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## Potentiality of the bat pass duration measure for studies dealing with bat activity

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1 **Title: Potentiality of the bat pass duration measure for studies dealing with bat activity**

2

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8 **ABSTRACT**

9 Acoustic detectors have become increasingly used by bat workers to investigate bat  
10 ecology and assess impacts of anthropogenic pressures. Within these studies, the metric  
11 used, “bat activity,” is based on the number of bat passes, without considering the bat pass  
12 duration (i.e., each event of a bat detected within the volume of an ultrasonic detector); we  
13 expected that bat pass duration may contain information about site quality in terms of  
14 potentialities for foraging. Because bats are expected to have a more sinuous trajectory and  
15 slower velocity when they exhibit foraging behaviour, as opposed to commuting behaviour,  
16 we hypothesize a greater bat pass duration in favourable habitats; during seasons with  
17 important energetic demands; or during night pic activity.

18 We datasets from a large-scale acoustic bat survey (n=2890 sites), allowing a total of  
19 24597 bat pass measures from 6 taxa, and performed GLMM modelling.

20 We detected a significant effect of habitat type on bat pass duration for five taxa.  
21 Smaller bat pass durations were detected in the beginning of the night. We detected longer  
22 pass durations during the lactation period or just before hibernating, while weather  
23 conditions or ageing and wear of the detector rarely influenced bat pass duration.

24 Bat pass duration appears to be a simple and easy measure for position calls on a  
25 gradient between commuting vs. foraging behaviour. We suggest that the traditional  
26 measure of bat activity may be weighted by bat pass duration by giving more weight to the  
27 events with potentially greater links to foraging behaviour.

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30

31 **1. INTRODUCTION**

32           Increasingly threatened worldwide (Mickleburgh et al. 2002), bats have the potential to  
33 be important biodiversity indicator species, as they are distributed globally and are long-lived  
34 species, and it has been suggested that their population trends reflect those of lower trophic  
35 level species (Jones et al. 2009). They are considered indicators of the response of  
36 biodiversity to anthropogenic pressure (Jones et al., 2009).

37           We have witnessed an exponential increase in the knowledge in the acoustic  
38 identification of bat species (Russo & Jones, 2002; Obrist et al., 2004; Barataud, 2015). In  
39 addition to this taxonomic knowledge, the cost of ultrasonic recorders has reduced and has  
40 resulted in the development of passive acoustic sensors that are able to record throughout  
41 the night. Acoustic detectors have been used to increase inventory completeness in bat  
42 assemblage studies (Mac Swiney et al 2008), and these methods have been proposed to form  
43 part of a single standardized monitoring protocol (Stahlschmidt and Brühl 2012). In addition,  
44 contrary to capture methods, radio tracking methods, roost surveys, and the use of  
45 ultrasonic detectors, all non-intrusive methods, are often the only logistically feasible  
46 methods (Stahlschmidt and Brühl 2012). Thus, since the two last decades, these approaches  
47 were widely used by researchers working for environmental consulting firms or government  
48 agencies (Adams et al. 2012), for example, during the evaluation of development projects.  
49 Acoustic detectors have become increasingly used by academic researchers to investigate the  
50 differential use of habitats by bats (Sherwin et al. 2000, Russo and Jones 2003) or to test  
51 various anthropogenic pressures such as the following: (i) agricultural intensification based  
52 on high levels of agrochemicals (Wickramasinghe et al 2003); (ii) non-lethal impacts of wind  
53 turbines, such as the disturbance of commuting and migration routes and local habitat loss  
54 (Hötker et al. 2006, Millon et al. 2015); or (iii) artificial light at night (Stone et al. 2009; Azam  
55 et al. 2015). Finally, monitoring of bat populations based on nocturnal acoustic standardized  
56 recordings are under development in an increasing number of countries, including the UK  
57 (Russ et al. 2008), USA (Herzog & Britzke 2009), Ireland (Roche et al. 2011), and France  
58 (Kerbiriou et al. 2010).

59           Within all these studies, the measure used, “bat activity,” is based on the number of  
60 bat passes. The metrics used for assessing bat activity vary among studies; for example,  
61 Hayes (1997) used the number of files recorded by bat detectors that include echolocation  
62 calls, while Tibbel and Kurta (2003) used the number of pulses in all files that were recorded  
63 in one night. In acoustic studies using time expansion bat detectors, a bat pass is defined as

64 one or more bat echolocation call during a record of sound at a x10 time expansion (Regnery  
65 et al. 2013). In these cases, the duration of the record is predefined by the ultra-sound  
66 detector (for example, 0.32 s for the Tranquility Transect (David Bale, Courtpan. Design Ltd,  
67 Cheltenham, UK), see Roche et al 2011, Regnery et al. 2013, Lacoeyuilhe et al. 2014). Other  
68 studies calculated bat activity as the number of bat passes per night, and bat pass was  
69 defined as a single or several bat calls emitted during a fixed interval (for example 5 s in  
70 Millon et al. (2015) study). Relative feeding activity is sometimes measured using a 'buzz  
71 ratio' (Rowse et al. 2016), which is the proportion of call sequences that included 'feeding  
72 buzzes' (buzzes are signals emitted by bats just before they try to catch insects, or when they  
73 drink or before landing). However, the ratio of feeding buzzes in a sample is regularly very  
74 low (~1% of whole contacts in the data set of the French bat-monitoring programme).

75 Curiously, at the time of writing, it appears that the measure of bat pass duration,  
76 (i.e., each event (expressed in seconds) of a bat detected within the detection volume of the  
77 ultrasonic detector, Fig. 1) has never been used; we expected this measure may contain  
78 information about site quality in terms of potentialities for foraging. Because bats are  
79 expected to have a more sinuous trajectory and slower velocity when they exhibit foraging  
80 behaviour, as opposed to commuting behaviour, between their roost and foraging areas or  
81 between two patch of foraging areas (Fig. 2), we thus hypothesize the following: (i) that sites  
82 or habitats with high levels of food resources may be characterized by sequences with  
83 greater bat pass duration on average than sites with low foraging resources; (ii) that bat pass  
84 duration may be lower in the first minutes after sunset when bats commute between their  
85 roost to their foraging areas; and (iii) that the pass duration may vary, with a longer pass  
86 duration on average during the spring when important energetic demands are imposed by  
87 pregnancy (Anthony et al. 1981, Ruedi 1993, Swift 1980) or in the autumn period when bats  
88 accumulate fat before hibernation.

89 However, acoustic recordings (here the bat pass duration) depend not only on the specificity  
90 of the transmitter (here the bats) but also on the receiver (here the detector) and the  
91 medium (here the air). For example, the speed of sound is influenced by the density of the  
92 medium and temperature. However, temperature and humidity could also indirectly  
93 influence the behaviour of bats due to their impact on feeding prey (O'Donnell 2000,  
94 Ciechanowski et al. 2007). In addition, acoustic recordings are expected to be influenced by  
95 technical choices such as the following: the microphone of the detector (Waters and Walsh

96 1994, Adams et al. 2012), bat detector height (Weller and Zabel 2002, Baerwald and Barclay  
97 2009, Collins and Jones 2009, Jones 2009), detector orientation (Weller and Zabel 2002), and  
98 distance of the signal from the detector (Adams et al. 2012). Moreover, long term acoustic  
99 monitoring involves also considering the wear of the microphones. Finally, methods to  
100 survey bat activity (mainly, line transects and stationary measurement) are expected to  
101 influence acoustic recordings (Stahlschmidt and Brühl 2012).

