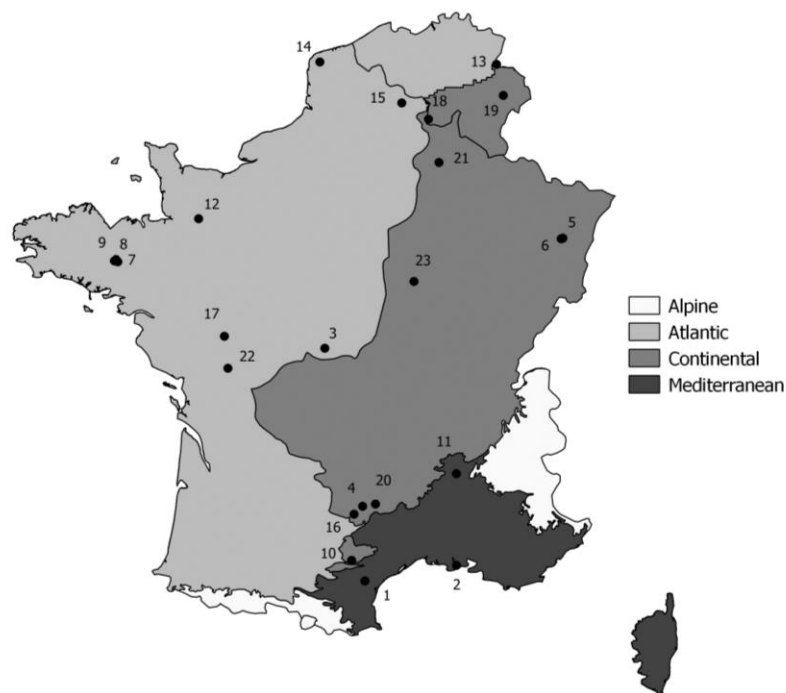


Figure 1: Study sites locations in France and Belgium and the different biogeographical areas.

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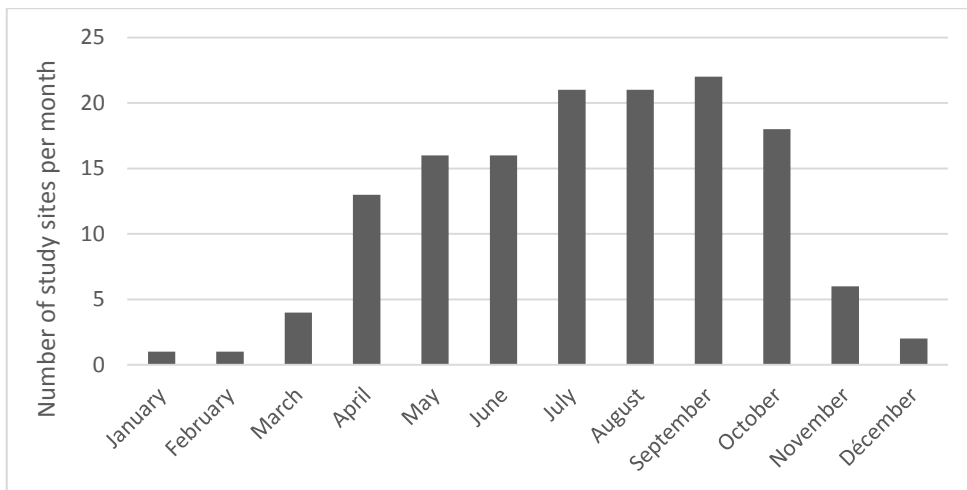


Figure 2: Cumulative number of sites surveyed per month for the six study years.

