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Title: Bat sonar and wing morphology predict species vertical niche

Running title: Bat traits predict species vertical niche

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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

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

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

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

In 2001, Schnitzler and Kalko described the concept of bat guilds, which was refined over time (Denzinger and Schnitzler, 2013; Denzinger et al., 2018). Guilds may be used to form consistent species groups for the study of sonar structures, habitat types, diet, foraging modes and other traits. In Denzinger et al. (2018), four guilds may be distinguished according to their acoustic strategies: (1) aerial hawkers or trawlers developed a strategy to efficiently locate prey in open and edge space using long quasi-constant frequency (QCF) calls (2) active gleaners mostly use short calls with high frequency compounds and frequency modulated (FM) calls resulting in large bandwidths, useful to detect prey or obstacles in high clutter (3) passive gleaners also use short calls with high frequencies and FM calls, but mostly listen to the rustling sounds of their prey while foraging, and use echolocation for orientation (4) some species also use a strategy implying long constant frequency calls with modulated frequency components (CF-FM) at high frequencies which allow them to evaluate flutter information from the prey 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 wing morphology and their use of the vertical dimension has never been thoroughly demonstrated. Since the

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

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

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

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

II. MATERIAL & METHODS

A. Acoustic recordings used to study bat altitudinal behaviour

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

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.

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

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

main part of the call). Yet, some sequences were so affected by atmospheric attenuation that there was no sufficient clue to attribute the sequence to a species. In addition, some species use sonar calls that are sometimes very close, even identical in certain flight circumstances, preventing identification to species level. These acoustic sequences that could not be identified at the species level were either classed in a group of species - when the vertical flight behaviours of all species were equivalent within the same group - or left unidentified and not used for further analysis (8.4 % of all bat passes). Here, *Myotis myotis* and *M. blythii* were identified as the “large *Myotis*” group, all other *Myotis* as the “small *Myotis*” group, and all *Plecotus* calls to the *Plecotus spp.* group. Species within those two groups present flight heights comparable to the other species of their group (Rodrigues *et al.*, 2015), and similar acoustic features (Barataud, 2015). Great care must be taken in the analysis of the results of the species *P. kuhlii* and *P. nathusii*, because acoustic features of these two species are simultaneously very variable and similar to each other. *V. murinus* is also difficult 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, 2018) from R (R Core Team, 2014). With two microphones, flight height cannot be precisely calculated, and TOAD were used to determine to which microphones bats were closer. A height threshold was defined for each site as the median height between the two microphones. Microphone median height was variable depending on study site (20-50 m) (Figure 2), but this variation did not greatly affect species proportion of flight at height (Figure 3). Using this threshold, bat calls were assigned to two classes following the method described in Roemer *et al.* (2017): “at height” if the source of the signal was above the threshold and “at ground level” if it was below the threshold. A ratio of the time spent at height was then calculated for each species. It must

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

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*.

D. Wing loading and aspect ratio

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.

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>Rhihip</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

