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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 locating
31 obstacles and prey with ultrasounds in complete darkness. To avoid interspecific competition,
32 it is likely that sonar features and wing morphology co-evolved with species vertical
33 distribution, but due to the technical difficulties of studying flight in the vertical dimension, this
34 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 activity
37 period (> 8,000 nights). We tested the correlation between the proportion of flights at height
38 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 vertical
40 space regardless of their acoustic strategies (i.e. gleaning, hawking or detecting prey flutter).

41 High wing aspect ratios and high wing loadings were associated with high proportions of time
42 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 are
51 more plastic (Dietz et al., 2009). In order to match these particular needs, this diet partitioning
52 is accompanied by morphological and behavioural differences. Illustrating those differences,
53 *Myotis nattereri*, a small bat (wingspan = 250-300 mm), is able to forage insects resting on
54 leaves under the forest cover while *Tadarida teniotis*, a large bat (wingspan = 400-450 mm),
55 forages on insect swarms in wide and elevated open spaces (Arthur and Lemaire, 2015). In
56 addition, the echolocation system, developed through evolution to sense the environment in the
57 dark, reflects the ability of each species to perceive obstacles and prey (Collen, 2012; Schnitzler
58 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 shape,
61 despite some overlap (Barataud, 2015; Fenton and Bell, 1981). Frequency in echolocation calls
62 varies from 9 kHz, as in calls emitted by *Euderma maculatum*, Vespertilionidae (Fullard and
63 Dawson, 1997) or *Tadarida teniotis*, Molossidae (Arlettaz, 1990), to 212 kHz, emitted by
64 *Cloeotis percivali*, Hipposideridae (Fenton and Bell, 1981). Because atmospheric attenuation
65 increases with call frequency, low frequency signals carry through greater distances than high

66 frequencies, which in turn procure the advantage of a higher structure resolution (Pye, 1979).
67 On the other hand, low frequencies are associated with long wavelengths, which are unsuitable
68 for the detection of targets such as small insects, and should be the major evolutionary constraint
69 for the use of low frequencies in echolocation (Barclay and Brigham, 1991; Waters et al., 1995).
70 Echolocation call length varies from 1 ms as by *Myotis brandtii*, Vespertilionidae, to more than
71 80 ms by *Rhinolophus ferrumequinum*, Rhinolophidae (Barataud, 2015). Long calls allow a
72 better detection of faint and distant echoes through the repeated addition of signal information
73 that evokes the activity of neurons tuned to the frequency of interest, and consequently increase
74 echolocation ranges (Neuweiler, 1989; Schnitzler et al., 2003). Long calls can also provide
75 information on prey fluttering and movement directionality (Trappe and Schnitzler, 1982),
76 while the emission of short calls decrease the issue of call-echo overlap (Jones, 1999). Finally,
77 call bandwidth varies from less than 1 kHz, as by *Nyctalus noctula*, Vespertilionidae (Barataud,
78 2015), to more than 170 kHz in some *Kerivoula* species (Vespertilionidae) (Kingston et al.,
79 1999). Large bandwidths enhance range accuracy and resolution (i.e. the differentiation of two
80 targets at close distances) (Pye, 1979; Siemers and Schnitzler, 2004) while small bandwidths,
81 combined with long call length, can also be used to detect prey fluttering or increase the
82 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, 1987).

91 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 of
96 many traits in bats.

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

109 Associations in echolocation, wing morphology and flight behaviour have only been
110 demonstrated for adaptation to clutter (Aldridge and Rautenbach, 1987; Siemers and Schnitzler,
111 2004), from studies using material positioned at ground level, with a limited detection range,
112 while bats use a three-dimensional space that can be as elevated as 3000 m for some species
113 (Peurach, 2003; Williams et al., 1973). The association between bat sonar or wing morphology
114 and their use of the vertical dimension has never been thoroughly demonstrated. Since the

115 vertical distribution of insects varies according to species (Reynolds et al., 2017), and since bats
116 differentiate in their diets (Dietz et al., 2009), the vertical distribution of the different bat guilds
117 is strongly expected to follow that of their prey (Norberg and Rayner, 1987; Roeleke et al.,
118 2018). Roemer et al. (2017) showed that bat guilds according to Denzinger and Schnitzler
119 (2013) could be ordered along the gradient of the rate of time spent at height. It was also shown
120 that the occurrence of certain insect orders in bat diet could be associated with certain bat sonar
121 and morphology features (Bogdanowicz et al., 1999). However, the contribution of sonar
122 features and wing morphology to the vertical separation of species was only described from
123 case studies on target species, or from a collection of heterogeneous observations (visual,
124 mistnetting, acoustic) of a bat community (Banse, 2010; Denzinger et al., 2018; Kalko et al.,
125 2008), and remains to be demonstrated with empirical and standardised measurements.

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

136 The aim of our study was to investigate the links between the vertical distribution of a
137 community of European insectivorous bats, the acoustic parameters of their sonar (peak
138 frequency, call duration and call bandwidth) and their wing morphology (wing aspect ratios and

139 wing loading). We expected (1) longer call durations to be associated with higher flight heights,
140 (2) higher peak frequencies to be associated with lower flight heights, (3) larger bandwidths to
141 be associated with lower flight heights, (4) narrower wings to be associated with higher flight
142 heights and (5) higher wing loadings to be associated with higher flight heights. To measure
143 bat position in the vertical space, we equipped wind masts with microphone arrays and
144 performed acoustic location of bat echolocation calls.

145

146 **II. MATERIAL & METHODS**

147 **A. Acoustic recordings used to study bat altitudinal behaviour**

148 Between 2011 and 2017, recordings were conducted at 48 sites in France and Belgium where
149 bat activity was monitored on 8,435 nights (mean = 175.7 standard deviation = 76.1, min = 19,
150 max = 352 nights per site). Microphones were installed on lattice or monopole wind masts of
151 50-100 m in height and the wind masts themselves were erected in open or semi-open habitats
152 (i.e. agricultural land, bocage, garrigue, wetlands or forest clearing). Arrays composed of two
153 microphones were achieved with two SMX-US, SMX-U1 (Wildlife Acoustics, USA) or SMX-
154 US (Biotope, France) microphones plugged to an SM2BAT or SM3BAT (all models, Wildlife
155 Acoustics, Massachusetts, USA). Microphones were inserted into tubes, facing downward, to
156 protect them from weather elements. A custom-made aluminium reflector placed below the
157 microphone at a 45° angle minimised the directionality of the setting. Microphones were
158 installed at heights ranging from 4 to 85 m (Figure 2 in suppl. mat.). Recorders were
159 programmed to start each day 30 min before sunset and stop 30 min after sunrise. Whole night
160 recordings were performed on study sites between 2013 and 2017 (38 sites), but from 2011 and
161 2012 (10 sites) samplings were collected for 10 minutes every 20 minutes. Gain was set at 36
162 dB, sampling rate at 192 kHz, trigger at 6 dB above background noise and trigger window at

163 2.5 sec. A 1 kHz high pass filter was used. Files were compressed in WAC4 format and analysed
164 in WAV format or directly recorded in WAV format.

