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# Bat sonar and wing morphology predict species vertical niche

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1 **Title: Bat sonar and wing morphology predict species vertical niche**

2 Running title: Bat traits predict species vertical niche

3

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28

29 **ABSTRACT**

30 The use of echolocation allows insectivorous bats to access unique foraging niches by  
31 locating obstacles and prey with ultrasounds in complete darkness. To avoid interspecific  
32 competition, it is likely that sonar features and wing morphology co-evolved with species  
33 vertical distribution, but due to the technical difficulties of studying flight in the vertical  
34 dimension, this has never been demonstrated with empirical measurements.

35 We equipped 48 wind masts with arrays of two microphones and located the vertical  
36 distribution of a community of 19 bat species and two species groups over their annual  
37 activity period (> 8,000 nights). We tested the correlation between the proportion of flights at  
38 height and the acoustic features of bat calls as well as their wing morphology.

39 We found that call peak frequency and bandwidth are good predictors of bat use of the  
40 vertical space regardless of their acoustic strategies (i.e. gleaning, hawking or detecting prey  
41 flutter). High wing aspect ratios and high wing loadings were associated with high  
42 proportions of time spent at height, confirming hypothesis from the literature.

43

44 **Keywords**

45 Wing aspect ratio; echolocation; bat vertical space use; acoustic location.

46

47 **I. INTRODUCTION**

48 Insectivorous bat species have developed through evolution the ability to commute and forage  
49 in complete darkness. Although feeding on similar resources (i.e. insects), most sympatric  
50 species specialise in their prey selection and therefore in their habitat selection, while some  
51 are more plastic (Dietz et al., 2009). In order to match these particular needs, this diet  
52 partitioning is accompanied by morphological and behavioural differences. Illustrating those  
53 differences, *Myotis nattereri*, a small bat (wingspan = 250-300 mm), is able to forage insects  
54 resting on leaves under the forest cover while *Tadarida teniotis*, a large bat (wingspan = 400-  
55 450 mm), forages on insect swarms in wide and elevated open spaces (Arthur and Lemaire,  
56 2015). In addition, the echolocation system, developed through evolution to sense the  
57 environment in the dark, reflects the ability of each species to perceive obstacles and prey  
58 (Collen, 2012; Schnitzler et al., 2003; Siemers and Schnitzler, 2004).

59 Indeed, bat echolocation calls are designed in such a way that most species may be  
60 differentiated from one another using call peak frequency, duration and bandwidth or call  
61 shape, despite some overlap (Barataud, 2015; Fenton and Bell, 1981). Frequency in  
62 echolocation calls varies from 9 kHz, as in calls emitted by *Euderma maculatum*,  
63 Vespertilionidae (Fullard and Dawson, 1997) or *Tadarida teniotis*, Molossidae (Arlettaz,  
64 1990), to 212 kHz, emitted by *Cloeotis percivali*, Hipposideridae (Fenton and Bell, 1981).  
65 Because atmospheric attenuation increases with call frequency, low frequency signals carry

66 through greater distances than high frequencies, which in turn procure the advantage of a  
67 higher structure resolution (Pye, 1979). On the other hand, low frequencies are associated  
68 with long wavelengths, which are unsuitable for the detection of targets such as small insects,  
69 and should be the major evolutionary constraint for the use of low frequencies in echolocation  
70 (Barclay and Brigham, 1991; Waters et al., 1995). Echolocation call length varies from 1 ms  
71 as by *Myotis brandtii*, Vespertilionidae, to more than 80 ms by *Rhinolophus ferrumequinum*,  
72 Rhinolophidae (Barataud, 2015). Long calls allow a better detection of faint and distant  
73 echoes through the repeated addition of signal information that evokes the activity of neurons  
74 tuned to the frequency of interest, and consequently increase echolocation ranges (Neuweiler,  
75 1989; Schnitzler et al., 2003). Long calls can also provide information on prey fluttering and  
76 movement directionality (Trappe and Schnitzler, 1982), while the emission of short calls  
77 decrease the issue of call-echo overlap (Jones, 1999). Finally, call bandwidth varies from less  
78 than 1 kHz, as by *Nyctalus noctula*, Vespertilionidae (Barataud, 2015), to more than 170 kHz  
79 in some *Kerivoula* species (Vespertilionidae) (Kingston et al., 1999). Large bandwidths  
80 enhance range accuracy and resolution (i.e. the differentiation of two targets at close  
81 distances) (Pye, 1979; Siemers and Schnitzler, 2004) while small bandwidths, combined with  
82 long call length, can also be used to detect prey fluttering or increase the detection range.