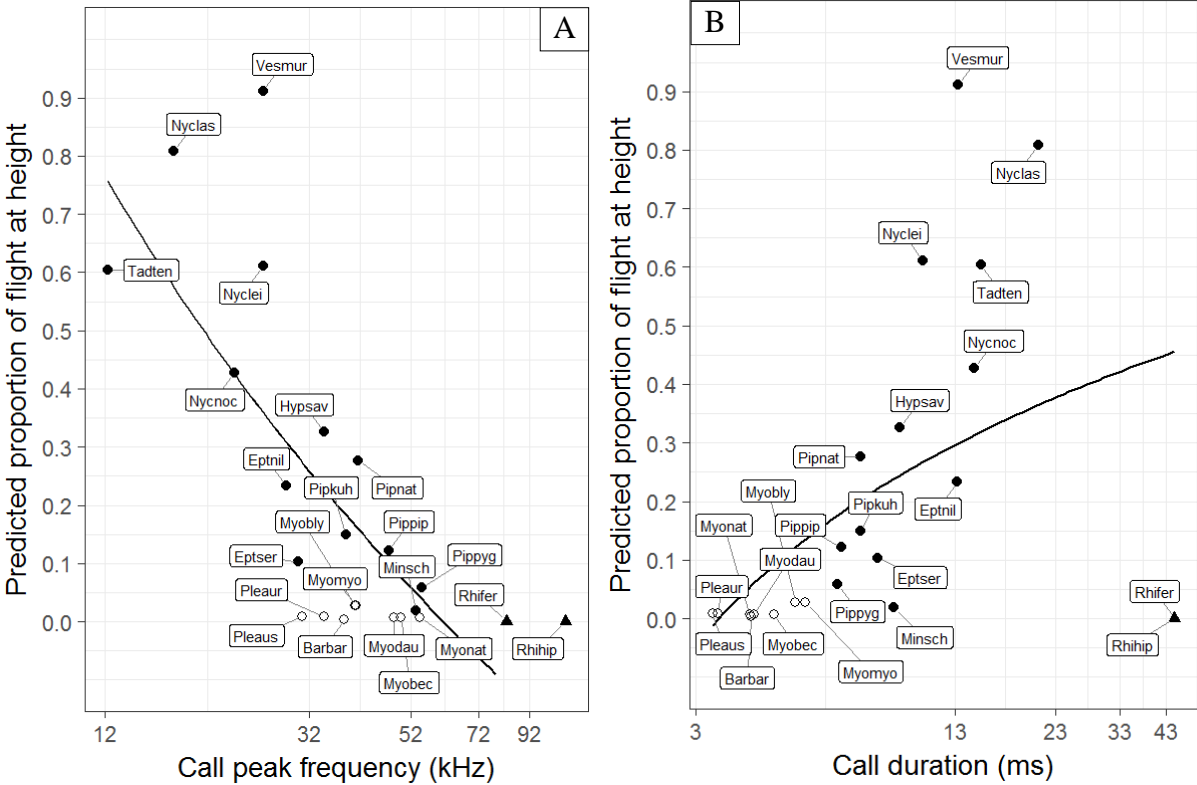
268 B. Correlations between proportion of flight at height and traits