165 B. Species identification and flight height classification

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

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

181 Some sequences may only contain faint calls, and yet contain enough clues to attribute the
182 sequence to a species, because the species does not completely overlap the acoustic repertoire
183 of another species (e.g. low frequency calls of *Tadarida teniotis* or low frequency calls of
184 *Hypsugo savii*). Call duration and bandwidth are the most affected by atmospheric attenuation,
185 yet other call parameters that are better preserved are sometimes sufficient to make an
186 identification (e.g. peak frequency, inter-call duration, frequency modulation (i.e. shape) of the

187 main part of the call). Yet, some sequences were so affected by atmospheric attenuation that
188 there was no sufficient clue to attribute the sequence to a species. In addition, some species use
189 sonar calls that are sometimes very close, even identical in certain flight circumstances,
190 preventing identification to species level. These acoustic sequences that could not be identified
191 at the species level were either classed in a group of species - when the vertical flight behaviours
192 of all species were equivalent within the same group - or left unidentified and not used for
193 further analysis (8.4 % of all bat passes). Here, *Myotis myotis* and *M. blythii* were identified as
194 the “large *Myotis*” group, all other *Myotis* as the “small *Myotis*” group, and all *Plecotus* calls to
195 the *Plecotus spp.* group. Species within those two groups present flight heights comparable to
196 the other species of their group (Rodrigues *et al.*, 2015), and similar acoustic features (Barataud,
197 2015). Great care must be taken in the analysis of the results of the species *P. kuhlii* and *P.*
198 *nathusii*, because acoustic features of these two species are simultaneously very variable and
199 similar to each other. *V. murinus* is also difficult to distinguish from *N. leisleri*, but *V. murinus*
200 is known to be rare in France and Belgium.

201 To classify flight heights, we used SonoChiro to automatically determine the time at which each
202 call started on each microphone. We then obtained the time differences of arrival (TOAD) for
203 each call detected using the `find.matches` function of Hmisc package (Harrell, 2018) from R (R
204 Core Team, 2014). With two microphones, flight height cannot be precisely calculated, and
205 TOAD were used to determine to which microphones bats were closer. A height threshold was
206 defined for each site as the median height between the two microphones. Microphone median
207 height was variable depending on study site (20-50 m) (Figure 2), but this variation did not
208 greatly affect species proportion of flight at height (Figure 3). Using this threshold, bat calls
209 were assigned to two classes following the method described in Roemer *et al.* (2017): “at
210 height” if the source of the signal was above the threshold and “at ground level” if it was below
211 the threshold. A ratio of the time spent at height was then calculated for each species. It must

212 be noted that in forest clearings, tree canopy was never higher than the median height between
213 both microphones. Therefore, bats positioned “at height” were flying in an open environment.

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

220 C. Acoustic parameters of species sonars

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

228 D. Wing loading and aspect ratio

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

234
$$\text{Aspect Ratio Index } ARI = \frac{d3 + FA}{d5} ,$$

235 where FA = length of the forearm, d3 = length of the third digit and d5 = length of the fifth
236 digit.

237
$$\text{Wing Loading Index } WLI = \frac{m}{(FA + d3) \times d5 \times 2} ,$$

238 where m = body mass.

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

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

246

247 **III. RESULTS**

248 In total, 639,734 bat passes were recorded. Table 1 shows bat passes identified at the species or
249 species group level.

250 Table 1 – Summary statistics for mean acoustic parameters (from Barataud, 2017, 2015), mean morphological variables (Dietz et al., 2009) and
 251 predicted proportion of flight at height. Species names are given with the first three letters of genus and species. CF: constant frequencies. FM:
 252 frequency modulated. QFC: quasi-constant frequencies. N calls = Number of calls measured in Barataud (2017). N flights = number of acoustic
 253 sequences used to calculate the proportion of flights at height. ARI: aspect ratio index for bat wings. WLI: wing loading index.

<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>Forearm length (mm)</i>	<i>Length of 5th digit (mm)</i>	<i>Length of 3rd digit (mm)</i>	<i>Mass (g)</i>	<i>ARI</i>	<i>WLI (10⁻⁴)</i>	<i>Proportion of flights at height</i>	<i>N flights</i>
<i>Barbar</i>		FM	37.85	4.11	16.85	55	40.00	50.50	67.00	8.50	2.12	7.87	0.00	6798
<i>Eptnil</i>		FM/QFC	28.59	13.18	8.41	167	40.65	50.50	65.00	11.00	2.09	10.31	0.15	169
<i>Eptser</i>		FM/QFC	30.40	8.38	26.75	225	53.00	64.00	88.00	21.50	2.20	11.91	0.06	13309
<i>Hypsav</i>		FM/QFC	34.28	9.54	13.11	81	34.65	42.50	57.50	7.00	2.17	8.94	0.23	8252
<i>Minsch</i>		FM/QFC	53.27	9.20	23.48	114	45.20	52.00	83.50	12.00	2.48	8.97	0.01	1835
<i>Myobec</i>	Small <i>Myotis</i>	FM	49.70	4.67	67.57	220	43.05	53.50	65.00	8.50	2.02	7.35	0.00	16560
<i>Myodau</i>		FM	47.91	4.17	60.02	201	37.55	45.50	59.00	8.00	2.12	9.11		
<i>Myonat</i>		FM	54.39	4.07	83.79	172	39.20	53.00	69.50	8.50	2.05	7.38		
<i>Myobly</i>	Large <i>Myotis</i>	FM	39.85	5.27	58.50	124	56.30	72.00	94.00	22.50	2.09	10.40	0.02	1213
<i>Myomyo</i>		FM	40.04	5.58	58.47	231	60.95	75.50	98.00	23.50	2.11	9.79		
<i>Nyclas</i>		FM/QFC	16.70	20.82	6.99	166	65.50	71.50	112.00	44.00	2.48	17.33	0.72	49
<i>Nyclei</i>		FM/QFC	25.59	10.82	8.26	123	42.55	47.00	74.00	15.50	2.48	14.15	0.49	27204
<i>Nycnoc</i>		FM/QFC	22.30	14.50	8.10	170	53.10	52.50	91.50	25.50	2.75	16.80	0.31	4845
<i>Pipkuh</i>		FM/QFC	38.09	7.64	15.02	142	33.85	42.50	57.50	6.50	2.15	8.37	0.10	56011
<i>Pipnat</i>		FM/QFC	40.35	7.65	11.80	123	34.65	44.50	59.50	8.00	2.12	9.55	0.19	10832
<i>Pippip</i>		FM/QFC	46.82	6.86	20.16	153	31.25	39.00	53.00	5.00	2.16	7.61	0.08	403619
<i>Pippyg</i>		FM/QFC	54.98	6.71	12.71	143	30.00	36.50	50.50	5.50	2.21	9.36	0.04	10709
<i>Pleaur</i>	<i>Plecotus</i> <i>spp.</i>	FM	34.40	3.40	27.60	224	39.15	50.50	65.00	7.50	2.06	7.13	0.00	7736
<i>Pleaus</i>		FM	30.90	3.30	19.70	216	40.00	51.50	67.50	8.00	2.09	7.23		
<i>Rhifer</i>		CF+FM	82.40	45.00	16.00	53	57.70	70.00	86.50	21.00	2.06	10.40	0.00	218
<i>Rhipip</i>		CF+FM	109.40	45.00	22.00	129	37.85	50.00	54.00	5.50	1.84	5.99	0.00	14
<i>Tadten</i>		FM/QFC	12.14	15.06	4.54	115	62.30	57.50	108.50	25.00	2.97	12.73	0.48	16671
<i>Vesmur</i>		FM/QFC	25.59	13.27	11.11	155	45.55	51.00	72.50	12.50	2.31	10.38	0.86	72