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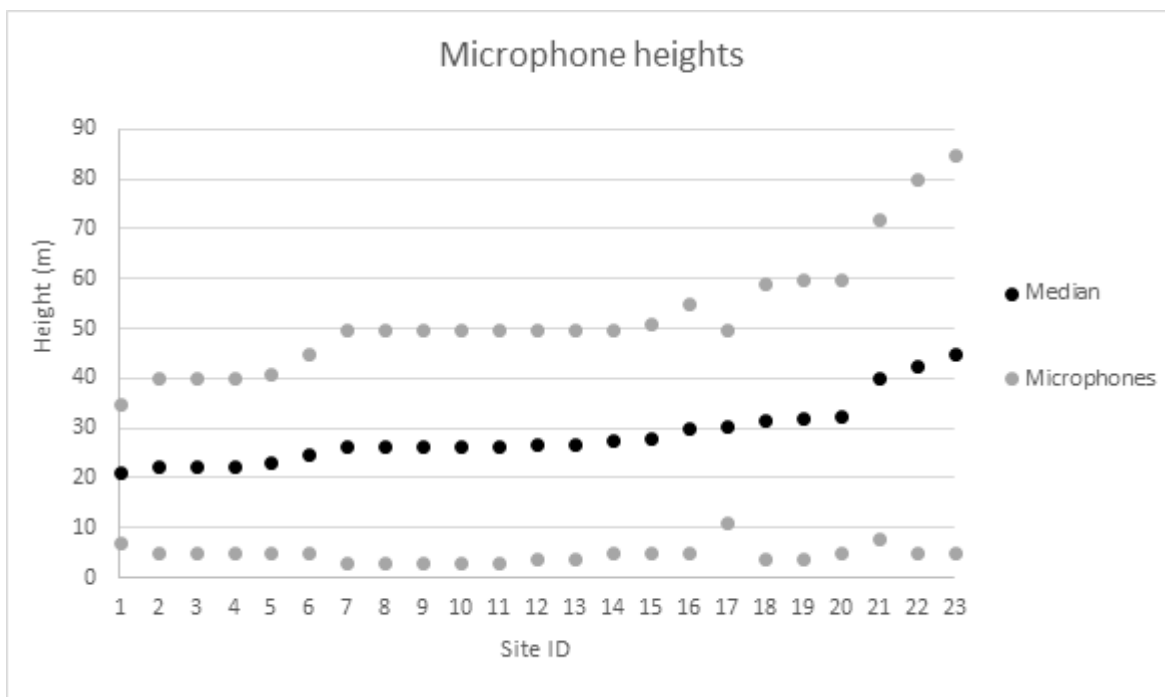


Figure 3: Microphone height and median height for all 23 study sites.

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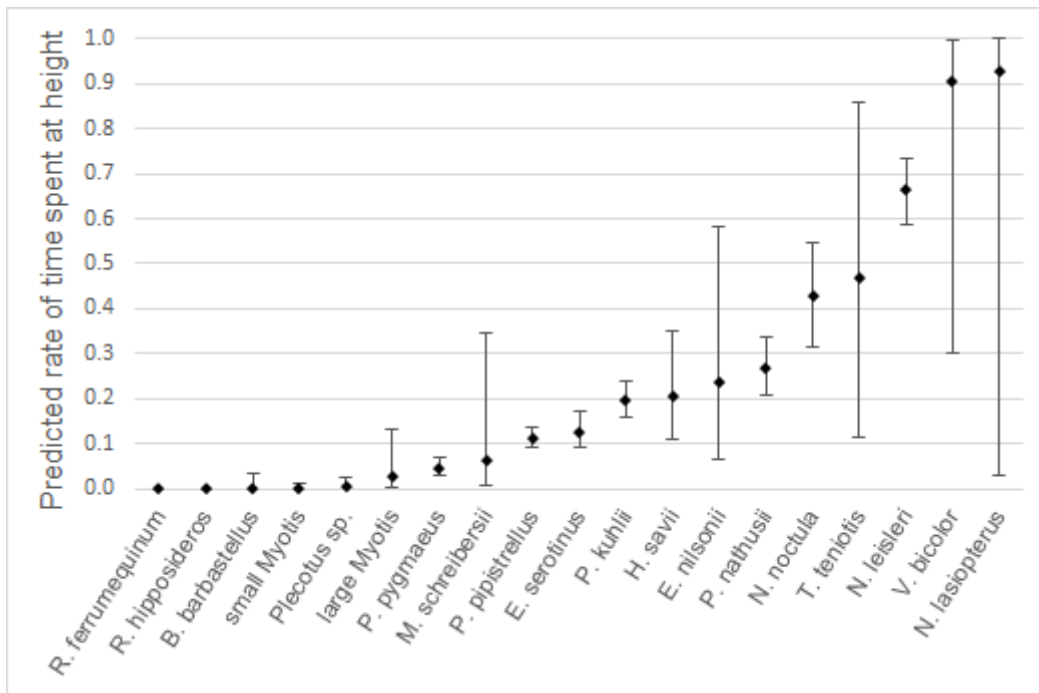