83 Aldridge and Rautenbach (1987) studied the links between call shape, wing morphology,  
84 manoeuvrability, habitat use and diet in South African insectivorous bats. They found that the  
85 differences in acoustic features and wing morphology explained resource partitioning in these  
86 species. High wing loading (larger wing area relative to mass) generally correlates with high  
87 flight speed while low wing loading favours good manoeuvrability, essential when foraging in  
88 clutter (Kalko et al., 2008; Norberg and Rayner, 1987). In addition, high wing aspect ratio  
89 (narrow wings) generally correlates with decreases in transport costs thanks to a low wing  
90 inertia, and favours good agility at high speeds (Kalko et al., 2008; Norberg and Rayner,

91 1987). These studies highly contributed to the understanding of the acoustic and morphologic  
92 characteristics leading to clutter - or closed - versus open space adaptations in bats (Fenton,  
93 1990). Several other studies also found strong relationships between body size or mass and  
94 acoustic parameters in many bat species all over the world (Bogdanowicz et al., 1999; Jones,  
95 1999; Penone et al., 2018; Thiagavel et al., 2017). These findings highlight the co-evolution  
96 of many traits in bats.

97 In 2001, Schnitzler and Kalko described the concept of bat guilds, which was refined over  
98 time (Denzinger and Schnitzler, 2013; Denzinger et al., 2018). Guilds may be used to form  
99 consistent species groups for the study of sonar structures, habitat types, diet, foraging modes  
100 and other traits. In Denzinger et al. (2018), four guilds may be distinguished according to their  
101 acoustic strategies: (1) aerial hawkers or trawlers developed a strategy to efficiently locate  
102 prey in open and edge space using long quasi-constant frequency (QCF) calls (2) active  
103 gleaners mostly use short calls with high frequency compounds and frequency modulated  
104 (FM) calls resulting in large bandwidths, useful to detect prey or obstacles in high clutter (3)  
105 passive gleaners also use short calls with high frequencies and FM calls, but mostly listen to  
106 the rustling sounds of their prey while foraging, and use echolocation for orientation (4) some  
107 species also use a strategy implying long constant frequency calls with modulated frequency  
108 components (CF-FM) at high frequencies which allow them to evaluate flutter information  
109 from the prey returning echoes.

110 Associations in echolocation, wing morphology and flight behaviour have only been  
111 demonstrated for adaptation to clutter (Aldridge and Rautenbach, 1987; Siemers and  
112 Schnitzler, 2004), from studies using material positioned at ground level, with a limited  
113 detection range, while bats use a three-dimensional space that can be as elevated as 3000 m  
114 for some species (Peurach, 2003; Williams et al., 1973). The association between bat sonar or

115 wing morphology and their use of the vertical dimension has never been thoroughly  
116 demonstrated. Since the vertical distribution of insects varies according to species (Reynolds  
117 et al., 2017), and since bats differentiate in their diets (Dietz et al., 2009), the vertical  
118 distribution of the different bat guilds is strongly expected to follow that of their prey  
119 (Norberg and Rayner, 1987; Roeleke et al., 2018). Roemer et al. (2017) showed that bat  
120 guilds according to Denzinger and Schnitzler (2013) could be ordered along the gradient of  
121 the rate of time spent at height. It was also shown that the occurrence of certain insect orders  
122 in bat diet could be associated with certain bat sonar and morphology features (Bogdanowicz  
123 et al., 1999). However, the contribution of sonar features and wing morphology to the vertical  
124 separation of species was only described from case studies on target species, or from a  
125 collection of heterogeneous observations (visual, mistnetting, acoustic) of a bat community  
126 (Banse, 2010; Denzinger et al., 2018; Kalko et al., 2008), and remains to be demonstrated  
127 with empirical and standardised measurements.

128 The study of animal use of the vertical space is a challenging task because of the technical  
129 difficulties this implies. Stereoscopic cameras are best suited for studies in a restricted volume  
130 because field of view is limited (Holderied and Jones, 2009). Tracking of animal movements  
131 with radar units only allow poor taxonomic resolution because target echoes provide limited  
132 information on animal size and flight behaviour (Bruderer and Popa-Lisseanu, 2005).  
133 Acoustic tracking of animal echolocation calls offers numerous advantages, such as species  
134 identification with the acoustic clues of their calls, an omnidirectional detection range, and an  
135 easy automation of the process (Holderied et al., 2008; Koblitz, 2018; Roemer et al., 2017). In  
136 addition, the installation of microphone arrays on wind masts allows acoustic location in a  
137 space situated at dozens of meters above ground, that is otherwise difficult to access (Roemer  
138 et al., 2017).