255 There was a continuous gradient in the vertical distribution of species from *Rhinolophus* bats
 256 that were never located at height to *Vespertilio murinus* that was located 86 % of the time at
 257 height. *Rhinolophus*, *Barbastella*, *Plecotus*, *Myotis*, *Miniopterus* species and *Pipistrellus*
 258 *pygmaeus* were located less than 5 % of the time at height. *Eptesicus serotinus*, *E. nilsonii*,
 259 *Hypsugo savii*, *P. kuhlii*, *P. pipistrellus* and *P. nathusii* were located between 5 and 25 % of the
 260 time at height. *Nyctalus*, *Tadarida* and *Vespertilio* species were located more than 30 % of the
 261 time at height.

262 A. Interdependence of traits

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

265 Table 2 – Kendall’s correlation tests between all acoustic variables. ARI: aspect ratio index for
 266 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

267

268 B. Correlations between proportion of flight at height and traits

269 Morphological and acoustic features were all correlated to the proportion of flights at height
 270 (Table 3, Figure 1). Compared to low-flying species, high-flying species used lower peak
 271 frequencies, narrower bandwidths, longer calls, and possessed narrower wings with higher wing
 272 loadings (Figure 1). In the correlation between the rate of flight at height and call duration,

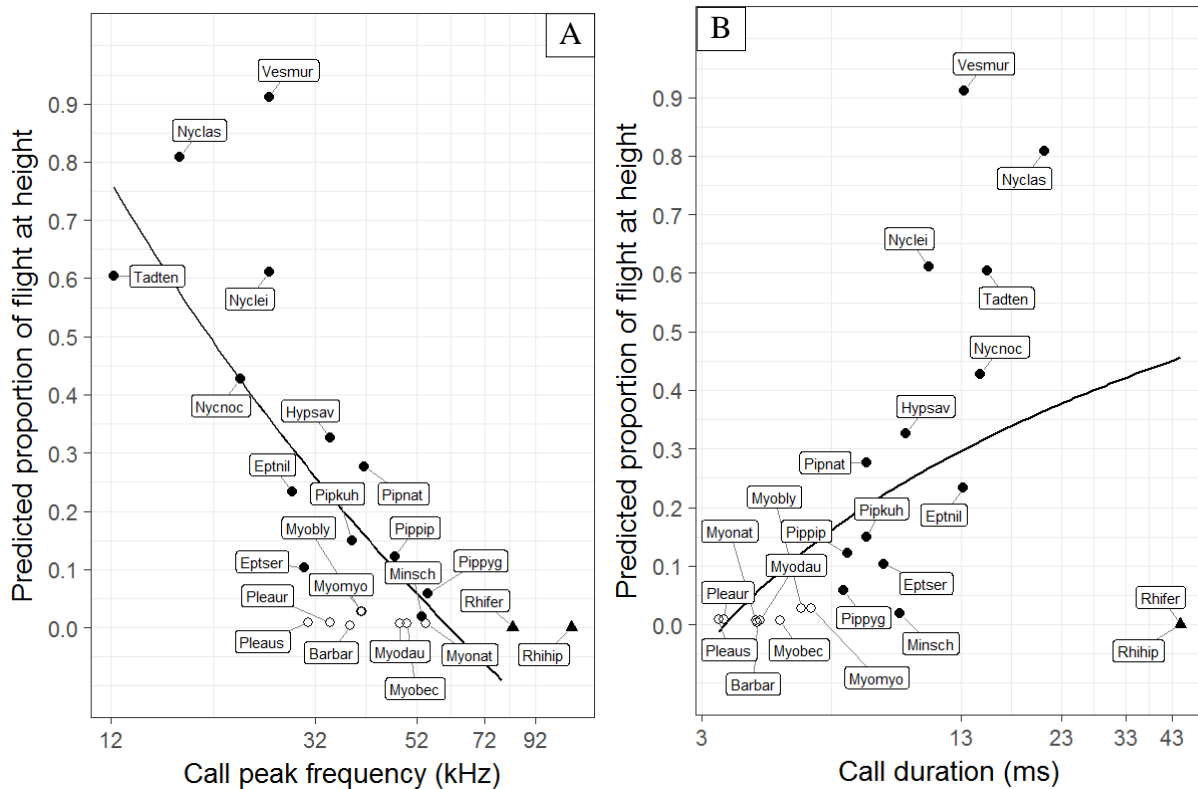
273 *Rhinolophus* species stood as outliers because they use extremely long call duration compared
 274 to other species flying near ground level (Figure 1b). Concerning call bandwidth, *Myotis* species
 275 were the outliers because they use extremely large bandwidth compared to other species flying
 276 near ground level (Figure 1c).