Figure 4 : Ratio of time spent at height for each species. Predicted rates are calculated from the GLMM output and are available in more details in Table A3 in the supplementary material.

484

Table 1 : Values taken from the literature to calculate a collision susceptibility index to WT. Mean activity at ground and at height microphones correspond to the values of our study sites which contain continuous recordings overnight (i.e. after 2013), for comparison with Actichiro.

Species	Mean activity (Positive minutes of activity /night) (Haquart , 2013)	Detection distance (m) (Barataud, 2015)	Number of carcasses FR (EUROBATS , 2015)	Collision susceptibility index	Mean activity at ground	Mean activity at height
small Myotis	19.59	15	3	3	2.32	0.02
<i>R. hipposideros</i>	0.66	5	0	8	0	0
<i>Plecotus sp.</i>	1.52	23	0	14	0.8	0.01
<i>R. ferrumequinum</i>	0.52	10	0	19	0.04	0
<i>B. barbastellus</i>	3.21	15	3	19	0.35	0
<i>M. schreibersii</i>	1.44	30	5	125	0.11	0.02
large Myotis	0.49	20	4	204	0.11	0.01
<i>P. pipistrellus</i>	79.85	35	622	273	27.08	5.86
<i>E. serotinus</i>	3.34	40	23	287	1.28	0.36
<i>P. kuhlii</i>	9.55	30	130	411	3.48	1.97
<i>P. pygmaeus</i>	5.93	25	125	532	2.61	0.33
<i>T. teniotis</i>	0.18	150	1	815	0.02	0.01
<i>H. savii</i>	1.78	40	36	833	0.2	0.11
<i>P. nathusii</i>	3.15	35	178	1991	1.36	0.89

<i>E. nilsonii</i>	0.02	50	0	2500	0	0
<i>N. noctula</i>	1.15	100	31	2783	0.07	0.14
<i>N. leisleri</i>	0.87	70	63	5155	0.6	0.7
<i>N. lasiopterus</i>	0.08	150	6	12755	0	0.02
<i>V. murinus</i>	0.01	50	8	81678	0	0.01

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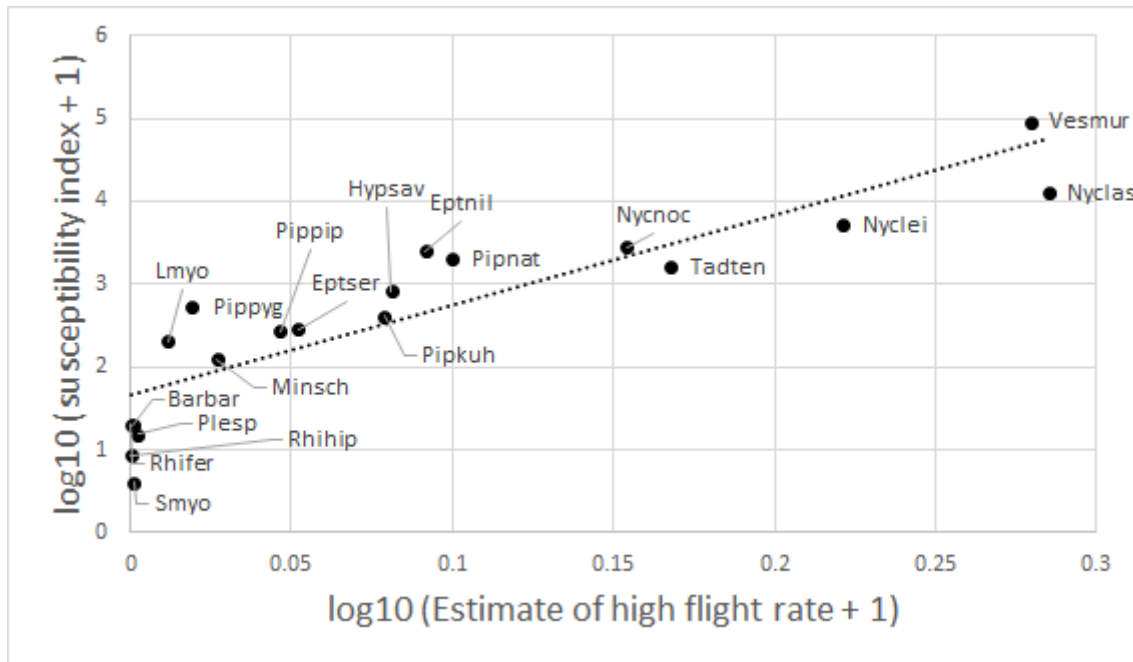