102         With the aim to test if bat pass duration was longer in favourable habitats, during  
103 seasons with high energetic constraints or during night pic activity, we mobilized two  
104 independent data sets (i.e., two protocols' recordings along line transects or stationary  
105 recordings) from the French bat-monitoring programme, a large scale acoustic bat survey  
106 that has involved numerous volunteers since 2006. These data sets offer the opportunity to  
107 simultaneously test multiple factors, such as habitat, season, hour in the night, weather  
108 condition, detector characteristics, and ageing of the detector, that are expected to influence  
109 acoustic recordings and more particularly, the bat pass duration of various species of bats. In  
110 addition, the protocol of this large survey avoids extreme weather conditions (i.e., lower  
111 temperatures, strong winds, and rain). Thus, the conditions of the recordings of these data  
112 are close to the conditions often selected for comparative studies (see Azam et al. 2015,  
113 Lacoecilhe et al. 2014)

114

## 115 **2. MATERIAL AND METHODS**

### 116 **2.1 Bat sampling**

117 The data were provided by the French bat-monitoring programme (FBMP)  
118 (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science programme running since  
119 2006 and coordinated by the French Museum of Natural History (MNHN). The FBMP is based  
120 on standardized echolocation recordings (Stahlschmidt and Brühl, 2012), where bat calls are  
121 detected using 2 types of bat detectors (Tranquility Transect Bat detector, Courtpan Design  
122 Ltd, UK; and D240x, Pettersson Elektronik AB) and were recorded on a Zoom H2 digital  
123 recorder (Samson Technologies, USA) at a sampling rate of 96 ks/s. Sound was stored on a  
124 Secured Card in Waveform Audio File Format, more commonly known as the WAV format.  
125 Each site is monitored twice: once during the period of 15 June to 31 July, when females are  
126 expected to give birth and feed their offspring; and second, during the period 15 August to  
127 31 September, when the young bats are flying, and individuals are expected to be less

128 dependent on their reproductive roost. The observers begin their sampling at thirty minutes  
129 after sunset, from season to season and year to year. Thus, this sampling occurred during the  
130 bat activity peak that begins 30 minutes after sunset and spans less than 3 hours (Roche et  
131 al. 2005). Observers sampled bats only when weather conditions were considered as  
132 favourable, i.e., no rain, temperature higher than 12°C, 30 minutes after sunset, and without  
133 strong winds (<20km/h). Two different versions are used (road survey by car and count  
134 point).

135

### 136 *2.2.1 Car transect survey*

137 Volunteer surveyors record bat activity while driving at a constant low-speed ( $25 \pm 5$  km/h)  
138 along a road circuit. Volunteer observers were asked to choose a road circuit of at least 30  
139 km and located within a 10-km radius around the volunteer's residence. Selecting a circuit  
140 met two requirements: the first concerned the safety of the volunteers, because the circuit  
141 must be performed at night at low speed; and the second objective was to design a circuit  
142 that proportionally crossed, as much as possible, the different habitats present in the area.  
143 Once the circuit was validated by the Museum, the starting plot was randomly chosen. Each  
144 circuit was then divided into 10 - 2 km transects where bat were recorded, separated by 1 km  
145 road portions where recording was not carried out (See ESM 1, Fig. S1-2). Such design  
146 allowed to obtain a quite good correlation between proportion of habitat sampled and  
147 proportion of habitat existing at the national scale ( $R^2 = 0.95$ ). Currently, the database is  
148 composed of 160 road circuits representing 1618 different transects (see ESM 1). The car  
149 transect survey is one of the three protocols used by the FBMP in order to monitor common  
150 bat population (for more details see Azam et al. 2016, Kerbiriou et al. 2018a, and ESM 1).

151

### 152 *2.2.2 Count point survey*

153 The protocol consists of a 2 km  $\times$  2 km square randomly chosen (by the Museum) in a radius  
154 of 10 km from the observer's home, within which a minimum of ten points are chosen by the  
155 observer, with at least five points being representative of the habitats of the square, the  
156 others being located in 'favourable' places for bats, such as riverbanks and wood edges. The  
157 ten points of a site were sampled (continuous recording during 6 minutes/point) during the  
158 same night. Currently, data have been gathered on 120 squares representing 1272 different

159 points (see ESM 1). The count point survey is the second protocols used by the FBMP in  
160 order to monitor common bat population (for more details see Kerbiriou et al. 2018b, and  
161 ESM 1

162

## 163 2.3. Biological data, species identification and the measure of bat pass duration

### 164 2.3.1. *Species identification*

165 Volunteers proceeded to species acoustic identification, while final data validation was made  
166 by Museum experts. Calls of genus *Myotis* were pooled in a *Myotis* spp. group due to their  
167 very low occurrence and some identification uncertainties (in this group less than 50% of bat  
168 passes were identified at the species level: *Myotis daubentonii*, *Myotis myotis*, *Myotis*  
169 *mystacinus*, *Myotis emarginatus*, and *Myotis nattereri*). Twenty-seven experienced  
170 volunteers proceeded to the measure of bat pass duration (Fig. 1) using Syrinx software  
171 version 2.6 (Burt 2006) for spectrogram analyses with settings provided by the MNHN. Bat  
172 passes containing social calls were excluded because the detection radius of social calls is  
173 expected to be drastically different from other echolocation calls.

174

### 175 2.3.2. *Variables expected to influence bat passes duration*

176 Bat activity is known to vary among habitats (Cramel and Safriel 1998, Russo and Jones 2003,  
177 Rainho 2007, Vandeveld et al. 2014), We hypothesize that in favourable habitats (for  
178 example, forest or wetlands), records will contain more bat passes with a hunting pattern,  
179 rather than in less favourable habitats (i.e., urbanized or intensive agricultural land), where  
180 we expect to record more bat passes with a commuting pattern. As commuting flights are  
181 faster and straighter on average than foraging flights, we hypothesized that the duration of  
182 bat passes will be greater in favourable foraging habitats. Volunteers involved in the FBMP  
183 provided a hierarchical description of the habitat surrounding the sampling point (each point  
184 count for the count point protocol and every 400 metres along the transect for the car survey  
185 protocol), from which we derived a simplified habitat classification. The Habitat type  
186 variable, used hereafter in the modelling, is a categorical variable with 8 classes: continuous  
187 urban areas (CU), discontinuous urban areas (DU), arable land (AL), heterogeneous  
188 agricultural areas including crops and pasture (HA), coniferous forest (CF), deciduous forest  
189 (DF), water courses (WC), and bodies of water (BW).

190 In addition, foraging behaviour also varies according to the habitat structure; for example,  
191 the *Myotis* group primarily included species considered to be gleaners, which capture the  
192 majority of their prey from substrates in cluttered environments (Arlettaz et al. 2001). Their  
193 prey are mainly diurnal Brachycera Diptera and non-volant arthropods, such as weevils,  
194 Lepidoptera larvae, harvestmen and spiders (Swift and Racey 2002; Dietz et al. 2007). In  
195 contrast, species of the genera *Pipistrellus*, *Eptesicus* and *Nyctalus* are considered to be aerial  
196 hawkers, which forage mostly on flying prey in open spaces (Dietz et al. 2007; Schnitzler et al.  
197 2003, Holderied and Von Helversen 2003). We thus built an index of clutter of the habitat  
198 (Clutter Index) derived from the hierarchical description of the habitat made by volunteers.  
199 The Clutter Index is an explicit seven-class gradient of habitat structure, ranging from (1)  
200 open habitat (i.e., farmland open fields without any trees or bushes) to (7) cluttered habitat  
201 (i.e., forests with a dense undergrowth layer) (for more details see Table XX, ESM1). We  
202 hypothesize that longer bat pass duration will be found in the foraging environments of  
203 species, that for *Myotis* spp., for example, bat pass duration will be greater in cluttered  
204 environments. Note however, that sound propagation could also be biased by the degree of  
205 cluttering of a habitat (Patriquin et al. 2003), so the net effect of habitat structure on bat pass  
206 duration is not easy to predict.