277 Table 3 – Kendall’s correlation tests between rate of flight at height and acoustic variables.
 278 ARI: aspect ratio index for bat wings. WLI: wing loading index.

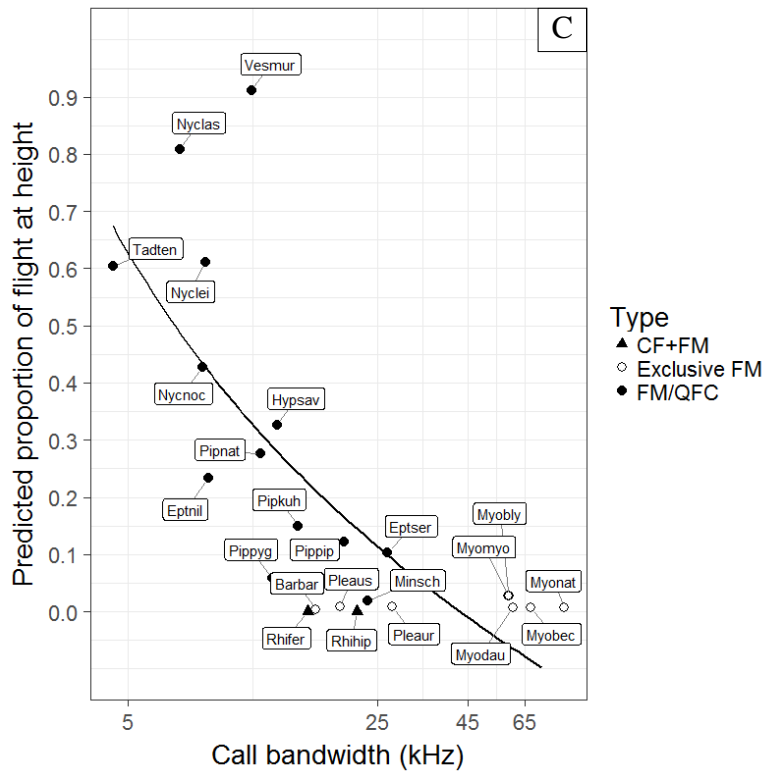
Variable 1	Variable 2	tau	p-value
Rate of flight at height	Peak	-0.59	<0.001
	Duration	0.44	<0.005
	Bandwidth	-0.56	<0.001
	ARI	0.58	<0.001
	WLI	0.48	<0.005

279

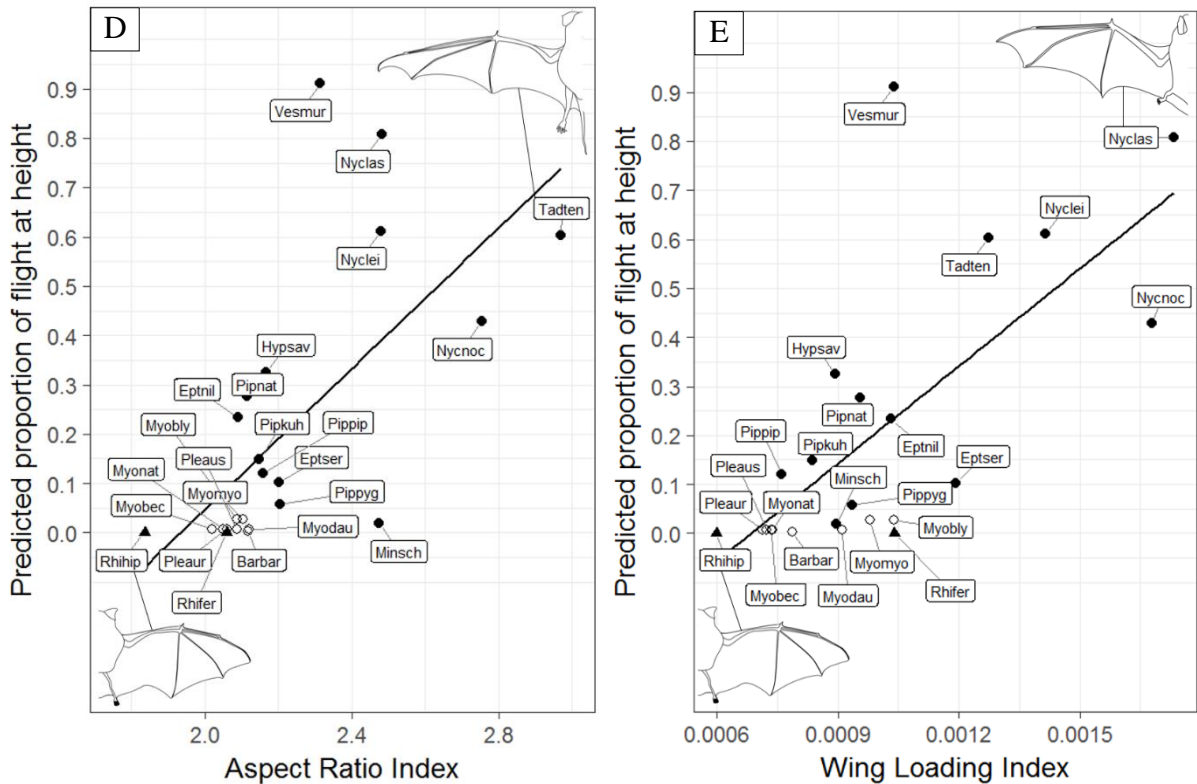
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282



283

284 Figure 1 – Correlation between the predicted proportion of flight at height and morphological
 285 and sonar variables. Etiquettes relate to the first three letters of genera and species names. The
 286 categories CF (constant frequencies), FM (frequency modulated), and QFC (quasi-constant

287 frequencies) refer to the acoustic strategy of the different species. The linear regression line is
288 shown. Acoustic parameters are presented on a logarithmic scale. Wing drawings represent the
289 extreme values.

290

291 **IV. DISCUSSION**

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

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

305 B. Bat traits predict bat vertical niche partitioning

306 We demonstrate for the first time that the acoustic features of bat sonar predict bat vertical
307 distribution regardless of species acoustic strategies. Call duration was a less reliable predictor
308 than call peak frequency and bandwidth since Rhinolophidae stood as outliers with a very long
309 call duration and an exclusive presence at ground level. This particularity is explained by their
310 echolocation strategy to detect prey flutter by emitting long constant frequencies (CF) calls

311 carrying short frequency modulated (FM) signals with a high duty cycle (Schnitzler and
312 Denzinger, 2011). Rhinolophidae are part of the Yinpterochiroptera suborder, that diverged 60
313 mya from the Yangochiroptera, (Teeling, 2009), to which the other bat families addressed here
314 belong.