139 The aim of our study was to investigate the links between the vertical distribution of a  
140 community of European insectivorous bats, the acoustic parameters of their sonar (peak  
141 frequency, call duration and call bandwidth) and their wing morphology (wing aspect ratios  
142 and wing loading). We expected (1) longer call durations to be associated with higher flight  
143 heights, (2) higher peak frequencies to be associated with lower flight heights, (3) larger  
144 bandwidths to be associated with lower flight heights, (4) narrower wings to be associated  
145 with higher flight heights and (5) higher wing loadings to be associated with higher flight  
146 heights. To measure bat position in the vertical space, we equipped wind masts with  
147 microphone arrays and performed acoustic location of bat echolocation calls.

148

## 149 **II. MATERIAL & METHODS**

### 150 A. Acoustic recordings used to study bat altitudinal behaviour

151 Between 2011 and 2017, recordings were conducted at 48 sites in France and Belgium where  
152 bat activity was monitored on 8,435 nights (mean = 175.7 standard deviation = 76.1, min =  
153 19, max = 352 nights per site). Microphones were installed on lattice or monopole wind masts  
154 of 50-100 m in height and the wind masts themselves were erected in open or semi-open  
155 habitats (i.e. agricultural land, bocage, garrigue, wetlands or forest clearing). Arrays  
156 composed of two microphones were achieved with two SMX-US, SMX-U1 (Wildlife  
157 Acoustics, USA) or SMX-US (Biotope, France) microphones plugged to an SM2BAT or  
158 SM3BAT (all models, Wildlife Acoustics, Massachusetts, USA). Microphones were inserted  
159 into tubes, facing downward, to protect them from weather elements. A custom-made  
160 aluminium reflector placed below the microphone at a 45° angle minimised the directionality  
161 of the setting. Microphones were installed at heights ranging from 4 to 85 m (Figure 2 in  
162 suppl. mat.). Recorders were programmed to start each day 30 min before sunset and stop



163 30 min after sunrise. Whole night recordings were performed on study sites between 2013 and  
164 2017 (38 sites), but from 2011 and 2012 (10 sites) samplings were collected for 10 minutes  
165 every 20 minutes. Gain was set at 36 dB, sampling rate at 192 kHz, trigger at 6 dB above  
166 background noise and trigger window at 2.5 sec. A 1 kHz high pass filter was used. Files were  
167 compressed in WAC4 format and analysed in WAV format or directly recorded in WAV  
168 format.

#### 169 B. Species identification and flight height classification

170 Files were decompressed with the WAC2WAV or the Kaleidoscope software (Wildlife  
171 Acoustics, Massachusetts, USA). Files were automatically cut in 5 second bouts after each  
172 triggered recording to be used as a proxy for a bat pass (Barré et al., 2018; Roemer et al.,  
173 2017). SonoChiro (Biotope, France) was used to automatically attribute calls to a species or a  
174 species group, and the verification of the result was done by manually checking acoustic  
175 sequences.

176 To identify bat species based on acoustic features, we followed the method developed by  
177 Barataud (2015), which is the most extensive study of European bat calls published today.  
178 Identification criteria are based on the association between acoustic call type, call shapes and  
179 measurable parameters (initial frequency, terminal frequency, signal length, maximum energy  
180 and its repartition ...), their rhythms (interval duration between calls) and the environment  
181 (distance to obstacles). With the knowledge accumulated today, this method allows the  
182 identification of 29 species out of the 34 extant in France and Belgium under good recording  
183 conditions. If a bat was recorded at both microphones at the same time, we checked the  
184 sequence which contained the most calls, and that was thus supposed to display the best  
185 acoustic quality.

186 Some sequences may only contain faint calls, and yet contain enough clues to attribute the  
187 sequence to a species, because the species does not completely overlap the acoustic repertoire  
188 of another species (e.g. low frequency calls of *Tadarida teniotis* or low frequency calls of  
189 *Hypsugo savii*). Call duration and bandwidth are the most affected by atmospheric  
190 attenuation, yet other call parameters that are better preserved are sometimes sufficient to  
191 make an identification (e.g. peak frequency, inter-call duration, frequency modulation (i.e.  
192 shape) of the main part of the call). Yet, some sequences were so affected by atmospheric  
193 attenuation that there was no sufficient clue to attribute the sequence to a species. In addition,  
194 some species use sonar calls that are sometimes very close, even identical in certain flight  
195 circumstances, preventing identification to species level. These acoustic sequences that could  
196 not be identified at the species level were either classed in a group of species - when the  
197 vertical flight behaviours of all species were equivalent within the same group - or left  
198 unidentified and not used for further analysis (8.4 % of all bat passes). Here, *Myotis myotis*  
199 and *M. blythii* were identified as the “large *Myotis*” group, all other *Myotis* as the “small  
200 *Myotis*” group, and all *Plecotus* calls to the *Plecotus spp.* group. Species within those two  
201 groups present flight heights comparable to the other species of their group (Rodrigues *et al.*,  
202 2015), and similar acoustic features (Barataud, 2015). Great care must be taken in the analysis  
203 of the results of the species *P. kuhlii* and *P. nathusii*, because acoustic features of these two  
204 species are simultaneously very variable and similar to each other. *V. murinus* is also difficult  
205 to distinguish from *N. leisleri*, but *V. murinus* is known to be rare in France and Belgium.