207 Second, we hypothesize that foraging behaviour could vary within the night, with smaller bat  
208 pass durations during the period of commuting between the roost and foraging areas (i.e.,  
209 early night); in addition, we also hypothesized that within a season, bat pass duration could  
210 vary according to the variation in energetic demands among seasons (Parsons et al. 2003):  
211 we expected to find longer bat pass durations during pregnancy in June and fat accumulation  
212 in the autumn. Thus, in our analysis, we take into account *Time after sunset* (in minutes) and  
213 *Date* (Julian date), and as we expected a non-linear effect, we also included the quadratic  
214 effect of these two variables.

215 Third, weather conditions are known to influence bat prey, i.e., invertebrates; thus, in our  
216 analysis, we take into account temperature (°C), humidity (%), cloud cover (% in four classes:  
217 0-25%, 25-50%, 50-75%, and 75-100%), and wind speed (km/h). Note that according to the  
218 FBMP protocol, volunteers are invited to avoid carrying out their field survey during extreme  
219 weather conditions (see ESM 2 for the distribution of these variables in the dataset).

220 Fourth, sound propagation is proportional to temperature, air composition (i.e., humidity,  
221 see Griffin 1971) and pressure. However, in the Earth's atmosphere, the chief factor affecting



222 sound propagation is the temperature, a variable previously selected for our analyses  
223 according to its potential impact on bat prey.

224 Fifth, the nature of the receiver (i.e., bat detector) is expected to influence the acoustic  
225 signal recorded: detection range differs according to the sensitivity of the detector and the  
226 directionality of the microphone (see Limpens et al. 2002). In addition, weatherproofing  
227 designs and microphone orientations are expected to impact the quantity and quality of the  
228 bat calls (Britzke et al. 2010). However, the survey was carried out (car or point count), and  
229 two models of detector are used by the volunteer network: Tranquility Transect and D240x.  
230 According to the type of microphone, electret for D240x and capacitive for the Tranquility  
231 Transect, we hypothesized that the Tranquility Transect, with a greater directionality, will  
232 record shorter durations of bat passes. In addition, to take into account ageing and wear (1 to  
233 9 years), we included the age of the detector as a variable as well as an interaction effect  
234 between the age of detector and model of detector.

235 Finally, we also take into account the protocol as a source of variation in bat pass duration,  
236 hypothesizing that bat pass duration will be greater with the point count protocol. In  
237 addition, for the car transect surveys, as the receiver is moving, it also depends on its speed,  
238 so we hypothesized a negative relationship between bat pass duration and car speed. Note  
239 however, that according to the requirement of the car transect survey (25 km/h  $\pm$  5 km/h)  
240 and compliance with instructions by volunteers, the variation of the car speed in the data set  
241 is relatively small (see ESM 2).

242

## 243 2.4. Statistical analysis

### 244 2.4.1. Influence of variables on the measure of bat pass duration

245 For each taxa and method used to survey bat activity (i.e., car transect and point count) we  
246 performed general linear mixed models (GLMM function *glmmPQL*, package R: MASS) using  
247 the duration of bat passes as a response variable with a Poisson error distribution according  
248 to the long tail pattern of bat passes duration (see ESM 3). The variables potentially  
249 influencing bat pass duration, such as habitat (habitat type or clutter index), date, time after  
250 sunset, weather conditions (temperature, humidity, cloud cover, and wind), receiver  
251 (detector model, age of detector, and the car speed for the car transect survey) were used as  
252 fixed effects. We included a quadratic effect for the date and time after sunset, and we used  
253 general additive mixed models (GAMM function *gamm*, package R: mgcv) for visualizing

254 these potentially non-linear effects. To account for possible spatial pseudo-replication  
255 involving several measurements taken from the same individual or environment, we included  
256 a group effect (named “date-point”) for identifying bat passes recorded within the same site  
257 at the same date as a random effect. In addition to taking temporal pseudo-replication into  
258 account, involving repeated measurements from the same volunteers, we included volunteer  
259 identity as one supplementary independent random effect. The fixed effects, except detector  
260 model and habitat type (categorical variable), were standardized so that the regression  
261 coefficients were comparable in magnitude (Schielzeth 2010). Before running each GLMM,  
262 we systematically evaluated the correlations among explanatory variables using Spearman’s  
263 rho for quantitative variables (Crawley 2009) to detect obvious correlation (See ESM 2).  
264 Second, we performed variance-inflation factors (VIF) on each model (Fox and Monette  
265 1992); all variables had a VIF<3, indicating no problem of multicollinearity in the explanatory  
266 variables of our models. Thus, we ran 12 models, one for each bat taxa (n=6) and for each  
267 protocol (car transect or point count), structured in the following way:

268

269 *[bat passes duration] ~ date + date<sup>2</sup> + time after sunset + time after sunset<sup>2</sup> + temperature +*  
270 *wind speed + humidity + cloud cover + detector model \* age of detector + clutter index or*  
271 *habitat type + 1|volunteer +1| date-point*

272

273 For the six models running on data from the car survey protocol, we added car speed as a  
274 fixed effect. According that, clutter index or habitat type are intrinsically correlated variables  
275 and could not be simultaneously included in the modelling; thus, we performed separate  
276 modelling.

277

### 278 **3. RESULTS**

279 The most common taxa (5 bats species: *P. kuhlij*, *P. pipistrellus* *E. serotinus*, *N. leisleri*,  
280 *N. noctula* and one genus: *Myotis*) accounted for 24597 bat passes (Table 1).

281

282 We detected relatively few effects of the clutter index: just a significant positive effect  
283 on bat pass duration for *N. leisleri* with data from the car survey (Table 2) and for *E. serotinus*  
284 with data from the count point survey (Table 3). Habitat type was slightly more significant,  
285 with two effects detected with data from the car survey (*P. pipistrellus* and *E. serotinus*) and

286 three effects with data from the count point survey (*P. kuhlii*, *E. serotinus* and *N. leisleri*)  
287 (Table 4).

288 For *P. pipistrellus*, we detected that greater bat pass durations were recorded in bodies of  
289 water (Fig. 4). For *P. kuhlii*, smaller bat pass durations were recorded in urban areas. For *E.*  
290 *serotinus*, greater bat pass durations were recorded in heterogeneous agricultural areas,  
291 deciduous forests and water courses, and smaller bat pass durations in continuous urban  
292 areas, discontinuous urban areas and arable land (Fig. 4).

293 We detected a significant effect of time after sunset for three species (*P. pipistrellus*,  
294 *E. serotinus* and *N. noctula*, for the latter species, only in the car transect survey). The  
295 observed pattern is congruent with our hypothesis: smaller bat pass duration was found in  
296 the beginning of the night (Tables 2 & 3; Fig. 3; ESM 4.2 & ESM 4.5), and in addition, a  
297 quadric effect was detected for *P. pipistrellus* and *E. serotinus* (for the latter species, only in  
298 the car transect survey), indicating an optimum of approximately 1 hour and a half after  
299 sunset (Table 2 & 3; Fig. 3; ESM 4.2 & ESM 4.5).

300 Some significant effects of the date have been detected for *P. pipistrellus*, *P. kuhlii*, *E.*  
301 *serotinus* and *N. noctula* and along with some species or survey type, an additional quadratic  
302 effect (Table 2 & 3). For the two *Pipistrellus* species, the fixed effect is positive, while for *E.*  
303 *serotinus* it is negative. When looking at fixed effects, this seems to be contrasted between  
304 species, while when looking at a non-linear effect (see ESM 4.3), species exhibit a similar  
305 convex quadratic pattern, with smaller bat pass durations in late July (~200<sup>th</sup> day) and an  
306 increase in bat pass durations after late August (~240<sup>th</sup> day).

