

Bat sonar and wing morphology predict species vertical niche

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28

29 ABSTRACT

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

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

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

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).

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

through greater distances than high frequencies, which in turn procure the advantage of a 66 67 higher structure resolution (Pye, 1979). On the other hand, low frequencies are associated with long wavelengths, which are unsuitable for the detection of targets such as small insects, 68 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 prev returning echoes.

Associations in echolocation, wing morphology and flight behaviour have only been demonstrated for adaptation to clutter (Aldridge and Rautenbach, 1987; Siemers and Schnitzler, 2004), from studies using material positioned at ground level, with a limited detection range, while bats use a three-dimensional space that can be as elevated as 3000 m 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 et al., 2017). 138

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

169 B. Species identification and flight height classification

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

Some sequences may only contain faint calls, and yet contain enough clues to attribute the 186 187 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.

To classify flight heights, we used SonoChiro to automatically determine the time at which each call started on each microphone. We then obtained the time differences of arrival (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.

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

227 C. Acoustic parameters of species sonars

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

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

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.

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

where m = body mass.

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

We first checked for normality in the distribution of raw or transformed variables. Most variables did not follow a normal distribution, hence the correlations between each pair of variables were tested with a Kendall correlation test. For data visualisation, we assigned species into exclusive frequency-modulated (FM), constant-frequency with modulated frequency components (CF+FM) and frequency-modulated or quasi-constant frequency (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

A. Acoustic location from wind masts, a powerful tool for the study of animal flightbehaviour

277 We studied to what extent the prevalence of bat species at elevated heights can be predicted by the acoustic features of their sonar and by their wing morphology. In the past, a study by 278 279 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

We demonstrate for the first time that the acoustic features of bat sonar predict bat vertical distribution regardless of species acoustic strategies. Call duration was a less reliable predictor than call peak frequency and bandwidth since Rhinolophidae stood as outliers with a very long call duration and an exclusive presence at ground level. This particularity is explained by their echolocation strategy to detect prey flutter by emitting long constant frequencies (CF) calls carrying short frequency modulated (FM) signals with a high duty cycle (Schnitzler and Denzinger, 2011). Rhinolophidae are part of the Yinpterochiroptera suborder, that diverged 60 mya from the Yangochiroptera, (Teeling, 2009), to which the otherbat 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.

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

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

their laryngeal capacity (Metzner and Müller, 2016; Pye, 1979). Several studies indeed found 346 347 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 larvnx 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 showed in B. barbastellus (Budenz et al., 2017), or they were already flying at height when 360 361 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).

Sonar features do not only vary interspecifically, and individuals can indeed adapt call 381 382 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.

The use of the aerosphere by bats makes them vulnerable to anthropogenic activities such as planes and wind turbines (Voigt et al., 2018). It was shown that bat species susceptibility to collisions with wind turbines is correlated to their proportion of time spent at height (Roemer et al., 2017). This classification of species susceptibility is of great importance in wind turbine impact assessment studies, which rely on the estimation of bat local abundance to estimate future impacts. However, this classification is only available for European bats and requires important time and human investments to be established for different bat communities. The correlation between species traits and proportion of flight at height presented in the current study should provide a proxy to predict species relative susceptibility to wind turbines in other geographical areas.

399

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412

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567 **TABLES**

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

Species	Group	Call type	Peak frequency (kHz)	Duration (ms)	Bandwidth (kHz)	N calls	ARI	WLI (10⁻⁴)	Proportion of flights at height	N flights
Barbar		FM	37.85	4.11	16.85	55	2.12	7.87	0.00	6798
Eptnil		FM/QFC	28.59	13.18	8.41	167	2.09	10.31	0.15	169
Eptser		FM/QFC	30.40	8.38	26.75	225	2.20	11.91	0.06	13309
Hypsav		FM/QFC	34.28	9.54	13.11	81	2.17	8.94	0.23	8252
Minsch		FM/QFC	53.27	9.20	23.48	114	2.48	8.97	0.01	1835
Myobec		FM	49.70	4.67	67.57	220	2.02	7.35		
Myodau	Small	FM	47.91	4.17	60.02	201	2.12	9.11	0.00	16560
Myonat	IVIYOUS	FM	54.39	4.07	83.79	172	2.05	7.38		
Myobly	Large	FM	39.85	5.27	58.50	124	2.09	10.40		
Муотуо	Myotis	FM	40.04	5.58	58.47	231	2.11	9.79	0.02	1213
Nyclas		FM/QFC	16.70	20.82	6.99	166	2.48	17.33	0.72	49
Nyclei		FM/QFC	25.59	10.82	8.26	123	2.48	14.15	0.49	27204
Nycnoc		FM/QFC	22.30	14.50	8.10	170	2.75	16.80	0.31	4845
Pipkuh		FM/QFC	38.09	7.64	15.02	142	2.15	8.37	0.10	56011
Pipnat		FM/QFC	40.35	7.65	11.80	123	2.12	9.55	0.19	10832
Pippip		FM/QFC	46.82	6.86	20.16	153	2.16	7.61	0.08	403619
Рірруд		FM/QFC	54.98	6.71	12.71	143	2.21	9.36	0.04	10709
Pleaur	Plecotus	FM	34.40	3.40	27.60	224	2.06	7.13	0.00	7706
Pleaus	spp.	FM	30.90	3.30	19.70	216	2.09	7.23	0.00	//36

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

- 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
	Peak	-0.59	< 0.001
	Duration	0.44	< 0.005
Rate of flight at height	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

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.
	Species Group Forearm length Length of 5th Length of 3rd Mass

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