206 To classify flight heights, we used SonoChiro to automatically determine the time at which  
207 each call started on each microphone. We then obtained the time differences of arrival  
208 (TOAD) for each call detected using the `find.matches` function of Hmisc package (Harrell,  
209 2018) from R (R Core Team, 2014). With two microphones, flight height cannot be precisely  
210 calculated, and TOAD were used to determine to which microphones bats were closer. A

211 height threshold was defined for each site as the median height between the two microphones.  
212 Microphone median height was variable depending on study site (20-50 m) (Figure 2), but  
213 this variation did not greatly affect species proportion of flight at height (Figure 3). Using this  
214 threshold, bat calls were assigned to two classes following the method described in Roemer et  
215 al. (2017): “at height” if the source of the signal was above the threshold and “at ground  
216 level” if it was below the threshold. A ratio of the time spent at height was then calculated for  
217 each species. It must be noted that in forest clearings, tree canopy was never higher than the  
218 median height between both microphones. Therefore, bats positioned “at height” were flying  
219 in an open environment.

220 A generalised linear mixed model (GLMM) was used to estimate rates of flight at height for  
221 each species. Bat pass height was modelled as a binomial variable (at height or at ground  
222 level) according to species as a fixed effect. The median height of microphones was  
223 introduced as a fixed effect to control for its potential influence. The local environment effect  
224 on flight behaviour was taken into account by introducing study sites as a random variable.  
225 The GLMM was built using the `glmmTMB` function (Magnusson et al., 2018) of R (R Core  
226 Team, 2014).

### 227 C. Acoustic parameters of species sonars

228 We chose to study the three main features defining bat call shapes and acoustic properties,  
229 namely call duration, peak frequency (i.e. the frequency at the maximum energy), and  
230 bandwidth. We referred to the work of Barataud (2017, 2015) to obtain the mean values of  
231 these three acoustic parameters for the species recorded in our study (Table 1). In the group  
232 small *Myotis*, we present results for *M. daubentonii*, *M. nattereri* and *M. bechsteinii*, which  
233 were the most common *Myotis* identified in our recordings. In the same manner, in the group  
234 *Plecotus spp.*, we present results for *P. auritus* and *P. austriacus*.

235 D. Wing loading and aspect ratio

236 We calculated indices of wing morphology based on bone measurements, which are the most  
237 practical and consistent indices, following the method of Bader et al. (2015). All  
238 morphological information was retrieved from Dietz et al. (2009). The latter authors provided  
239 the minimum and maximum values per species, from which we calculated a mean value that  
240 we used for further analyses.

$$\text{Aspect Ratio Index } ARI = \frac{d3 + FA}{d5} ,$$

241 where FA = length of the forearm, d3 = length of the third digit and d5 = length of the fifth  
242 digit.

$$\text{Wing Loading Index } WLI = \frac{m}{(FA + d3) \times d5 \times 2} ,$$

243 where m = body mass.

244 E. Correlations between rate of flight at height and species traits

245 We first checked for normality in the distribution of raw or transformed variables. Most  
246 variables did not follow a normal distribution, hence the correlations between each pair of  
247 variables were tested with a Kendall correlation test. For data visualisation, we assigned  
248 species into exclusive frequency-modulated (FM), constant-frequency with modulated  
249 frequency components (CF+FM) and frequency-modulated or quasi-constant frequency  
250 (FM/QCF) categories, according to their acoustic strategies (Barataud, 2015).

251

252 **III. RESULTS**

253 In total, 639,734 bat passes were recorded. Table 1 shows bat passes identified at the species  
254 or species group level. There was a continuous gradient in the vertical distribution of species  
255 from *Rhinolophus* bats that were never located at height to *Vespertilio murinus* that was  
256 located 86 % of the time at height. *Rhinolophus*, *Barbastella*, *Plecotus*, *Myotis*, *Miniopterus*  
257 species and *Pipistrellus pygmaeus* were located less than 5 % of the time at height. *Eptesicus*  
258 *serotinus*, *E. nilsonii*, *Hypsugo savii*, *P. kuhlii*, *P. pipistrellus* and *P. nathusii* were located  
259 between 5 and 25 % of the time at height. *Nyctalus*, *Tadarida* and *Vespertilio* species were  
260 located more than 30 % of the time at height.