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,

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

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



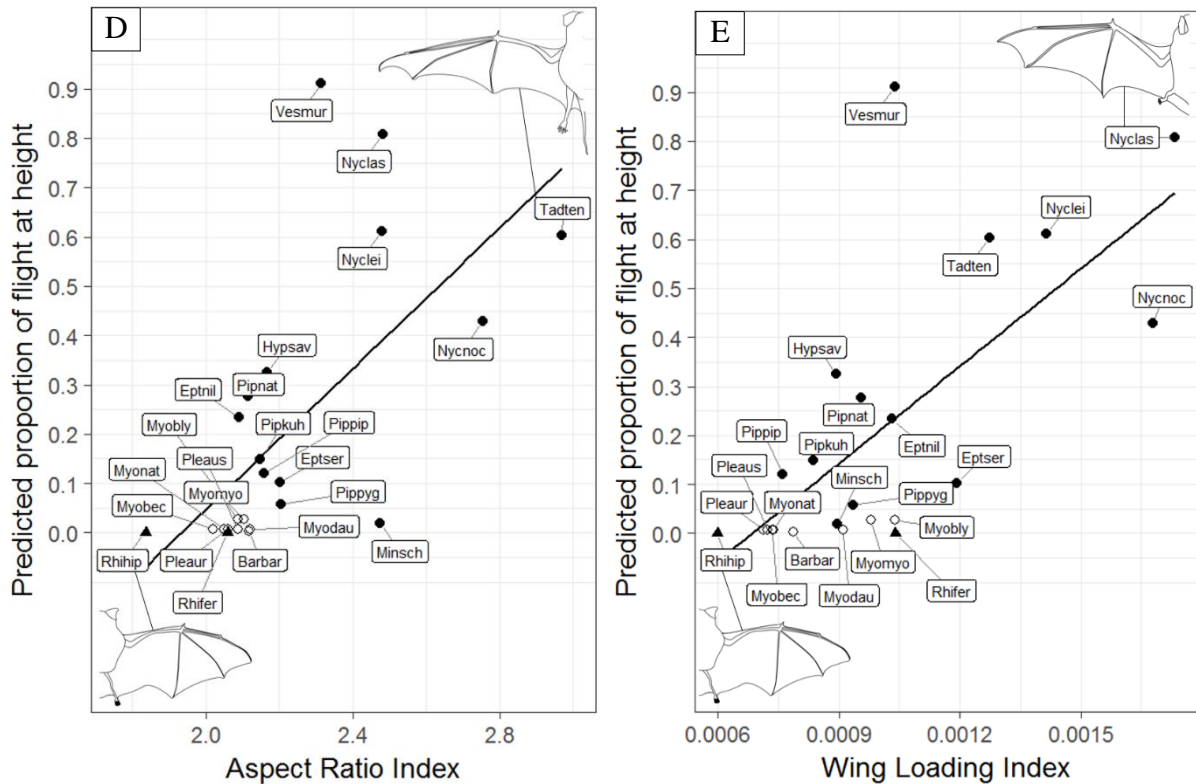
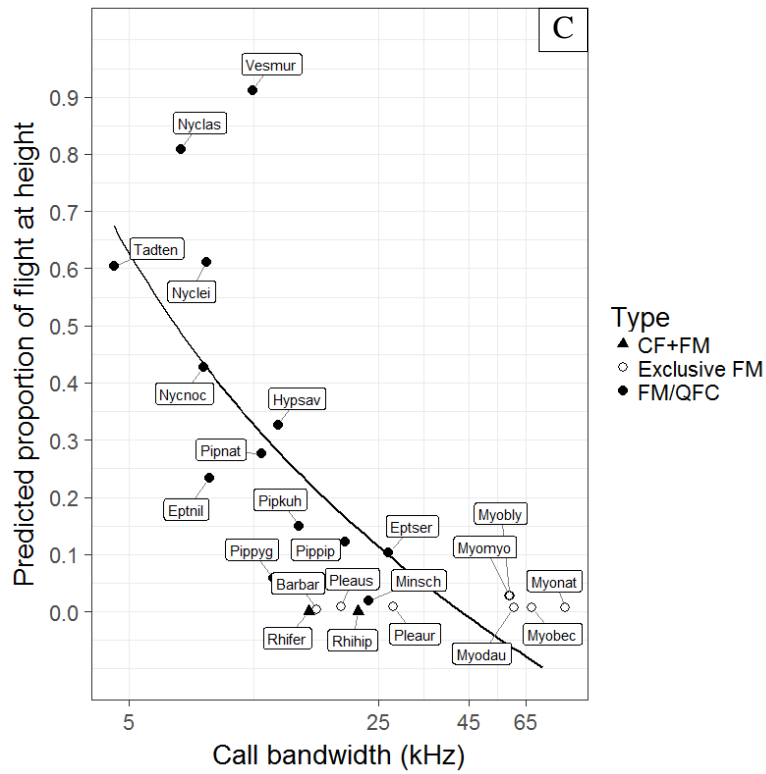


Figure 1 – Correlation between the predicted proportion of flight at height and morphological and sonar variables. Etiquettes relate to the first three letters of genera and species names. The categories CF (constant frequencies), FM (frequency modulated), and QFC (quasi-constant

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

IV. DISCUSSION

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

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 Jensen and Miller (1999) with a vertical array of three microphones on a 15 meter pole elucidated the links between echolocation features and flight height in *E. serotinus*, a European bat. A study by Kloepper and Kinniry (2018) suggested that the features of echolocation calls in *Tadarida brasiliensis*, an American bat, vary in function of their flight height. However, our study is the first to assess this relationship in a bat community. The use of wind masts allowed a long-term monitoring of bat flight behaviour and an objective assessment of species vertical flight distribution. The automation of the process allowed us to equip 48 masts over the French and Belgian territories and analyse their results. The combination of long-term monitoring and of the high amount of study sites was an advantage in obtaining enough data for rare species (e.g. *E. nilssonii*) or species with short detection ranges (e.g. *R. hipposideros*).

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 other bat families addressed here belong.

Our study also shows the first correlations based on empirical measures between bat wing morphology and their vertical distribution. It confirmed our hypotheses that narrow wings 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).