307 Weather conditions (humidity, temperature, cloud cover, and wind) rarely influence  
308 bat pass duration, with less than 10% of significant effects. An effect of the bat detector is  
309 detected for *P. pipistrellus* and *Myotis* spp., with the Tranquility Transect detector recording  
310 smaller bat pass durations than the D240x. Ageing and wear of detector are only detected for  
311 data from the car survey and for some species, but with some opposite effects (Table 2 & 3),  
312 and the interaction between bat detector type and age indicates that when significant, this  
313 effect differs among species.

314

#### 315 **4. DISCUSSION**

316 When considering the influence of habitat on bat pass durations, the clutter index  
317 appears to weakly influence, while we detected more effects of the categorical habitat

318 variables. When a significant effect of habitat is detected, as we hypothesized, greater bat  
319 pass durations were recorded in habitats considered as favourable for the species: for *E.*  
320 *serotinus*, heterogeneous agricultural areas including crops and pastures (Catto et al. 1996,  
321 Robinson and Stebbings 1997, Arthur et al. 2014), deciduous forest (Russo and Jones 2003;  
322 Rainho 2007), and water courses (Ciechanowski 2002, Bartonicka et al. 2003, Russo and Jones  
323 2003, Kanuch et al. 2006, Rainho 2007, Arthur et al. 2014); or for *P. pipistrellus*, bodies of  
324 water (Nicholls and Racey 2006, Vandeveldel et al. 2014). Congruently, habitats with smaller  
325 bat pass duration are, for *E. serotinus*, habitats that regularly identify as not selected or with  
326 lower bat activity: urban areas (Davidson-Watts et al. 2006, Arthur et al. 2014) and arable  
327 land (Davidson-Watts et al. 2006, Nicholls and Racey 2006). Surprisingly, for *P. kuhlii*, a  
328 species that exhibits a mid-level of bat activity in urban areas (Vandeveldel et al. 2014) and  
329 that is considered an anthophilous species (Tomassini et al. 2014), we recorded a smaller bat  
330 pass duration in continuous urban areas. Among the hypotheses, for explaining that clutter  
331 index is rarely significant, we can first note that sound transmission can vary among the same  
332 type of habitat, i.e., between forest types of deciduous, coniferous, and mixed (Patriquin et  
333 al. 2003); second, the sound attenuation effect by vegetation density may differ according to  
334 sound frequency studied (Patriquin et al. 2003); and third, we may suspect the opposite  
335 effect of the degree of cluttering of habitat on sound propagation (i.e., attenuation) and the  
336 selection of clutter habitat by some species, such as *Myotis*. Another non-exclusive  
337 hypothesis could be linked to the roughness of the construction of the clutter index. If we  
338 detect a greater effect of habitat type than clutter index, note that we detect effects for only  
339 half of the species, again we can hypothesize the accuracy of the habitat classes (only 8  
340 classes) we built that do not allow consideration, for example, of the maturity of the forest  
341 (Regnery et al. 2013), agricultural intensification (Wickramasinghe et al. 2003), or type of  
342 bank in aquatic habitats (Scott et al. 2010). In addition, the species studied are among the  
343 most generalist species (Lacoeuilhe et al. 2016).

344         As expected, we detected a significant effect of time after sunset in bat pass duration  
345 for half of the species studied. When significant, the pattern is congruent with our  
346 prediction: smaller bat pass durations are recorded in the beginning of the night due to a  
347 greater percentage of individuals leaving the colony to reach foraging sites and then exhibit  
348 commuting flight. A maximum bat pass duration is detected approximately 1 hour and a half

349 after sunset, which matches the activity pattern of individuals outside the roost during the  
350 night, as described by Swift (1980) for *P. pipistrellus* or by Catto et al. (1995) for *E. serotinus*.

351 As predicted, we also detected a variation in bat pass duration within the year for  
352 some species; the non-linear effect (see ESM 4.3) showed a convex quadratic pattern with  
353 smaller bat pass durations after late July (~200<sup>th</sup> day of the year) and an increase of bat pass  
354 durations after early September (~240<sup>th</sup> day of the year). The longer pass durations observed  
355 before the 200<sup>th</sup> day of the year match the lactation period: the parturition of *P. pipistrellus* is  
356 known to occur over a ten-day period in late June (~170<sup>th</sup> day of the year), lactation lasts 4-5  
357 weeks, and weaning was completed when the adults left the roost approximately 2 weeks  
358 later (~210<sup>th</sup> day of the year) (Swift and Racey 1981, Dietz et al. 2007). Catto and Racey  
359 (1995) found the lactation period for *E. serotinus* to be from the end of June to the third  
360 week of July (i.e., 180 to 200<sup>th</sup> day of the year). Jones (1995) found a similar pattern for *N.*  
361 *noctula*, where most of the females were lactating between 2 June and 19 July. The increase  
362 of bat pass durations after the 240<sup>th</sup> day of the year (early September) matches the seasonal  
363 weight changes observed in bats and related to fat deposition, particularly brown adipose  
364 tissue, which is a prerequisite for hibernation (Arévalo et al. 1990).

365 We detected relatively few significant effects of weather conditions, but it should be  
366 noted that the requirement of the FBMP implies that records are performed only when  
367 weather conditions are considered as favourable (see Material and Methods); so, our dataset  
368 includes a limited range of weather conditions. An effect of the bat detector was detected for  
369 *P. pipistrellus* and *Myotis* spp., and as expected, the more directional detector (Tranquility  
370 Transect) recorded smaller bat pass durations. Ageing effects and the interactions between  
371 bat detector type and the age of detector are not easy to read because the ageing of the  
372 detector is partially related to volunteer experience (as volunteers have their own materials).  
373 Note that in these two protocols (car survey transect and count point), the time spent  
374 outside by the equipment, and thus exposure to weather such as humidity, is relatively short  
375 explaining probably the non-detection of aging of detector.; In a third protocol under  
376 development in the FBMP, based on a stationary detector (SM2, SM3, SM4 Wildlife Acoustic,  
377 USA) running in the field for several weeks per year, we observed real microphone failures  
378 after one to two years of survey.

379

380 We found results that confirm the three main hypotheses that we formulated on bat pass  
381 duration: (i) longer bat pass durations within selected habitats for foraging; (ii) smaller bat  
382 pass durations in the first minutes after sunset; and (iii) longer bat pass durations during  
383 periods with important energetic demands. While we did not detect results that clearly  
384 reject our hypotheses, we did, however, not simultaneously detect these effects for each  
385 species. For *P. pipistrellus*, and *E. serotinus* to a lesser extent, our main predictions were  
386 found; note that *P. pipistrellus* is by far the species for which we have the largest number of  
387 measures (~8000 and ~10000 measures, respectively, for the count point survey and the car  
388 transect survey). This volume of sample appears impressive according to the recorded  
389 sample of 4-6 minutes of recording per point, manual identification and manual measure of  
390 bat pass duration; however, the recent reduced cost of acoustic recorders has resulted in an  
391 exponential development of Passive Acoustic Monitoring (PAM) involving, for example, a  
392 third protocol in the FMBP. PAM produces considerable amounts of data, while before we  
393 recorded 4-6 minutes per site in the two previous protocols, now these detectors allow  
394 recording the entire night; so, regularly, several hundred bat passes could be recorded per  
395 night, site and species (see for example Charbonnier et al. 2014), even in habitats with  
396 regularly low bat activity, such as agriculture land (see Millon et al. 2015). In addition to the  
397 arrival of a new generation of passive recorders on the market, the development of a  
398 software toolbox (Bas et al. in press) allows the detection of every sound event and extracts  
399 numerous features, so that sounds could be well characterized during the same process and  
400 used to produce species identification and characteristics of the call (buzz, social call, etc.).  
401 Thus, in the near future, we expect that analysing bat pass durations will not be limited by  
402 the amount of data.