#### 261 A. Interdependence of traits

262 Correlation tests for all species showed that all morphological and acoustic features were  
263 inter-correlated, except for call peak frequency versus call duration (Table 2).

#### 264 B. Correlations between proportion of flight at height and traits

265 Morphological and acoustic features were all correlated to the proportion of flights at height  
266 (Table 3, Figure 1). Compared to low-flying species, high-flying species used lower peak  
267 frequencies, narrower bandwidths, longer calls, and possessed narrower wings with higher  
268 wing loadings (Figure 1). In the correlation between the rate of flight at height and call  
269 duration, *Rhinolophus* species stood as outliers because they use extremely long call duration  
270 compared to other species flying near ground level (Figure 1b). Concerning call bandwidth,  
271 *Myotis* species were the outliers because they use extremely large bandwidth compared to  
272 other species flying near ground level (Figure 1c).

273

## 274 IV. DISCUSSION

275 A. Acoustic location from wind masts, a powerful tool for the study of animal flight  
276 behaviour

277 We studied to what extent the prevalence of bat species at elevated heights can be predicted  
278 by the acoustic features of their sonar and by their wing morphology. In the past, a study by  
279 Jensen and Miller (1999) with a vertical array of three microphones on a 15 meter pole  
280 elucidated the links between echolocation features and flight height in *E. serotinus*, a  
281 European bat. A study by Kloepper and Kinniry (2018) suggested that the features of  
282 echolocation calls in *Tadarida brasiliensis*, an American bat, vary in function of their flight  
283 height. However, our study is the first to assess this relationship in a bat community. The use  
284 of wind masts allowed a long-term monitoring of bat flight behaviour and an objective  
285 assessment of species vertical flight distribution. The automation of the process allowed us to  
286 equip 48 masts over the French and Belgian territories and analyse their results. The  
287 combination of long-term monitoring and of the high amount of study sites was an advantage  
288 in obtaining enough data for rare species (e.g. *E. nilssonii*) or species with short detection  
289 ranges (e.g. *R. hipposideros*).

290 B. Bat traits predict bat vertical niche partitioning

291 We demonstrate for the first time that the acoustic features of bat sonar predict bat vertical  
292 distribution regardless of species acoustic strategies. Call duration was a less reliable  
293 predictor than call peak frequency and bandwidth since Rhinolophidae stood as outliers with a  
294 very long call duration and an exclusive presence at ground level. This particularity is  
295 explained by their echolocation strategy to detect prey flutter by emitting long constant  
296 frequencies (CF) calls carrying short frequency modulated (FM) signals with a high duty  
297 cycle (Schnitzler and Denzinger, 2011). Rhinolophidae are part of the Yinpterochiroptera

298 suborder, that diverged 60 mya from the Yangochiroptera, (Teeling, 2009), to which the other  
299 bat families addressed here belong.

300 Our study also shows the first correlations based on empirical measures between bat wing  
301 morphology and their vertical distribution. It confirmed our hypotheses that narrow wings  
302 with high wing loadings are best suited for flying at greater heights.

303 In the bat community that we sampled, the proportion of time spent at height might be  
304 correlated to the availability in the prey on which each species specialises, but the  
305 opportunistic high-flying species (e.g. *Nyctalus*, *Tadarida*) could also exploit more elevated  
306 altitudes to actively avoid spatial competition with other species (Dietz et al., 2009; Roeleke  
307 et al., 2018). Indeed, the low frequency calls providing long detection ranges to high-flying  
308 bats are also less effective in detecting the small prey they feed on than the high frequency  
309 calls of species found at lower heights (e.g. *Pipistrellus*) (Waters et al., 1995).

### 310 C. Constraints of bat flight at great heights

311 We show that the use of the vertical space in European bats is ordered from *Rhinolophus*  
312 species (always flying near ground level or near background) to *Nyctalus* and *Tadarida*  
313 species (prevailing at height). In fact, guild categories used to define bat adaptation to clutter  
314 (i.e. narrow, edge and open space foragers (Denzinger and Schnitzler, 2013)) may be ordered  
315 along this same gradient from narrow foragers (low-flying species) to open space foragers  
316 (high-flying species). Manoeuvrability and the challenging detection of very thin obstacles, or  
317 prey at a very small distance from background elements seem to be the main issues limiting  
318 species foraging success when flying through cluttered environments (Fenton et al., 2016;  
319 Norberg and Rayner, 1987; Sleep and Brigham, 2003). On the other hand, it is interesting to  
320 discuss what limits the ability of bats to reach elevated heights.