C. Constraints of bat flight at great heights

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

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

In the first instance, we demonstrated that high-flying species possess high aspect ratios and high wing loadings. For foraging purposes, high-flyers cover greater distances than low-flyers (Dietz et al., 2009), possibly because insects are scarcer at height (Reynolds et al., 2017). Economic flights over long distances are facilitated by a low wing inertia, which is associated with a high aspect ratio (Norberg and Rayner, 1987; Pennycuick, 2008). Since high aspect ratios are often associated with short wings, high-flyers tend to also have high wing loadings (Norberg and Rayner, 1987). In order to sustain a powered flight, species with higher wing loadings must fly faster, which is precisely an optimal strategy when travelling through long distances between two foraging grounds (Grodzinski et al., 2009; Norberg and Rayner, 1987), but also for long-distance migration (Hedenström, 2009). It was suggested that the swift aspect of *Miniopterus schreibersii* could be linked to agile flight in high-altitude hawking (Norberg and Rayner, 1987). Our results do not support this hypothesis, since this species was very rarely recorded at height. The relatively high aspect ratio of *M. schreibersii* is probably associated with good agility during fast flights near ground level. This species indeed covers very long distances overnight (up to 40 km) to actively avoid intraspecific competition for food in the vicinity of its very large colonies (Dietz et al., 2009). As a fast flyer (Holderied and Jones, 2009), this species does not have a higher wing loading than the average, because its wings are longer than average due to the unusual length of its third digit, but its wide uropatagium allows for a manoeuvrability not seen in other species with narrow wings (Dietz 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 that body size is inversely correlated with echolocation call peak frequency – when acoustic strategies are taken into account - which corroborates this hypothesis (Bogdanowicz et al., 1999; Jones, 1999; Penone et al., 2018; Thiagavel et al., 2017). Calls used for social communication may be much lower than the echolocation repertoire (Chaverri et al., 2018), but their production is based on the same biomechanical properties of the larynx than the production of echolocation calls (Kobayasi et al., 2012). Indeed, in isolated larynxes, it was demonstrated that below a certain air flow threshold, the emitted frequencies correspond to the register of echolocation frequencies, but passing this threshold, the emitted frequencies correspond to the register of social communication (much lower frequencies) (Kobayasi et al., 2012). This jumping from one frequency register to another is similar to yodelling.

Nonetheless, we found that species with high-pitched vocalisations (e.g. *Myotis sp.* or *M. schreibersii*) could also – although rarely – be found at elevated heights. These individuals 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 they came across the wind mast. Individuals can lower their call frequency to perceive obstacles from a greater distance (Jensen and Miller, 1999; Schaub and Schnitzler, 2007), however we do not expect species such as *Myotis sp.* to be able to modify their sonar in such a way that they could perceive ground level when flying at more than 20 m, their estimated maximal detection range in open spaces (Barataud, 2015). High-pitched echolocators are more likely to explore wind masts from the bottom, but they could possibly rely only on vision to perceive long-distance obstacles and use their sonar to sense small obstacles such as other flying animals (Boonman et al., 2013).

D. Conclusion and perspectives

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

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

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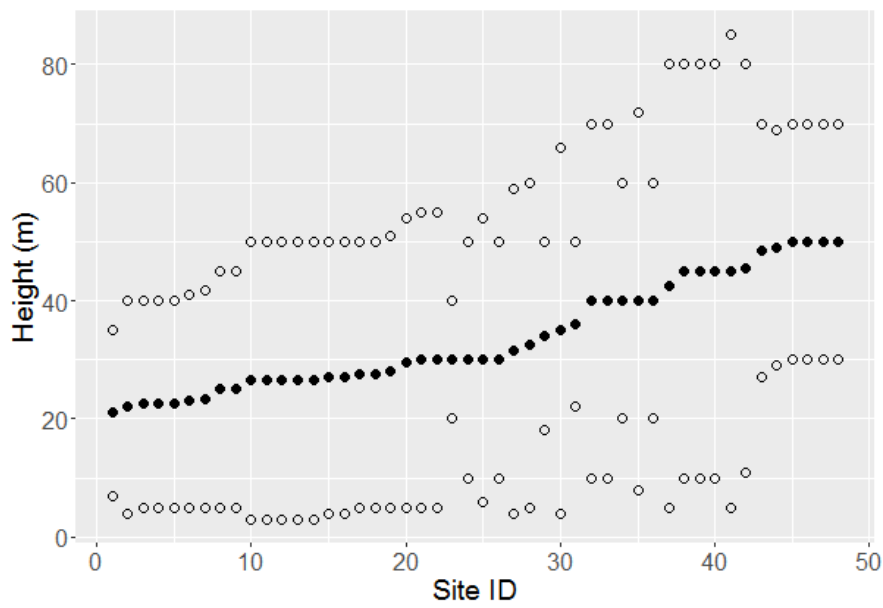
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579

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

581 filled circles show the median height.