403 Our results suggest that bat pass duration is a simple and easy measure that can be  
404 used as a position indicator on a gradient between commuting vs. foraging behaviour.  
405 However, in studies and environmental expertise investigating the differential use of habitats  
406 by bats, the traditional measure of bat activity (i.e., number of bat passes per time unit)  
407 could be, for example, weighted by bat pass duration for giving more weight to events with a  
408 potentially greater link to foraging behaviour. Our results obtained by correlative approaches  
409 could be validated via field experiments based on 4 microphone array recordings to model  
410 flight behaviour (Bas et al. 2015). Such an approach will allow perform direct relationship

411 between a flight behaviour (commuting vs foraging) and echolocation calls characteristics  
412 (including bat pass duration).

413

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424

## 425 **REFERENCES**

426

427 Adams AM, Jantzen MK, Hamilton RM, Fenton MB. 2012. Do you hear what I hear?  
428 Implications of detector selection for acoustic monitoring of bats. *Method Ecol Evol.* 3:992–  
429 998.

430

431 Anthony ELP, Stack MH, Kunz TH. 1981. Night roosting and the nocturnal time budget of the  
432 little brown bat, *Myotis lucifugus*: effects of reproductive status, preys density, and  
433 environmental conditions. *Oecologia.* 51:151-156.

434

435 Arévalo F, Burgos MJ, del Hoyo N, López-Luna P. 1990. Seasonal variations in the lipid  
436 composition of white and brown tissues in the bat *Pipistrellus pipistrellus*. *Comp Biochem*  
437 *Phys. B.* 95(3):535-539.

438

439 Arlettaz R, Jones J, Racey PA. 2001. Effect of acoustic clutter on prey detection by bats.  
440 *Nature.* 414:742–745.

441

442 Arthur L, Lemaire M, Dufrière L, Le Viol I, Julien JF, Kerbiriou C. 2014 Understanding bat-  
443 habitat associations and the effects of monitoring on long-term roost success using a  
444 volunteer dataset. *Acta Chiropterol.* 16:397-411.  
445

446 Azam C., Le Viol I., Julien J.-F., Bas Y., Kerbiriou C. 2016. Disentangling the relative effect of  
447 light pollution, impervious surfaces and intensive agriculture on bat activity with a national-  
448 scale monitoring program. *Landscape Ecology.* 31(10), 2471–2483

449 Baerwald EF, Barclay RMR. 2009. Geographic Variation in Activity and Fatality of Migratory  
450 Bats at Wind Energy Facilities. *J Mammal* 90(6):1341-1349.

451

452 Barataud M. 2015. Acoustic Ecology of European Bats, Species identification, study of their  
453 habitat and foraging behavior. Biotope, Mèze; Muséum national d’histoire naturelle, Paris  
454 (Inventaires et biodiversité Series), 352 p.  
455

456 Bartonicka T, Zukal J. 2003. Flight activity and habitat use of four bat species in a small town  
457 revealed by bat detectors. *Folia Zool.* 52:155-166.  
458

459 Bas Y, Charbonnier M, Kiri Ing R, Julien JF. 2015. Using acoustic flight path reconstruction to  
460 distinguish foraging and commuting behaviour, then predicting it a posteriori from call  
461 features. 4th Berlin Bat meeting: Movement Ecology of Bats Mars2015. Berlin Deutschland.  
462

463 Britzke ER, Slack BA, Armstrong MP, Loeb SC. 2010. Effects of orientation and  
464 weatherproofing on the detection of bat echolocation calls. *J. Fish Wild Manag.* 1:136–141.  
465

466 Burt J. 2006. Syrinx a software for real time spectrographic recording, analysis and playback  
467 of sound. Available from: <http://www.syrinxpc.com>.  
468

469 Catto CMC, Racey PA, Stephenson PJ. 1995. Activity patterns of the serotine bat (*Eptesicus*  
470 *serotinus*) at a roost in southern England *J Zool.* 235:635–644.  
471



472 Catto C, Hutson AM, Racey PA, Stephenson PJ. 1996. Foraging behaviour and habitat use of  
473 the serotine bat (*Eptesicus serotinus*) in southern England J Zool. 238:623-633.  
474

475 Charbonnier Y, Barbaro L, Theillout A, Jactel H. 2014. Numerical and Functional Responses of  
476 Forest Bats to a Major Insect Pest in Pine Plantations. PLoS ONE. 9(10): e109488.  
477 doi:10.1371/journal.pone.0109488  
478

479 Ciechanowski M. 2002. Community structure and activity of bats (Chiroptera) over different  
480 water bodies. Mamm Biol. 67:276-285.  
481

482 Ciechanowski M, Zajac T, Bilas A, Dunajski R. 2007. Spatiotemporal variation in activity of bat  
483 species differing in hunting tactics: effects of weather, moonlight, food abundance, and  
484 structural clutter. Rev Can Zool. 85:1249–1263.  
485

486 Cleveland CJ, Betke M, Federico P, Frank JD, Hallam TG, Horn J, López Juan D, McCracken GF,  
487 Medellín RA, Moreno-Valdez A, Sansone CG, Westbrook JK, Kunz TH. 2006. Economic value of  
488 the pest control service provided by Brazilian free-tailed bats in south-central Texas. Front  
489 Ecol Environ. 4(5):238-243.  
490

491 Collins J, Jones G. 2009. Differences in Bat Activity in Relation to Bat Detector Height:  
492 Implications for Bat Surveys at Proposed Windfarm Sites. Chiropterol. 11(2):343-350.  
493

494 Cramel Y, Safriel U. 1998. Habitat use by bats in a Mediterranean ecosystem in Israel,  
495 conservation implication. Biol Cons. 84:245-250.  
496

497 Crawley MJ. 2009. The R book. John Wiley & Sonc, Chicago, USA.  
498

499 Davidson-Watts I, Walls S, Jones G. 2006. Differential habitat selection by *Pipistrellus*  
500 *pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic  
501 species of echolocating bats. Biol Cons. 133:118-127.  
502

503 Dietz C, Nill D, Von Helversen O, Lina PH., Hutson AM. 2007. Bats of Britain, Europe and  
504 Northwest Africa. Franck-Kosmos Verlags, London, UK, pp. 400pp.  
505

506 Fox J, Monette G. 1992. Generalized collinearity diagnostics. J Am Statist Assoc. 87:178–183.  
507

508 Griffin DR. 1971. The importance of atmospheric attenuation for the echolocation of bats  
509 (Chiroptera), Anim Behav. 19(1):55-61.  
510

511 Hayes JP. 1997. Temporal Variation in Activity of Bats and the Design of Echolocation-  
512 Monitoring Studies. J Mam. 78(2):21.  
513

514 Herzog C. Britzke E. 2009. Progress Update for Acoustic Monitoring of Summer Bats.  
515 Available from:  
516 <http://whitenosesyndrome.org/sites/default/files/resource/herzognysdecbritzkeusaceprogre>  
517 [ssupdateacousticmonitoringsummerbats](http://whitenosesyndrome.org/sites/default/files/resource/herzognysdecbritzkeusaceprogre)  
518

519 Holderied MW, Von Helversen O. 2003. Echolocation range and wingbeat period match in  
520 aerial-hawking bats. Proc R Soc B: Biol. Sci. 270:2293–2299.  
521

522 Hötker H, Thomsen K-M, Jeromin H. 2006. Impacts on biodiversity of exploitation of  
523 renewable energy sources: the example of birds and bats - facts, gaps in knowledge,  
524 demands for further research, and ornithological guidelines for the development of  
525 renewable energy exploitation. Michael-Otto-Institut im NABU, Bergenhusen.  
526