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

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

325 C. Constraints of bat flight at great heights

326 We show that the use of the vertical space in European bats is ordered from *Rhinolophus* species
327 (always flying near ground level or near background) to *Nyctalus* and *Tadarida* species
328 (prevailing at height). In fact, guild categories used to define bat adaptation to clutter (i.e.
329 narrow, edge and open space foragers (Denzinger and Schnitzler, 2013)) may be ordered along
330 this same gradient from narrow foragers (low-flying species) to open space foragers (high-
331 flying species). Manoeuvrability and the challenging detection of very thin obstacles, or prey
332 at a very small distance from background elements seem to be the main issues limiting species
333 foraging success when flying through cluttered environments (Fenton et al., 2016; Norberg and

334 Rayner, 1987; Sleep and Brigham, 2003). On the other hand, it is interesting to discuss what
335 limits the ability of bats to reach elevated heights.

336 In the first instance, we demonstrated that high-flying species possess high aspect ratios and
337 high wing loadings. For foraging purposes, high-flyers cover greater distances than low-flyers
338 (Dietz et al., 2009), possibly because insects are scarcer at height (Reynolds et al., 2017).
339 Economic flights over long distances are facilitated by a low wing inertia, which is associated
340 with a high aspect ratio (Norberg and Rayner, 1987; Pennycuick, 2008). Since high aspect ratios
341 are often associated with short wings, high-flyers tend to also have high wing loadings (Norberg
342 and Rayner, 1987). In order to sustain a powered flight, species with higher wing loadings must
343 fly faster, which is precisely an optimal strategy when travelling through long distances between
344 two foraging grounds (Grodzinski et al., 2009; Norberg and Rayner, 1987), but also for long-
345 distance migration (Hedenström, 2009). It was suggested that the swift aspect of *Miniopterus*
346 *schreibersii* could be linked to agile flight in high-altitude hawking (Norberg and Rayner,
347 1987). Our results do not support this hypothesis, since this species was very rarely recorded at
348 height. The relatively high aspect ratio of *M. schreibersii* is probably associated with good
349 agility during fast flights near ground level. This species indeed covers very long distances
350 overnight (up to 40 km) to actively avoid intraspecific competition for food in the vicinity of
351 its very large colonies (Dietz et al., 2009). As a fast flyer (Holderied and Jones, 2009), this
352 species does not have a higher wing loading than the average, because its wings are longer than
353 average due to the unusual length of its third digit, but its wide uropatagium allows for a
354 manoeuvrability not seen in other species with narrow wings (Dietz et al., 2009).

355 In the second instance, we demonstrated that high-flying bats use shallower – and generally
356 longer – calls than low flying species. This call structure carries signals through greater
357 distances than high frequencies because it is more tolerant to atmospheric attenuation (Pye,

358 1979). It can be argued that small bats have difficulties producing low frequency echolocation
359 calls since their production requires large body structures, and species are therefore limited by
360 their laryngeal capacity (Metzner and Müller, 2016; Pye, 1979). Several studies indeed found
361 that body size is inversely correlated with echolocation call peak frequency – when acoustic
362 strategies are taken into account - which corroborates this hypothesis (Bogdanowicz et al.,
363 1999; Jones, 1999; Penone et al., 2018; Thiagavel et al., 2017). Calls used for social
364 communication may be much lower than the echolocation repertoire (Chaverri et al., 2018), but
365 their production is based on the same biomechanical properties of the larynx than the production
366 of echolocation calls (Kobayasi et al., 2012). Indeed, in isolated larynxes, it was demonstrated
367 that below a certain air flow threshold, the emitted frequencies correspond to the register of
368 echolocation frequencies, but passing this threshold, the emitted frequencies correspond to the
369 register of social communication (much lower frequencies) (Kobayasi et al., 2012). This
370 jumping from one frequency register to another is similar to yodelling.

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

383 D. Conclusion and perspectives

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

395 Sonar features do not only vary interspecifically, and individuals can indeed adapt call
396 frequency, duration and bandwidth to commute or forage in different environments (Barataud,
397 2015; Moss and Surlykke, 2001; Russo et al., 2017). Studies on *E. serotinus* and *V. murinus*
398 (QFC strategy) show that their repertoire is quite variable up to a dozen meters from the
399 background, and then stabilises past that threshold (Jensen and Miller, 1999; Schaub and
400 Schnitzler, 2007). However, it is not known whether this holds true for other echolocating
401 strategies (e.g. FM and CF-FM) and to what extent bat flight height may be predicted
402 intraspecifically from sonar features.

403 The use of the aerosphere by bats makes them vulnerable to anthropogenic activities such as
404 planes and wind turbines (Voigt et al., 2018). It was shown that bat species susceptibility to
405 collisions with wind turbines is correlated to their proportion of time spent at height (Roemer
406 et al., 2017). This classification of species susceptibility is of great importance in wind turbine

407 impact assessment studies, which rely on the estimation of bat local abundance to estimate
408 future impacts. However, this classification is only available for European bats and requires
409 important time and human investments to be established for different bat communities. The
410 correlation between species traits and proportion of flight at height presented in the current
411 study should provide a proxy to predict species relative susceptibility to wind turbines in other
412 geographical areas.

413

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426

427 **REFERENCES**

428 Aldridge, H. D. J. N., and Rautenbach, I. L. (1987). "Morphology, Echolocation and Resource
429 Partitioning in Insectivorous Bats," *J. Anim. Ecol.*, **56**, 763. doi:10.2307/4947

430 Arlettaz, R. (1990). "Contribution à l'éco-éthologie du Molosse de Cestoni, *Tadarida teniotis*
431 (Chiroptera), dans les Alpes valaisannes (sud-ouest de la Suisse)," "Contribution to the
432 eco-ethology of the European free-tailed bat, *Tadarida teniotis* (Chiroptera,
433 Molossidae), in the Alps of the Valais (south-western Switzerland)," *Z. Für*
434 *Säugetierkd.*, **55**, 28–42.

435 Arthur, L., and Lemaire, M. (2015). *Les chauves-souris de France, Belgique, Luxembourg et*
436 *Suisse, Bats of France, Belgium, Luxemburg and Switzerland*, Biotope Editions, Mèze;
437 Paris, 544 pages.