321 In the first instance, we demonstrated that high-flying species possess high aspect ratios and  
322 high wing loadings. For foraging purposes, high-flyers cover greater distances than low-flyers  
323 (Dietz et al., 2009), possibly because insects are scarcer at height (Reynolds et al., 2017).  
324 Economic flights over long distances are facilitated by a low wing inertia, which is associated  
325 with a high aspect ratio (Norberg and Rayner, 1987; Pennycuick, 2008). Since high aspect  
326 ratios are often associated with short wings, high-flyers tend to also have high wing loadings  
327 (Norberg and Rayner, 1987). In order to sustain a powered flight, species with higher wing  
328 loadings must fly faster, which is precisely an optimal strategy when travelling through long  
329 distances between two foraging grounds (Grodzinski et al., 2009; Norberg and Rayner, 1987),  
330 but also for long-distance migration (Hedenström, 2009). It was suggested that the swift  
331 aspect of *Miniopterus schreibersii* could be linked to agile flight in high-altitude hawking  
332 (Norberg and Rayner, 1987). Our results do not support this hypothesis, since this species was  
333 very rarely recorded at height. The relatively high aspect ratio of *M. schreibersii* is probably  
334 associated with good agility during fast flights near ground level. This species indeed covers  
335 very long distances overnight (up to 40 km) to actively avoid intraspecific competition for  
336 food in the vicinity of its very large colonies (Dietz et al., 2009). As a fast flyer (Holderied  
337 and Jones, 2009), this species does not have a higher wing loading than the average, because  
338 its wings are longer than average due to the unusual length of its third digit, but its wide  
339 uropatagium allows for a manoeuvrability not seen in other species with narrow wings (Dietz  
340 et al., 2009).

341 In the second instance, we demonstrated that high-flying bats use shallower – and generally  
342 longer – calls than low flying species. This call structure carries signals through greater  
343 distances than high frequencies because it is more tolerant to atmospheric attenuation (Pye,  
344 1979). It can be argued that small bats have difficulties producing low frequency echolocation  
345 calls since their production requires large body structures, and species are therefore limited by



346 their laryngeal capacity (Metzner and Müller, 2016; Pye, 1979). Several studies indeed found  
347 that body size is inversely correlated with echolocation call peak frequency – when acoustic  
348 strategies are taken into account - which corroborates this hypothesis (Bogdanowicz et al.,  
349 1999; Jones, 1999; Penone et al., 2018; Thiagavel et al., 2017). Calls used for social  
350 communication may be much lower than the echolocation repertoire (Chaverri et al., 2018),  
351 but their production is based on the same biomechanical properties of the larynx than the  
352 production of echolocation calls (Kobayasi et al., 2012). Indeed, in isolated larynxes, it was  
353 demonstrated that below a certain air flow threshold, the emitted frequencies correspond to  
354 the register of echolocation frequencies, but passing this threshold, the emitted frequencies  
355 correspond to the register of social communication (much lower frequencies) (Kobayasi et al.,  
356 2012). This jumping from one frequency register to another is similar to yodelling.

357 Nonetheless, we found that species with high-pitched vocalisations (e.g. *Myotis sp.* or *M.*  
358 *schreibersii*) could also – although rarely – be found at elevated heights. These individuals  
359 either came from the foot of the mast and flew to the top of the mast, a behaviour which was  
360 showed in *B. barbastellus* (Budenz et al., 2017), or they were already flying at height when  
361 they came across the wind mast. Individuals can lower their call frequency to perceive  
362 obstacles from a greater distance (Jensen and Miller, 1999; Schaub and Schnitzler, 2007),  
363 however we do not expect species such as *Myotis sp.* to be able to modify their sonar in such a  
364 way that they could perceive ground level when flying at more than 20 m, their estimated  
365 maximal detection range in open spaces (Barataud, 2015). High-pitched echolocators are  
366 more likely to explore wind masts from the bottom, but they could possibly rely only on  
367 vision to perceive long-distance obstacles and use their sonar to sense small obstacles such as  
368 other flying animals (Boonman et al., 2013).

369 D. Conclusion and perspectives

370 Our study contributes to the comprehension of bat use of the vertical dimension, which is  
371 often difficult to explore due to technical limitations. We demonstrated that bat vertical niche  
372 partitioning is not only constrained by species ability to move and detect prey in cluttered  
373 environments, but it is also constrained by their ability to commute and forage at elevated  
374 heights with optimal flight energetic costs and with sonar adaptations for long-distance  
375 perception of their environment. There are probably many other morphologic traits that were  
376 not tested in our study and that may be correlated with species use of the vertical space. For  
377 example, long and narrow pinnae (external ears) or tragi (small eminence of the external ear),  
378 possibly accounting for the accuracy of vertical localization (Fenton et al., 2016), are  
379 generally found in low flyers, while short and round pinnae and tragi are found in bats  
380 prevailing at height (see Dietz et al., 2009).