527 Jones G. 1995. Flight performance, echolocation and foraging behaviour in noctule bats  
528 *Nyctalus noctula*. J. Zool. 237:303–312.  
529

530 Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA. 2009. Carpenoctem: the importance of  
531 bats as bioindicators. Endangered Species Research. 8:93–115.  
532

533 Kanuch P, Danko S, Celuch M, Kristin A, Pjencak P, Matis S, Smid J. 2006. Relating bat species  
534 presence to habitat features in natural forests of Slovakia (Central Europe). *Mamm Biol.*  
535 73:147-155.  
536

537 Kerbiriou C, Bas Y, Dufrêne L, Robert A, Julien JF. 2010. Long term trends monitoring of bats,  
538 from biodiversity indicator production to species specialization assessment. *Society for*  
539 *Conserv. Biol.* In: 24th Annual Meeting, 3–7 July 2010, Edmonton, Alberta, Canada.  
540

541 Kerbiriou C., Azam C., Touroult J., Marmet J., Julien J.F., Pellissier V., 2018a. Common bats are  
542 more abundant within Natura 2000 areas. *Biological Conservation* 217: 66-74  
543

544 Kerbiriou C., Parisot-Laprun M. Julien J.-F. 2018b. Potential of restoration of gravel-sand pits  
545 for Bats. *Ecological Engineering* In press.  
546

547 Kunz, TH, Braun de Torrez E, Bauer D, Lobo T, Fleming TH. 2011. Ecosystem services  
548 provided by bats. *Ann. NY Acad. Sci.* 1223:1–38.  
549

550 Lacoëuilhe A, Machon N, Julien JF, Le Bocq A, Kerbiriou C 2014. The Influence of Low  
551 Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE.* 9(10):  
552 e103042. doi:10.1371/journal.pone.0103042  
553

554 Lacoëuilhe A, Machon N, Julien JF, Kerbiriou C. 2016. Effects of hedgerows on bats and bush  
555 crickets at different spatial scales. *Acta Oecol.* 71:61–72.  
556

557 Limpens HJGA, McCracken GF. 2002 Choosing a Bat Detector: Theoretical and Practical  
558 Aspects 28-37 In Brigham M., Kalko E.K.V., Jones G., Parsons S., Limpens H.J.G.A. (eds) *Bat*  
559 *Echolocation Research, tools, techniques and analysis.*  
560

561 Limpens HJGA, McCracken GF. 2004. Choosing a bat detector: theoretical and practical  
562 aspects. *Bat Echolocation Research: Tools, Techniques, and Analysis* eds Brigham RM, Kalko

563 EKV, Jones G, Parsons S, Limpens HJGA, pp. 28–37, Bat Conservation International, Austin,  
564 TX.

565

566 MacSwiney G, Clarke FM, Racey, PA. 2008. What you see is not what you get: the role of  
567 ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. J  
568 Appl Ecol. 45:1364–1371.

569

570 Mickleburgh SP, Hutson AM, Racey PA. 2002. A review of the global conservation status of  
571 bats. Oryx. 36:18-34.

572

573 Millon L, Julien J-F, Julliard R, Kerbiriou C. 2015. Bat activity in intensively farmed landscapes  
574 with wind turbines and offset measures. Ecol Eng. 75:250–257.

575

576 Nicholls B, Racey PA. 2006 Habitat selection as a mechanism of resource partitioning in two  
577 cryptic bat species *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*. Ecography. 29:697-708.

578

579 Obrist MK, Boesch R, Flückiger PF. 2004. Variability in echolocation call design of 26 Swiss bat  
580 species: consequences, limits and options for automated field identification with a synergetic  
581 pattern recognition approach. Mammalia. 68(4):307-322.

582

583 O'Donnell CFJ. 2000. Influence of season, habitat, temperature, and invertebrate availability  
584 on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New  
585 Zeal J Zool. 27(3):207-221.

586

587 Parsons KN, Jones G, Greenaway F. 2003. Swarming activity of temperate zone  
588 microchiropteran bats: effects of season, time of night and weather conditions. J Zool.  
589 261(3):257-264.

590

591 Patriquin KJ, Hogberg LK, Chruszcz BJ, Barclay RMR. 2003. The influence of habitat structure  
592 on the ability to detect ultrasound using bat detectors. Wildlife Soc B. 31(2):475-481.

593

594 Rainho A. 2007. Summer foraging habitats of bats in a Mediterranean region of the Iberian  
595 Peninsula. *Acta Chiropterol.* 9:171-181.  
596

597 Regnery B, Couvet D, Kubarek L, Julien J-F, Kerbiriou C. 2013. Tree microhabitats as indicators  
598 of bird and bat communities in Mediterranean forests. *Ecological Indicators.* 34:221-230  
599

600 Robinson MF, Stebbings RE. 1997. Home range and habitat use by serotine bat, *Eptesicus*  
601 *serotinus*, *J Zool.*243:117-136.  
602

603 Roche N, Catto C, Langton S, Aughney T, Russ J. 2005. Development of a Car-Based Bat  
604 Monitoring Protocol for the Republic of Ireland. *Irish Wildlife Manuals*, No. 19. National Parks  
605 and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin,  
606 Ireland.  
607

608 Roche N, Langton S. Aughney T. Russ J. M. Marnell F. Lynn D, Catto. C. 2011. A car-based  
609 monitoring method reveals new information on bat populations and distributions in Ireland.  
610 *Anim Cons.* 14:642–651.  
611

612 Rowse EG, Harris S, Jones G 2016. The Switch from Low-Pressure Sodium to Light Emitting  
613 Diodes Does Not Affect Bat Activity at Street Lights. *PLoS ONE* 11(3): e0150884.  
614

615 Ruedi M. 1993. Variations de la fréquentation de gîtes nocturnes par *Myotis daubentoni*  
616 pendant la période de reproduction. Rôle des précipitations et de la température.  
617 *Mammalia.* 57:307-315.  
618

619 Russ J, Briggs P, Wembridge D. 2008. The Bats & Roadside Mammals Survey Bat Conservation  
620 Trust. Final Report on Fourth Year of Study. Available from:  
621 <https://sites.google.com/site/ibatsresources/publications>.  
622

623 Russo D, Jones G. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera)  
624 from Italy by analysis of time-expanded recordings of echolocation calls. *J Zool.* 258:91–103.  
625

626 Russo D, Jones G. 2003. Use of foraging habitats by bats in a Mediterranean area determined  
627 by acoustic surveys: conservation implications. *Ecography*. 26:197–209.  
628

629 Schielzeth H. 2010 Simple means to improve the interpretability of regression coefficients.  
630 *Methods Ecol Evol*. 1:103–113.  
631

632 Sherwin RE, Gannon WL, Haymond S. 2000. The efficacy of acoustic techniques to infer  
633 differential. Use of habitat by bats. *Acta Chiropterol*. 2:145-153.  
634

635 Schnitzler HU, Moss CF, Denzinger A. 2003. From spatial orientation to food acquisition in  
636 echolocating bats. *Trends Ecol Evol*. 18:386–394.  
637

638 Stahlschmidt, P. & Brühl, C.A. (2012) Bats as bioindicators – the need of a standardized  
639 method for acoustic bat activity surveys. *Methods Ecol and Evol*. 3:503–508.  
640

641 Stone EL, Jones G, Harris S. 2009. Street lighting disturbs commuting bats. *Curr. Biol*.  
642 19:1123–1127.  
643

644 Swift SM. 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in North-east  
645 Scotland. *J Zool*. 190:285-295.  
646

647 Swift S, Racey P. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus*  
648 *pipistrellus*) from year to year *J Reprod Fertil*. 61:123-129.  
649

650 Swift S, Racey P. 2002. Gleaning as a foraging strategy in Natterer's bat *Myotis nattereri*.  
651 *Behav Ecol Sociobiol*. 52:408–416.  
652

653 Tomassini A, Colangelo P, Agnelli P, Jones G, Russo D. 2014. Cranial size has increased over  
654 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or  
655 urbanization? *J Biogeogr*. 41:944–953.  
656

657 Tibbels AE, Kurta A. 2003. Bat activity is low in thinned and unthinned stands of red pine. Can  
658 J Forest Res. 33:2436–2442.