Figure 5: Ratio of time spent at height in function to susceptibility to WT collision. Spearman correlation coefficient  $\rho = 0.94$ ;  $p = 4.58e-06$ . Species names are the three first letters of the genus and of the species name excepted for small *Myotis* (Smyo) and large *Myotis* (Lmyo).

## Supplementary material

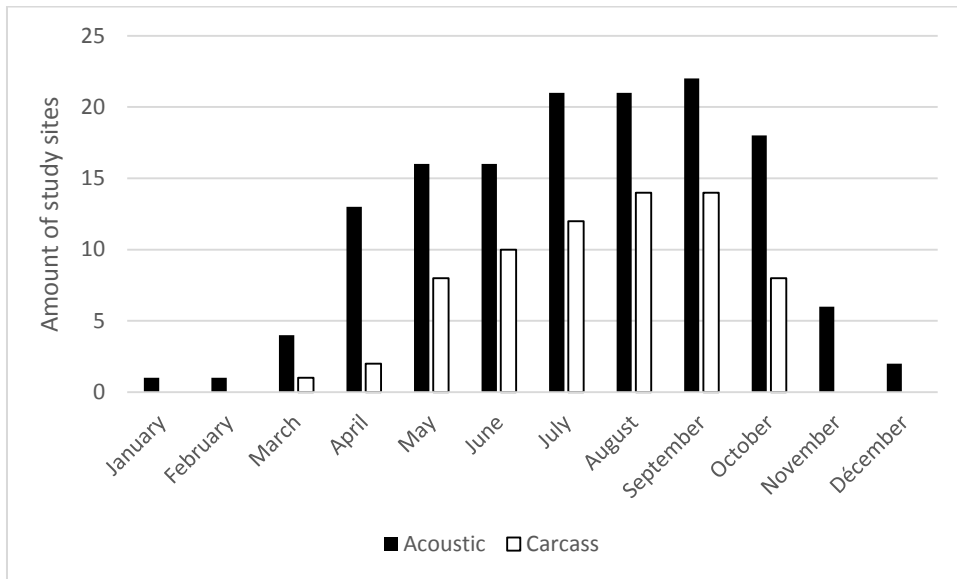


Figure A1: Annual distribution of the acoustic surveys at wind masts used for flight height assessment (black) and of the carcass searches at wind farms (white) (when data was available).