438 Bader, E., Jung, K., Kalko, E. K., Page, R. A., Rodriguez, R., and Sattler, T. (2015). "Mobility
439 explains the response of aerial insectivorous bats to anthropogenic habitat change in the
440 Neotropics," *Biol. Conserv.*, **186**, 97–106.

441 Banse, G. (2010). "Ableitung des Kollisionsrisikos von Fledermäusen an Windenergieanlagen
442 über biologische Parameter," "Calculation of bat collision risks at wind turbines using
443 biological parameters" *Nyctalus NF*, **15**, 64–74.

444 Barataud, M. (2015). *Acoustic ecology of European bats: species identification, study of their*
445 *habitats and foraging behaviour*, Biotope éditions, 344 pages.

446 Barataud, M. (2017, January). "Update of the 3rd edition (2015) of Acoustic ecology of
447 European bats http://ecologieacoustique.fr/?page_id=1713 consulted on the
448 10/03/2018.," Retrieved from http://ecologieacoustique.fr/?page_id=1713

449 Barclay, R. M., and Brigham, R. M. (1991). "Prey detection, dietary niche breadth, and body
450 size in bats: why are aerial insectivorous bats so small?," *Am. Nat.*, **137**, 693–703.

451 Barré, K., Le Viol, I., Bas, Y., Julliard, R., and Kerbiriou, C. (2018). "Estimating habitat loss
452 due to wind turbine avoidance by bats: Implications for European siting guidance," *Biol.*
453 *Conserv.*, **226**, 205–214.

454 Bogdanowicz, W., Fenton, M. B., and Daleszczyk, K. (1999). “The relationships between
455 echolocation calls, morphology and diet in insectivorous bats,” *J. Zool.*, **247**, 381–393.
456 doi:10.1111/j.1469-7998.1999.tb01001.x

457 Boonman, A., Bar-On, Y., and Yovel, Y. (2013). “It’s not black or white—on the range of
458 vision and echolocation in echolocating bats,” *Front. Physiol.*, , doi:
459 10.3389/fphys.2013.00248. doi:10.3389/fphys.2013.00248

460 Bruderer, B., and Popa-Lisseanu, A. G. (2005). “Radar data on wing-beat frequencies and flight
461 speeds of two bat species,” *Acta Chiropterologica*, **7**, 73–82. doi:10.3161/1733-
462 5329(2005)7[73:RDOWFA]2.0.CO;2

463 Budenz, T., Gessner, B., Lüttmann, J., Molitor, F., Servatius, K., and Veith, M. (2017). “Up
464 and down: *B. barbastellus* explore lattice towers,” *Hystrix*, **28**, 272–276.

465 Chaverri, G., Ancillotto, L., and Russo, D. (2018). “Social communication in bats,” *Biol. Rev.*,
466 Collen, A. (2012). *The evolution of echolocation in bats: a comparative approach* (Doctoral
467 dissertation), University College London.

468 Denzinger, A., and Schnitzler, H.-U. (2013). “Bat guilds, a concept to classify the highly diverse
469 foraging and echolocation behaviors of microchiropteran bats,” *Front. Physiol.*, , doi:
470 10.3389/fphys.2013.00164. doi:10.3389/fphys.2013.00164

471 Denzinger, A., Tschapka, M., and Schnitzler, H.-U. (2018). “The role of echolocation strategies
472 for niche differentiation in bats,” *Can. J. Zool.*, **96**, 171–181. doi:10.1139/cjz-2017-
473 0161

474 Dietz, C., Nill, D., and Helversen, O. von (2009). *Bats of Britain, Europe and Northwest Africa*,
475 A & C Black, 406 pages.

476 Fenton, B. (1990). “The foraging behaviour and ecology of animal-eating bats,” *Can. J. Zool.*,
477 **68**, 411–422.

478 Fenton, M. B., and Bell, G. P. (1981). “Recognition of Species of Insectivorous Bats by Their
479 Echolocation Calls,” *J. Mammal.*, **62**, 233–243. doi:10.2307/1380701

480 Fenton, M. B., Grinnell, A., Popper, A. N., and Fay, R. R. (Eds.) (2016). *Bat bioacoustics*,
481 Springer handbook of auditory research, Springer Science+Business Media, New York,
482 304 pages.

483 Fullard, J. H., and Dawson, J. W. (1997). “The echolocation calls of the spotted bat *Euroderma*
484 *maculatum* are relatively inaudible to moths,” *J. Exp. Biol.*, **200**, 129–137.

485 Grodzinski, U., Spiegel, O., Korine, C., and Holderied, M. W. (2009). “Context-dependent
486 flight speed: evidence for energetically optimal flight speed in the bat *Pipistrellus*
487 *kuhlii* ?,” *J. Anim. Ecol.*, **78**, 540–548. doi:10.1111/j.1365-2656.2009.01526.x

488 Harrell, F. E. (2018). *Hmisc: Harrell Miscellaneous*,. Retrieved from [https://CRAN.R-](https://CRAN.R-project.org/package=Hmisc)
489 [project.org/package=Hmisc](https://CRAN.R-project.org/package=Hmisc)

490 Hedenström, A. (2009). “Optimal migration strategies in bats,” *J. Mammal.*, **90**, 1298–1309.

491 Holderied, M. W., Baker, C. J., Vespe, M., and Jones, G. (2008). “Understanding signal design
492 during the pursuit of aerial insects by echolocating bats: tools and applications,” *Integr.*
493 *Comp. Biol.*, **48**, 74–84.

494 Holderied, M. W., and Jones, G. (2009). “Flight Dynamics,” *Ecol. Behav. Methods Study Bats*,.

495 Jensen, M. E., and Miller, L. A. (1999). “Echolocation signals of the bat *Eptesicus serotinus*
496 recorded using a vertical microphone array: effect of flight altitude on searching
497 signals,” *Behav. Ecol. Sociobiol.*, **47**, 60–69. doi:10.1007/s002650050650

498 Jones, G. (1999). “Scaling of echolocation call parameters in bats,” *J. Exp. Biol.*, **202**, 3359–
499 3367.

500 Kalko, E. K., Estrada Villegas, S., Schmidt, M., Wegmann, M., and Meyer, C. F. (2008).
501 “Flying high—assessing the use of the aerosphere by bats,” *Integr. Comp. Biol.*, **48**, 60–
502 73.