659

660 Vandeveldde JC, Bouhours A, Julien JF, Couvet C, Kerbiriou C. 2014. Activity of European  
661 common bats along railway verges. Ecol Eng. 64:49-56.

662

663 Waters DA, Walsh AL. 1994. The influence of bat detector brand on the quantitative  
664 estimation of bat activity. Bioacoustic 5:205-221

665

666 Weller T, Zabel CJ 2002. Variation in Bat Detections due to Detector Orientation in a Forest.  
667 Wildlife SocBul. 30:922-930

668

669 Wickramasinghe LP, Harris S, Jones G, Vaughan N. 2003. Bat activity and species richness on  
670 organic and conventional farms: impact of agricultural intensification. J App Ecol. 40:984–  
671 993.

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673

674 **Table 1.** Number of bat calls recorded according to type of survey. Bold indicates the taxa  
 675 studied specifically thereafter.

676

	Count point survey	Car transect survey
<i>Pipistrellus kuhlii</i>	805	981
<i>Pipistrellus pipistrellus</i>	8117	11132
<i>Eptesicus serotinus</i>	130	713
<i>Nyctalus leisleri</i>	226	531
<i>Nyctalus noctula</i>	143	414
<i>Myotis ssp.</i>	1131	274

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679 **Table 2.** Averaged partial regression coefficient and p-value from GLMM of the fixed effects  
 680 included in the analysis performed on data from the car transect survey. Bold indicates a P-  
 681 value < 0.05.

682

	<i>P. pipistrellus</i>	<i>P. kuhlii</i>	<i>E. serotinus</i>	<i>N. Leisleri</i>	<i>N. noctula</i>	<i>Myotis ssp</i>
Clutter index	$P=0.102$	$P=0.183$	$P=0.311$	<b><math>P=0.024</math></b> <b><math>\beta=0.063</math></b>	$P=0.089$	$P=0.967$
Time after sunset	<b><math>P&lt;0.001</math></b> <b><math>\beta=0.074</math></b>	$P=0.151$	<b><math>P=0.001</math></b> <b><math>\beta=0.111</math></b>	$P=0.426$	$P=0.198$	$P=0.582$
Time after sunset <sup>2</sup>	<b><math>P=0.006</math></b> <b><math>\beta=-0.046</math></b>	<b><math>P=0.004</math></b> <b><math>\beta=-0.066</math></b>	<b><math>P=0.002</math></b> <b><math>\beta=-0.061</math></b>	$P=0.910$	$P=0.702$	$P=0.908$
Date	<b><math>P&lt;0.001</math></b> <b><math>\beta=0.033</math></b>	$P=0.775$	<b><math>P=0.031</math></b> <b><math>\beta=-0.082</math></b>	$P=0.281$	$P=0.439$	$P=0.071$
Date <sup>2</sup>	<b><math>P&lt;0.001</math></b> <b><math>\beta=0.081</math></b>	$P=0.652$	$P=0.043$	$P=0.226$	$P=0.401$	$P=0.572$
Temperature	$P=0.599$	$P=0.722$	<b><math>P=0.001</math></b> <b><math>\beta=0.095</math></b>	$P=0.059$	$P=0.179$	$P=0.625$
Humidity	$P=0.110$	$P=0.670$	$P=0.457$	$P=0.193$	$P=0.958$	$P=0.782$
Cloud cover	$P=0.121$	$P=0.798$	$P=0.240$	$P=0.790$	$P=0.953$	$P=0.793$
Wind	$P=0.933$	$P=0.163$	$P=0.700$	$P=0.837$	$P=0.887$	$P=0.477$
Bat detector	<b><math>P&lt;0.001</math></b> <b><math>D240x&gt;TT</math></b>	$P=0.751$	$P=0.177$	$P=0.163$	$P=0.468$	$P=0.851$
Age	<b><math>P=0.018</math></b> <b><math>\beta=0.012</math></b>	$P=0.055$	$P=0.436$	$P=0.068$	<b><math>P=0.007</math></b> <b><math>\beta=-0.211</math></b>	<b><math>P=0.019</math></b> <b><math>\beta=-0.026</math></b>
Bat detector : Age	<b><math>P=0.004</math></b> <b><math>\beta_{TT}=-0.366</math></b>	$P=0.460$	<b><math>P=0.023</math></b> <b><math>\beta_{TT}=0.225</math></b>	$P=0.455$	<b><math>P=0.039</math></b> <b><math>\beta_{TT}=0.285</math></b>	$P=0.161$
Car speed	<b><math>P&lt;0.001</math></b> <b><math>\beta=-0.145</math></b>	$P=0.280$	$P=0.857$	$P=0.275$	$P=0.051$	$P=0.905$

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686 **Table 3.** Averaged partial regression coefficient and p-value from GLMM of the fixed effects  
 687 included in the analysis performed on data from the count point survey. Bold indicates a P-  
 688 value < 0.05.

689  
 690

	<i>P. pipistrellus</i>	<i>P. kuhli</i>	<i>E. serotinus</i>	<i>N. Leisleri</i>	<i>N. noctula</i>	<i>Myotis ssp</i>
Clutter index	<i>P</i> =0.527	<i>P</i> =0.890	<b><i>P</i>=0.017</b> <b><i>β</i>=0.163</b>	<i>P</i> =0.574	<i>P</i> =0.389	<i>P</i> =0.245
Time after sunset	<b><i>P</i>=0.010</b> <b><i>β</i>=0.059</b>	<i>P</i> =0.057	<b><i>P</i>=0.003</b> <b><i>β</i>=0.391</b>	<i>P</i> =0.414	<b><i>P</i>=0.006</b> <b><i>β</i>=-0.312</b>	<i>P</i> =0.727
Time after sunset <sup>2</sup>	<b><i>P</i>&lt;0.001</b> <b><i>β</i>=-0.037</b>	<i>P</i> =0.079	<i>P</i> =0.233	<i>P</i> =0.528	<i>P</i> =0.798	<i>P</i> =0.244
Date	<b><i>P</i>=0.012</b> <b><i>β</i>=0.052</b>	<b><i>P</i>=0.015</b> <b><i>β</i>= 0.107</b>	<i>P</i> =0.298	<i>P</i> =0.748	<i>P</i> =0.393	<i>P</i> =0.818
Date <sup>2</sup>	<i>P</i> =0.926	<i>P</i> =0.475	<i>P</i> =0.636	<i>P</i> =0.161	<b><i>P</i>=0.001</b> <b><i>β</i>=-0.538</b>	<i>P</i> =0.927
Temperature	<i>P</i> =0.214	<i>P</i> =0.849	<i>P</i> =0.892	<i>P</i> =0.858	<i>P</i> =0.166	<i>P</i> =0.569
Humidity	<b><i>P</i>=0.011</b> <b><i>β</i>=0.054</b>	<i>P</i> =0.063	<i>P</i> =0.285	<b><i>P</i>=0.022</b> <b><i>β</i>=-0.200</b>	<i>P</i> =0.349	<i>P</i> =0.547
Cloud cover	<b><i>P</i>=0.018</b> <b><i>β</i>=-0.052</b>	<i>P</i> =0.240	<i>P</i> =0.269	<i>P</i> =0.811	<i>P</i> =0.934	<i>P</i> =0.013
Wind	<i>P</i> =0.938	<i>P</i> =0.910	<i>P</i> =0.452	<i>P</i> =0.066	<i>P</i> =0.298	<b><i>P</i>=0.032</b> <b><i>β</i>=0.087</b>
Bat detector	<b><i>P</i>&lt;0.001</b> <b><i>D</i>240x&gt;<i>TT</i></b>	<i>P</i> =0.214	<i>P</i> =0.479	<i>P</i> =0.160	<i>P</i> =0.597	<b><i>P</i>&lt;0.001</b> <b><i>D</i>240x&gt;<i>TT</i></b>
Age	<i>P</i> =0.282	<i>P</i> =0.657	<i>P</i> =0.524	<i>P</i> =0.202	<i>P</i> =0.563	<i>P</i> =0.567
Bat detector : Age	<b><i>P</i>&lt;0.001</b> <b><i>β</i><sub>TT</sub>=-0.256</b>	<i>P</i> =0.260	<i>P</i> =0.986	<b><i>P</i>=0.012</b> <b><i>β</i><sub>TT</sub>=-0.518</b>	<i>P</i> =0.731	<b><i>P</i>=0.011</b> <b><i>β</i><sub>TT</sub>=-0.208</b>