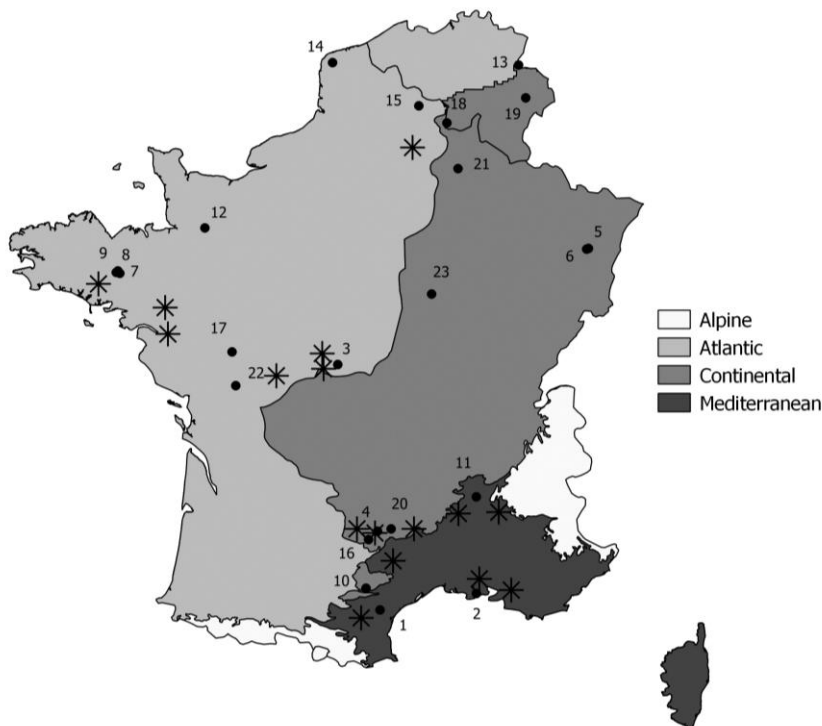


Figure A2: Spatial distribution of the wind masts used for flight height assessment (dots) and of the wind farms where carcass searches were performed (stars) (when data was available). The different biogeographical areas are showed for France and Belgium.

Table A1: Comparison of activity (number of bat passes) recorded from both microphones. Species names are the three first letters of the genus and of the species name excepted for small Myotis (Smyo) and large Myotis (Lmyo).  $R^2$  is the correlation between the activity recorded at the ground

microphone and the activity recorded at the upper microphone where each study site in an observation. NA stands for species that were not observed at height (i.e. *Rhinolophus*) and for species that were not recorded at more than 15 study sites.

Source Species	< median height		> median height		Total	Percentage of bat passes recorded from ground mic	R <sup>2</sup> between ground and height mic
	Ground mic	Ground and height mic	Ground and height mic	Height mic			
<i>Barbar</i>	4,600	55	1	6	4,662	99.87	0.14
<i>Eptnil</i>	123	6	5	33	167	80.24	NA
<i>Eptser</i>	7,631	696	219	768	9,314	91.75	0.39
<i>Hypsav</i>	666	56	24	135	881	84.68	NA
<i>Minsch</i>	192	4	9	9	214	95.79	NA
<i>L Myotis</i>	617	14	3	22	656	96.65	0.55
<i>S Myotis</i>	8,104	118	3	30	8,255	99.64	0.03
<i>Nyclas</i>	1	1	3	24	29	17.24	NA
<i>Nyclei</i>	1,629	353	626	2,684	5,292	49.28	0.85
<i>Nycnoc</i>	1,298	194	292	445	2,229	80.04	0.80
<i>Pipkuh</i>	33,454	2,779	491	6,136	42,860	85.68	0.79
<i>Pipnat</i>	3406	135	90	1,869	5,500	66.02	0.74
<i>Pippip</i>	207,392	5,029	1,608	22,856	236,885	90.35	0.52
<i>Pippyg</i>	8,743	66	59	471	9,339	94.96	NA
<i>Plesp</i>	4,023	44	2	22	4,091	99.46	0.23
<i>Rhifer</i>	198				198	100	NA
<i>Rhihip</i>	9				9	100	NA
<i>Tadten</i>	38	5	21	21	85	75.29	NA
<i>Vesmur</i>	4	4	16	50	74	32.43	NA

Table A2: Data used for estimations of species density. Sampling effort for each of the biogeographical areas in Haquart (2013).

Biogeographical area	Number of sampling sites	Area (km <sup>2</sup> )	Number of sampling sites per 1000 km <sup>2</sup>
<i>Alpine</i>	28	30,658	0.91
<i>Atlantic</i>	768	268,155	2.86
<i>Continental</i>	169	184,203	0.92
<i>Mediterranean (Corsica excluded)</i>	752	56,918	13.21

Table A3: Ratio of time spent at height for each species. Predicted rates are calculated from the GLMM output. Standard error for *Rhinolophus* species could not be estimated (NE)

because of the nonexistence of occurrences at height.