381 Sonar features do not only vary interspecifically, and individuals can indeed adapt call  
382 frequency, duration and bandwidth to commute or forage in different environments (Barataud,  
383 2015; Moss and Surlykke, 2001; Russo et al., 2017). Studies on *E. serotinus* and *V. murinus*  
384 (QFC strategy) show that their repertoire is quite variable up to a dozen meters from the  
385 background, and then stabilises past that threshold (Jensen and Miller, 1999; Schaub and  
386 Schnitzler, 2007). However, it is not known whether this holds true for other echolocating  
387 strategies (e.g. FM and CF-FM) and to what extent bat flight height may be predicted  
388 intraspecifically from sonar features.

389 The use of the aerosphere by bats makes them vulnerable to anthropogenic activities such as  
390 planes and wind turbines (Voigt et al., 2018). It was shown that bat species susceptibility to  
391 collisions with wind turbines is correlated to their proportion of time spent at height (Roemer  
392 et al., 2017). This classification of species susceptibility is of great importance in wind turbine  
393 impact assessment studies, which rely on the estimation of bat local abundance to estimate

394 future impacts. However, this classification is only available for European bats and requires  
395 important time and human investments to be established for different bat communities. The  
396 correlation between species traits and proportion of flight at height presented in the current  
397 study should provide a proxy to predict species relative susceptibility to wind turbines in other  
398 geographical areas.

399

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566

567 **TABLES**

568 Table 1 – Summary statistics for mean acoustic parameters (from Barataud, 2017, 2015),  
569 mean morphological variables and predicted proportion of flight at height. Species names are  
570 given with the first three letters of genus and species. CF: constant frequencies. FM:  
571 frequency modulated. QFC: quasi-constant frequencies. N calls = Number of calls measured  
572 in Barataud (2017). N flights = number of acoustic sequences used to calculate the proportion  
573 of flights at height. ARI: aspect ratio index for bat wings. WLI: wing loading index. See  
574 Table 4 for details about the morphological values used to calculate ARI and WLI.

<i>Species</i>	<i>Group</i>	<i>Call type</i>	<i>Peak frequency (kHz)</i>	<i>Duration (ms)</i>	<i>Bandwidth (kHz)</i>	<i>N calls</i>	<i>ARI</i>	<i>WLI (10<sup>-4</sup>)</i>	<i>Proportion of flights at height</i>	<i>N flights</i>
<i>Barbar</i>		FM	37.85	4.11	16.85	55	2.12	7.87	0.00	6798
<i>Eptnil</i>		FM/QFC	28.59	13.18	8.41	167	2.09	10.31	0.15	169
<i>Eptser</i>		FM/QFC	30.40	8.38	26.75	225	2.20	11.91	0.06	13309
<i>Hypsav</i>		FM/QFC	34.28	9.54	13.11	81	2.17	8.94	0.23	8252
<i>Minsch</i>		FM/QFC	53.27	9.20	23.48	114	2.48	8.97	0.01	1835
<i>Myobec</i>	Small <i>Myotis</i>	FM	49.70	4.67	67.57	220	2.02	7.35	0.00	16560
<i>Myodau</i>		FM	47.91	4.17	60.02	201	2.12	9.11		
<i>Myonat</i>		FM	54.39	4.07	83.79	172	2.05	7.38		
<i>Myobly</i>	Large <i>Myotis</i>	FM	39.85	5.27	58.50	124	2.09	10.40	0.02	1213
<i>Myomyo</i>		FM	40.04	5.58	58.47	231	2.11	9.79		
<i>Nyclas</i>		FM/QFC	16.70	20.82	6.99	166	2.48	17.33	0.72	49
<i>Nyclei</i>		FM/QFC	25.59	10.82	8.26	123	2.48	14.15	0.49	27204
<i>Nycnoc</i>		FM/QFC	22.30	14.50	8.10	170	2.75	16.80	0.31	4845
<i>Pipkuh</i>		FM/QFC	38.09	7.64	15.02	142	2.15	8.37	0.10	56011
<i>Pipnat</i>		FM/QFC	40.35	7.65	11.80	123	2.12	9.55	0.19	10832
<i>Pippip</i>		FM/QFC	46.82	6.86	20.16	153	2.16	7.61	0.08	403619
<i>Pippyg</i>		FM/QFC	54.98	6.71	12.71	143	2.21	9.36	0.04	10709
<i>Pleaur</i>	<i>Plecotus</i> spp.	FM	34.40	3.40	27.60	224	2.06	7.13	0.00	7736
<i>Pleaus</i>		FM	30.90	3.30	19.70	216	2.09	7.23		

<i>Rhifer</i>		CF+FM	82.40	45.00	16.00	53	2.06	10.40	0.00	218
<i>Rhip</i>		CF+FM	109.40	45.00	22.00	129	1.84	5.99	0.00	14
<i>Tadten</i>		FM/QFC	12.14	15.06	4.54	115	2.97	12.73	0.48	16671
<i>Vesmur</i>		FM/QFC	25.59	13.27	11.11	155	2.31	10.38	0.86	72

575

576 Table 2 – Kendall’s correlation tests between all acoustic variables. ARI: aspect ratio index

577 for bat wings. WLI: wing loading index. NS: not significant.