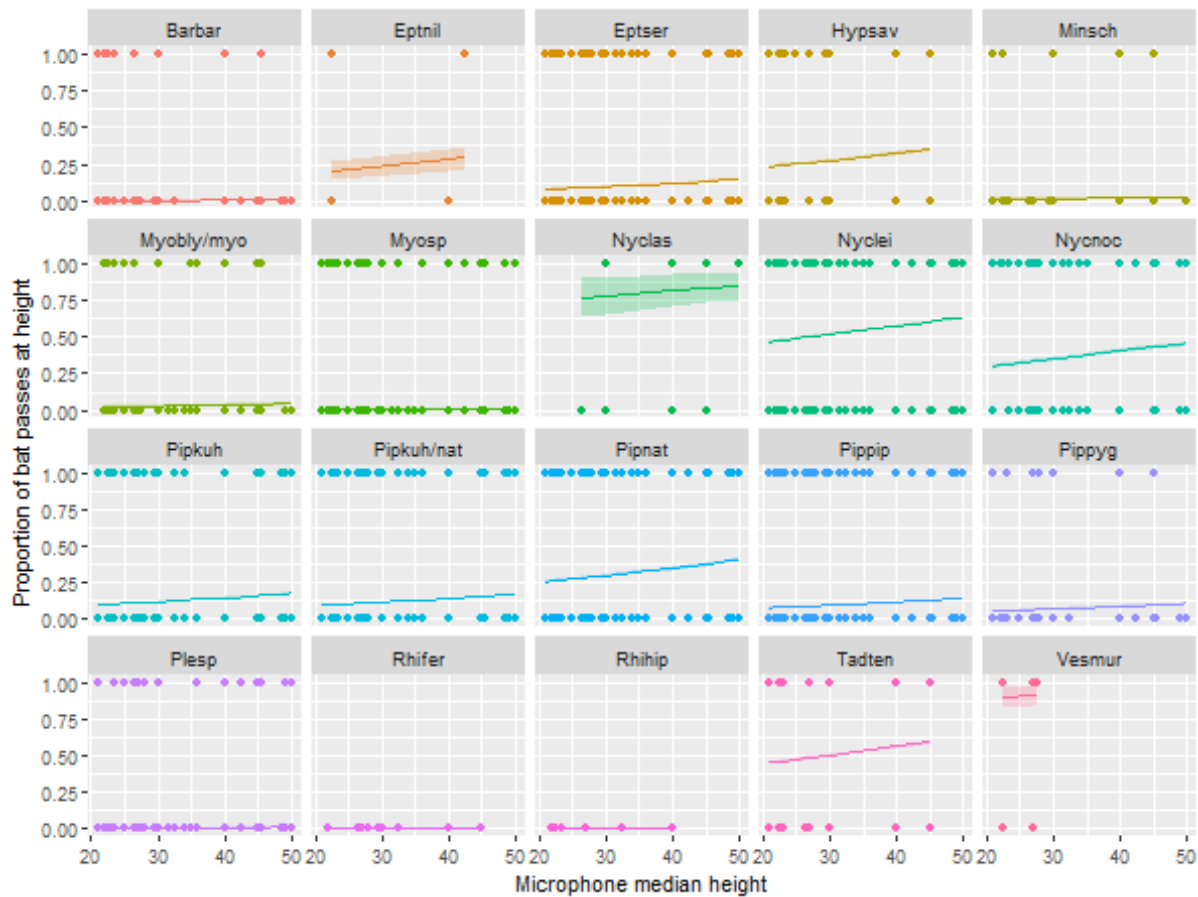


Figure 3 – Influence of microphone median height on the proportion of bat flights at height. The regression line is shown (modelled with a binomial generalized linear model with microphone median height and species as fixed effect). Species names are given with the first three letters of species and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

APPENDIX

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

Species	Group	Forearm length (mm)	Length of 5 th digit (mm)	Length of 3 rd digit (mm)	Mass (g)
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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>	Small <i>Myotis</i>	43.05	53.50	65.00	8.50
<i>Myodau</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