503 Kingston, T., Jones, G., Akbar, Z., and Kunz, T. H. (1999). "Echolocation signal design in
504 Kerivoulineae and Murininae (Chiroptera: Vespertilionidae) from Malaysia.,"
505 Kloepper, L. N., and Kinniry, M. (2018). "Recording animal vocalizations from a UAV: bat
506 echolocation during roost re-entry," *Sci. Rep.*, **8**, 7779.

507 Kobayasi, K. I., Hage, S. R., Berquist, S., Feng, J., Zhang, S., and Metzner, W. (2012).
508 "Behavioural and neurobiological implications of linear and non-linear features in
509 larynx phonations of horseshoe bats," *Nat. Commun.*, **3**, 1184.

510 Koblitz, J. C. (2018). "Arrayvolution-Using microphone arrays to study bats in the field," *Can.*
511 *J. Zool.*,.

512 Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., Bentham, K.
513 van, et al. (2018). *glmmTMB: Generalized Linear Mixed Models using Template Model*
514 *Builder.*, Retrieved from <https://CRAN.R-project.org/package=glmmTMB>

515 Metzner, W., and Müller, R. (2016). "Ultrasound production, emission, and reception," *Bat*
516 *Bioacoustics*, Springer, pp. 55–91.

517 Moss, C. F., and Surlykke, A. (2001). "Auditory scene analysis by echolocation in bats," *J.*
518 *Acoust. Soc. Am.*, **110**, 2207–2226. doi:10.1121/1.1398051

519 Neuweiler, G. (1989). "Foraging Ecology and Audition in Echolocating Bats," *Trends Ecol.*
520 *Evol.*, **4**, 7.

521 Norberg, U. M., and Rayner, J. M. (1987). "Ecological morphology and flight in bats
522 (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and
523 echolocation," *Phil Trans R Soc Lond B*, **316**, 335–427.

524 Pennycuick, C. J. (2008). *Modelling the flying bird*, Elsevier, Vol. 5.

525 Penone, C., Kerbiriou, C., Julien, J.-F., Marmet, J., and Le Viol, I. (2018). "Body size
526 information in large-scale acoustic bat databases," *PeerJ*, **6**, e5370.
527 doi:10.7717/peerj.5370

528 Peurach, S. C. (2003). “High-altitude Collision between an Airplane and a Hoary Bat, *Lasiurus*
529 *cinereus*,” *Bat Res. News*, **44**, 2–3.

530 Pye, J. D. (1979). “Why ultrasound?,” *Endeavour*, **3**, 57–62.

531 R Core Team (2014). *R: A language and environment for statistical computing*, R Foundation
532 for Statistical Computing, Vienna, Austria. Retrieved from <http://www.R-project.org/>

533 Reynolds, D. R., Chapman, J. W., and Drake, V. A. (2017). “Riders on the Wind: The
534 Aeroecology of Insect Migrants,” In P. B. Chilson, W. F. Frick, J. F. Kelly, and F.
535 Liechti (Eds.), *Aeroecology*, Springer International Publishing, Cham, pp. 145–178.
536 doi:10.1007/978-3-319-68576-2_7

537 Roeleke, M., Johannsen, L., and Voigt, C. C. (2018). “How Bats Escape the Competitive
538 Exclusion Principle—Seasonal Shift From Intraspecific to Interspecific Competition
539 Drives Space Use in a Bat Ensemble,” *Front. Ecol. Evol.*, , doi:
540 10.3389/fevo.2018.00101. doi:10.3389/fevo.2018.00101

541 Roemer, C., Disca, T., Coulon, A., and Bas, Y. (2017). “Bat flight height monitored from wind
542 masts predicts mortality risk at wind farms,” *Biol. Conserv.*, **215**, 116–122.
543 doi:10.1016/j.biocon.2017.09.002

544 Russo, D., Ancillotto, L., and Jones, G. (2017). “Bats are still not birds in the digital era:
545 echolocation call variation and why it matters for bat species identification,” *Can. J.*
546 *Zool.*, **96**, 63–78. doi:10.1139/cjz-2017-0089

547 Schaub, A., and Schnitzler, H. U. (2007). “Echolocation behavior of the bat *Vespertilio murinus*
548 reveals the border between the habitat types ‘edge’ and ‘open space,’” *Behav. Ecol.*
549 *Sociobiol.*, **61**, 513–523. doi:10.1007/s00265-006-0279-9

550 Schnitzler, H.-U., and Denzinger, A. (2011). “Auditory fovea and Doppler shift compensation:
551 adaptations for flutter detection in echolocating bats using CF-FM signals,” *J. Comp.*
552 *Physiol. A*, **197**, 541–559.

553 Schnitzler, H.-U., and Kalko, E. K. V. (2001). "Echolocation by Insect-Eating Bats,"
554 BioScience, **51**, 557. doi:10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2

555 Schnitzler, H.-U., Moss, C. F., and Denzinger, A. (2003). "From spatial orientation to food
556 acquisition in echolocating bats," Trends Ecol. Evol., **18**, 386–394. doi:10.1016/S0169-
557 5347(03)00185-X

558 Siemers, B. M., and Schnitzler, H.-U. (2004). "Echolocation signals reflect niche differentiation
559 in five sympatric congeneric bat species," Nature, **429**, 657–661.
560 doi:10.1038/nature02547

561 Sleep, D. J., and Brigham, R. M. (2003). "An experimental test of clutter tolerance in bats," J.
562 Mammal., **84**, 216–224.

563 Teeling, E. C. (2009). "Hear, hear: the convergent evolution of echolocation in bats?," Trends
564 Ecol. Evol., **24**, 351–354.