Species	GLMM value	Standard error	Predicted rate	N bat passes
<i>R. ferrumequinum</i>	-24.30	NE	0	198
<i>R. hipposideros</i>	-22.93	NE	0	9
<i>B. barbastellus</i>	-6.38	3.06	0.002	4,662
small <i>Myotis</i>	-5.94	1.43	0.003	8,255
<i>Plecotus sp.</i>	-5.29	1.67	0.005	4,091
large <i>Myotis</i>	-3.58	1.7	0.027	656
<i>P. pygmaeus</i>	-3.05	0.44	0.045	9,339
<i>M. schreibersii</i>	-2.68	2.04	0.064	214
<i>P. pipistrellus</i>	-2.06	0.23	0.113	236,885
<i>E. serotinus</i>	-1.93	0.36	0.127	9,314
<i>P. kuhlii</i>	-1.41	0.25	0.197	42,860
<i>H. savii</i>	-1.36	0.75	0.205	881
<i>E. nilsonii</i>	-1.18	1.51	0.235	167
<i>P. nathusii</i>	-1.01	0.33	0.267	5,500
<i>N. noctula</i>	-0.30	0.48	0.427	2,229
<i>T. teniotis</i>	-0.12	1.93	0.470	85
<i>N. leisleri</i>	0.68	0.34	0.664	5,292
<i>V. bicolor</i>	2.23	3.06	0.903	74
<i>N. lasiopterus</i>	2.57	6.03	0.929	29

Table A4: Detailed number of bat passes located at ground or at height for all species, before pooling species into groups for further analysis.

Species	Ground	Height	Total
<i>B. barbastellus</i>	4,655	7	4,662
<i>Chiroptera sp.</i>	317	73	390
<i>Eptesicus/Nyctalus/Vespertillio sp.</i>	1,205	1,101	2,306
<i>E. nilssonii</i>	129	38	167
<i>E. serotinus</i>	8,327	987	9,314
<i>H. savii</i>	722	159	881
<i>M. schreibersii</i>	196	18	214
<i>M. alcathoe</i>	1		1
<i>M. bechsteinii</i>	150		150
<i>M. brandtii</i>	9		9
<i>M. capaccinii</i>	1		1
<i>M. dasycneme</i>	3		3
<i>M. dasycneme (probable)</i>		1	1
<i>M. daubentonii</i>	236	2	238
<i>M. emmarginatus</i>	38		38
Large <i>Myotis</i>	631	25	656



<i>M. mystacinus</i>	48		48
<i>M. mystacinus/brandtii</i>	6		6
<i>M. nattereri</i>	781		781
<i>Small myotis</i>	6,949	30	6,979
<i>N. lasiopterus</i>	2	27	29
<i>N. leisleri</i>	1,982	3,310	5,292
<i>N. noctula</i>	1,492	737	2,229
<i>P. kuhlii/nathusii</i>	6,256	1,114	7,370
<i>P. kuhlii</i>	36,233	6,627	42,860
<i>P. nathusii</i>	3,541	1,959	5,500
<i>P. pipistrellus</i>	212,421	24,464	236,885
<i>P. pygmaeus</i>	8,809	530	9,339
<i>Plecotus sp.</i>	3,582	17	3,599
<i>P. auritus</i>	382	3	385
<i>P. austriacus</i>	99	1	100
<i>R. ferrumequinum</i>	198		198
<i>R. hipposideros</i>	9		9
<i>T. teniotis</i>	43	42	85
<i>V. murinus</i>	8	66	74
Total	299,461	41,336	340,797