Variable 1	Variable 2	tau	p-value
Peak	Duration	-0.22	NS
Peak	Bandwidth	0.50	<0.001
Duration	Bandwidth	-0.51	<0.001
ARI	Peak	-0.45	<0.005
ARI	Duration	0.37	<0.05
ARI	Bandwidth	-0.51	<0.001
WLI	Peak	-0.41	<0.01
WLI	Duration	0.48	<0.005
WLI	Bandwidth	-0.46	<0.005
WLI	ARI	0.46	<0.005

578

579 Table 3 – Kendall’s correlation tests between rate of flight at height and acoustic variables.

580 ARI: aspect ratio index for bat wings. WLI: wing loading index.

Variable 1	Variable 2	tau	p-value
Rate of flight at height	Peak	-0.59	<0.001
	Duration	0.44	<0.005
	Bandwidth	-0.56	<0.001
	ARI	0.58	<0.001
	WLI	0.48	<0.005

581

582 **FIGURE CAPTIONS**

583

584 Figure 1 – Correlation between the predicted proportion of flight at height and morphological

585 and sonar variables. Etiquettes relate to the first three letters of genera and species names. The

586 categories CF (constant frequencies), FM (frequency modulated), and QFC (quasi-constant  
587 frequencies) refer to the acoustic strategy of the different species. The linear regression line is  
588 shown. Acoustic parameters are presented on a logarithmic scale. Wing drawings represent  
589 the extreme values.

590

591

## 592 **SUPPLEMENTARY FIGURE CAPTIONS**

593

594 Figure 2 – Microphone heights for each study site. Open circles show microphone height and  
595 filled circles show the median height.

596

597 Figure 3 – Influence of microphone median height on the proportion of bat flights at height.  
598 The regression line is shown (modelled with a binomial generalized linear model with  
599 microphone median height and species as fixed effect). Species names are given with the first  
600 three letters of species and genus. 95 % confidence intervals are shown.

601

## 602 **APPENDIX**

603 Table 4 – Mean morphological values used to calculate ARI (aspect ratio index for bat wings)  
604 and WLI (wing loading index). These values were retrieved from Dietz et al. (2009). Species  
605 names are given with the first three letters of genus and species.

<i>Species</i>	<i>Group</i>	<i>Forearm length</i>	<i>Length of 5<sup>th</sup></i>	<i>Length of 3<sup>rd</sup></i>	<i>Mass</i>
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		<b>(mm)</b>	<b>digit (mm)</b>	<b>digit (mm)</b>	<b>(g)</b>
<i>Barbar</i>		40.00	50.50	67.00	8.50
<i>Eptnil</i>		40.65	50.50	65.00	11.00
<i>Eptser</i>		53.00	64.00	88.00	21.50
<i>Hypsav</i>		34.65	42.50	57.50	7.00
<i>Minsch</i>		45.20	52.00	83.50	12.00
<i>Myobec</i>		43.05	53.50	65.00	8.50
<i>Myodau</i>	Small <i>Myotis</i>	37.55	45.50	59.00	8.00
<i>Myonat</i>		39.20	53.00	69.50	8.50
<i>Myobly</i>	Large <i>Myotis</i>	56.30	72.00	94.00	22.50
<i>Myomyo</i>		60.95	75.50	98.00	23.50
<i>Nyclas</i>		65.50	71.50	112.00	44.00
<i>Nyclei</i>		42.55	47.00	74.00	15.50
<i>Nycnoc</i>		53.10	52.50	91.50	25.50
<i>Pipkuh</i>		33.85	42.50	57.50	6.50
<i>Pipnat</i>		34.65	44.50	59.50	8.00
<i>Pippip</i>		31.25	39.00	53.00	5.00
<i>Pippyg</i>		30.00	36.50	50.50	5.50
<i>Pleaur</i>	<i>Plecotus</i> <i>spp.</i>	39.15	50.50	65.00	7.50
<i>Pleaus</i>		40.00	51.50	67.50	8.00
<i>Rhifer</i>		57.70	70.00	86.50	21.00
<i>Rhihip</i>		37.85	50.00	54.00	5.50
<i>Tadten</i>		62.30	57.50	108.50	25.00
<i>Vesmur</i>		45.55	51.00	72.50	12.50

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