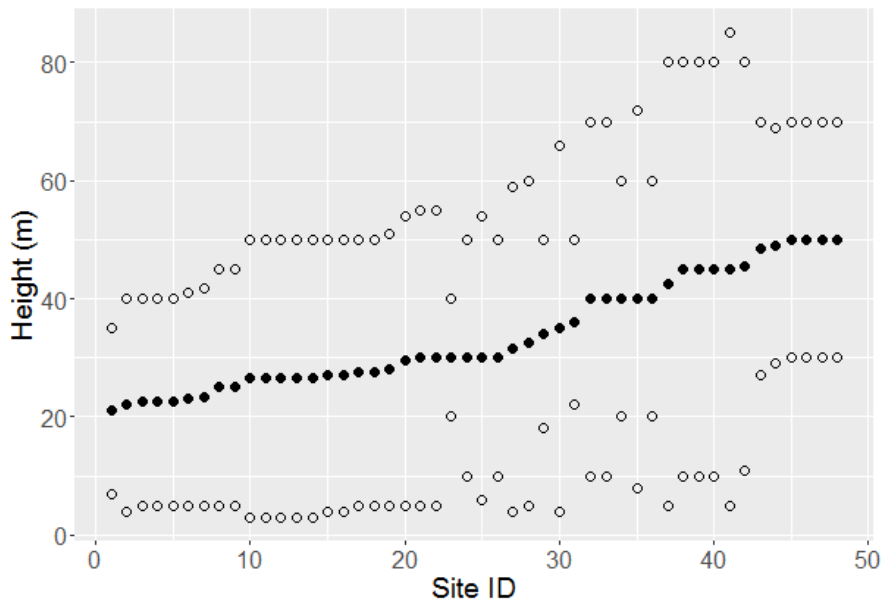
565 Thiagavel, J., Santana, S. E., and Ratcliffe, J. M. (2017). "Body Size Predicts Echolocation Call
566 Peak Frequency Better than Gape Height in Vespertilionid Bats," Sci. Rep., , doi:
567 10.1038/s41598-017-00959-2. doi:10.1038/s41598-017-00959-2

568 Trappe, M., and Schnitzler, H.-U. (1982). "Doppler-Shift Compensation in Insect-Catching
569 Horseshoe Bats," Naturwissenschaften, **62**, 193–194.

570 Voigt, C. C., Currie, S. E., Fritze, M., Roeleke, M., and Lindecke, O. (2018). "Conservation
571 Strategies for Bats Flying at High Altitudes," BioScience, **68**, 427–435.

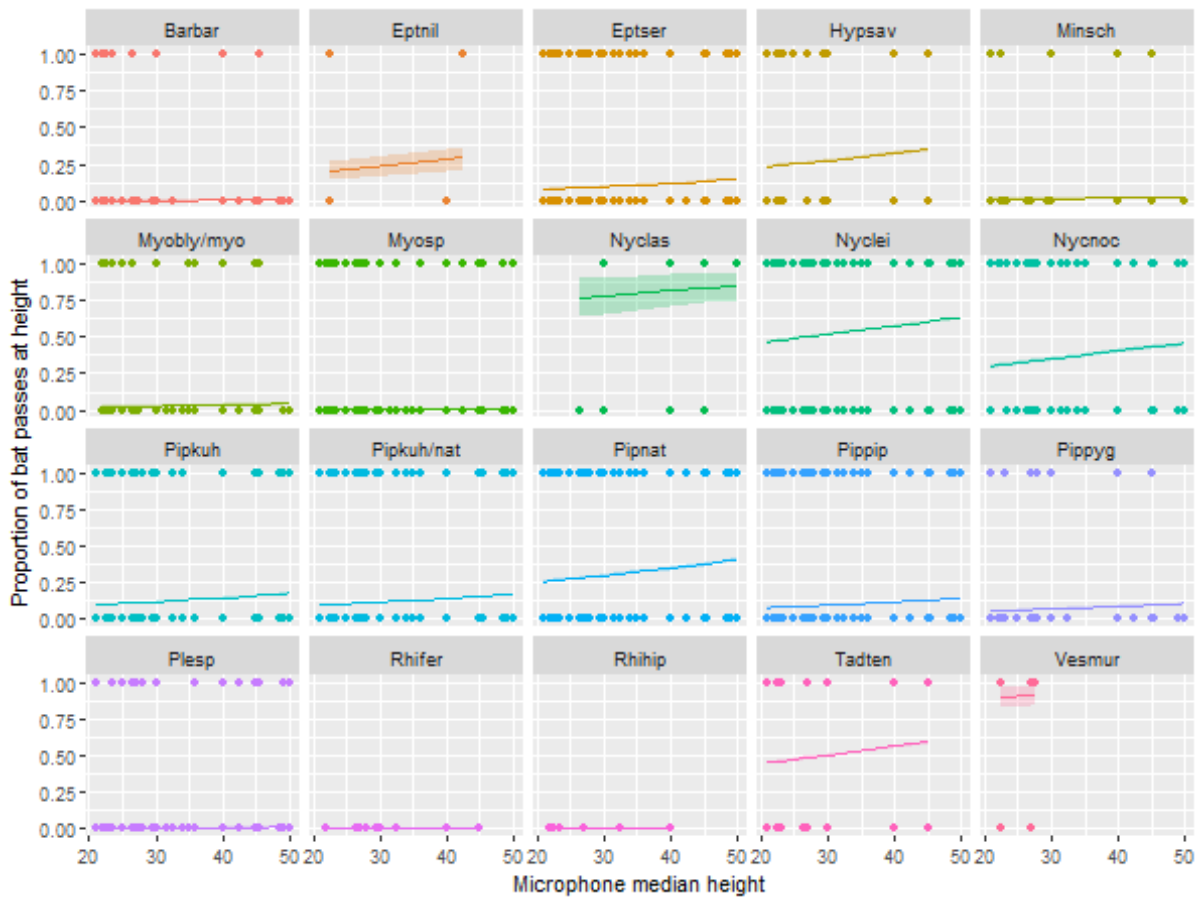
572 Waters, D. A., Rydell, J., and Jones, G. (1995). "Echolocation Call Design and Limits on Prey
573 Size: A Case Study Using the Aerial-Hawking Bat *Nyctalus leisleri*," Behav. Ecol.
574 Sociobiol., **37**, 321–328.

575 Williams, T. C., Ireland, L. C., and Williams, J. M. (1973). "High Altitude Flights of the Free-
576 Tailed Bat, *Tadarida brasiliensis*, Observed with Radar," J. Mammal., **54**, 807–821.
577 doi:10.2307/1379076



579

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



582

583 Figure 3 – Influence of microphone median height on the proportion of bat flights at height.

584 The regression line is shown (modelled with a binomial generalized linear model with

585 microphone median height and species as fixed effect). Species names are given with the first

586 three letters of species and genus. 95 % confidence intervals are shown.

587

588 **APPENDIX**

589 Table 4 – Mean morphological values used to calculate ARI (aspect ratio index for bat wings)

590 and WLI (wing loading index). These values were retrieved from Dietz et al. (2009). Species

591 names are given with the first three letters of genus and species.

<i>Species</i>	<i>Group</i>	<i>Forearm length (mm)</i>	<i>Length of 5th digit (mm)</i>	<i>Length of 3rd digit (mm)</i>	<i>Mass (g)</i>
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<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

592