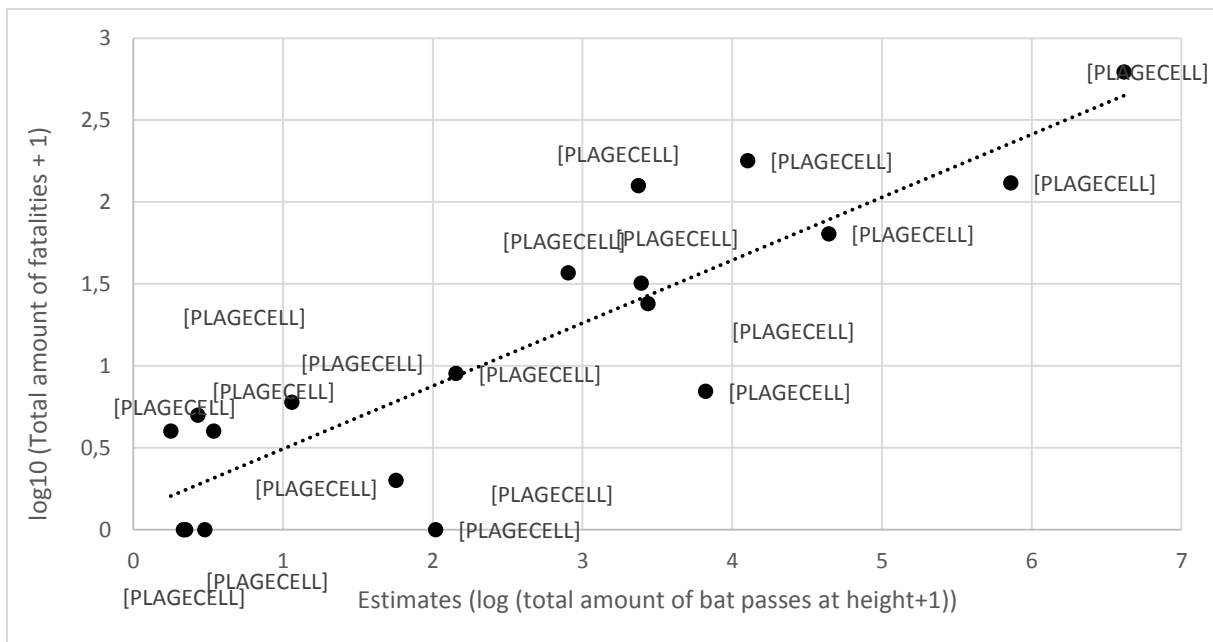


Figure A3: Correlation between the raw count of bat carcasses and the estimated species number of bat passes at height ( $\rho = 0.84$ ). We used the same generalised linear mixed model (GLMM) structure as the one described in Material and Methods to estimate the numbers of bat passes at

height (and respectively at ground) for each species. These estimates were then correlated to species fatality counts.

Table A5: Detail of the proportion of bat passes between microphones at ground and height for the three different biogeographical regions. Species names are the three first letters of the genus and of the species name excepted for small *Myotis* (Smyo) and large *Myotis* (Lmyo).

<i>Source localisation</i>	<i>Atlantic</i>		<i>Continental</i>		<i>Mediterranean</i>	
	Ground	Height	Ground	Height	Ground	Height
<i>Barbar</i>	4,472	5	174	1	9	1
<i>Eptnil</i>			129	38		
<i>Eptser</i>	6,450	750	469	81	1,408	156
<i>Hypsav</i>		2	33	2	689	155
<i>Minsch</i>			15	1	181	17
<i>L Myotis</i>	163	8	442	17	26	
<i>S Myotis</i>	4,927	16	2,987	5	308	12
<i>Nyclas</i>			2	27		
<i>Nyclei</i>	1,115	1,090	511	1,746	356	474
<i>Nycnoc</i>	1,463	683	13	31	16	23
<i>Pipkuh</i>	14,238	790	4,836	189	17,159	5,648
<i>Pipnat</i>	1,357	771	344	938	1840	250
<i>Pippip</i>	99,881	8,789	80,993	13,119	31,547	2,556
<i>Pippyg</i>	69	3	9		8,731	527
<i>Plesp</i>	3,508	17	395	2	164	5
<i>Rhifer</i>	184		2		12	
<i>Rhihip</i>	5		2		2	
<i>Tadten</i>			6	7	37	35
<i>Vesmur</i>	3	4	2	59	3	3