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693 **Table 4.** Effects of habitat type on bat call duration. Bold indicates P-value < 0.05; for effects  
 694 of the other variable that were similar to those found with clutter index analysis, see ESM 4.5  
 695 for details.

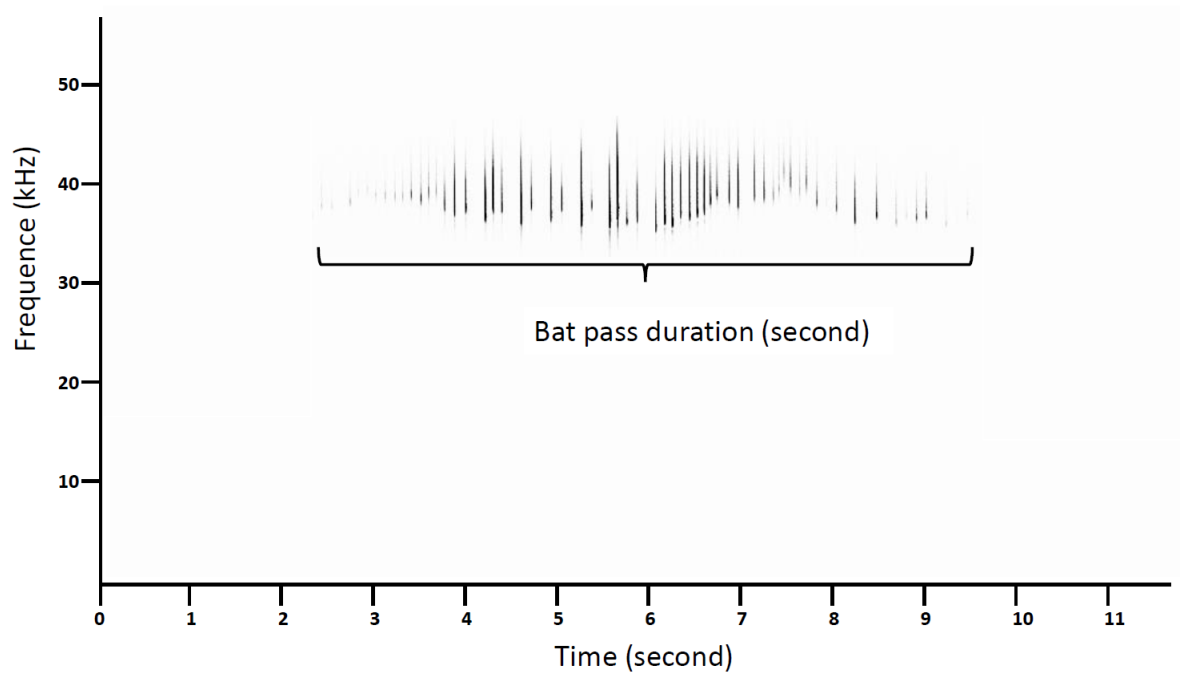
696

	<i>P. pipistrellus</i>	<i>P. kuhli</i>	<i>E. serotinus</i>	<i>N. Leisleri</i>	<i>N. noctula</i>	<i>Myotis ssp</i>
Car transect survey	<b><i>P</i>&lt;0.0001</b>	<i>P</i> =0.52	<b><i>P</i>=0.027</b>	<i>P</i> =0.45	<i>P</i> =0.67	<i>P</i> =0.25
Count point survey	<i>P</i> =0.81	<b><i>P</i>=0.021</b>	<b><i>P</i>=0.044</b>	<b><i>P</i>=0.002</b>	<i>P</i> =0.46	<i>P</i> =0.37

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701 **Figure 1.** Bat pass duration

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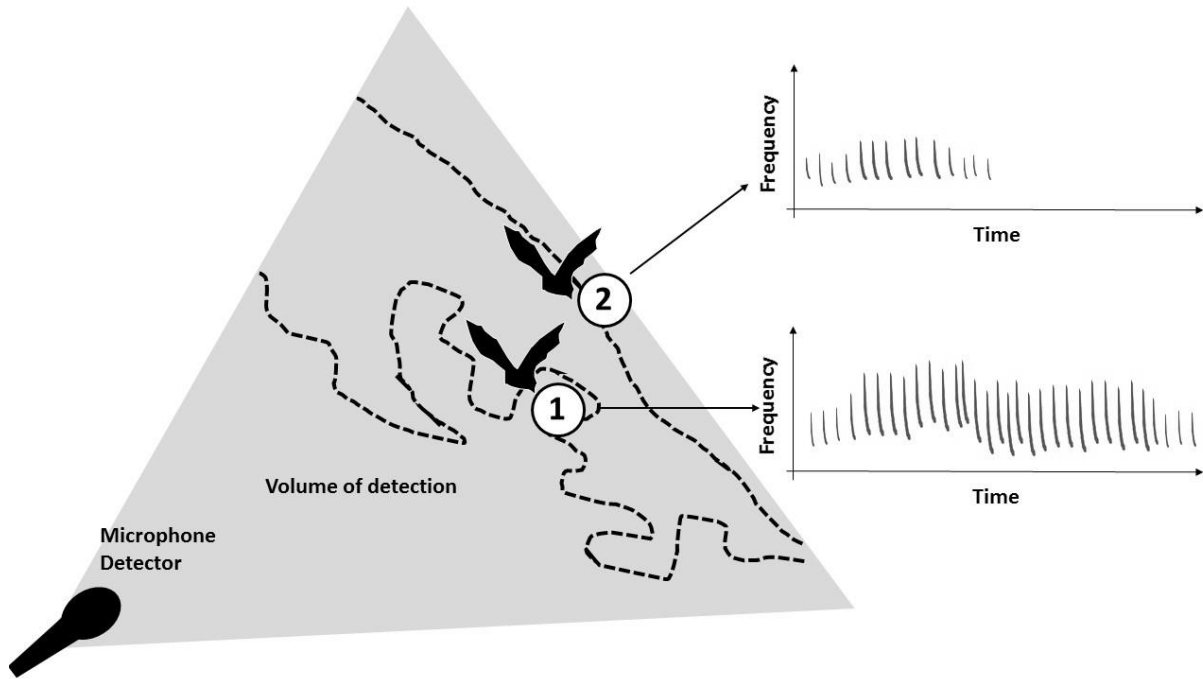
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706 **Figure 2.** Difference of bat pass duration according to the type of trajectory: (1) a sinuous  
707 trajectory exhibited when a bat forages; and (2) a strait trajectory when a bat exhibits a  
708 commuting flight.

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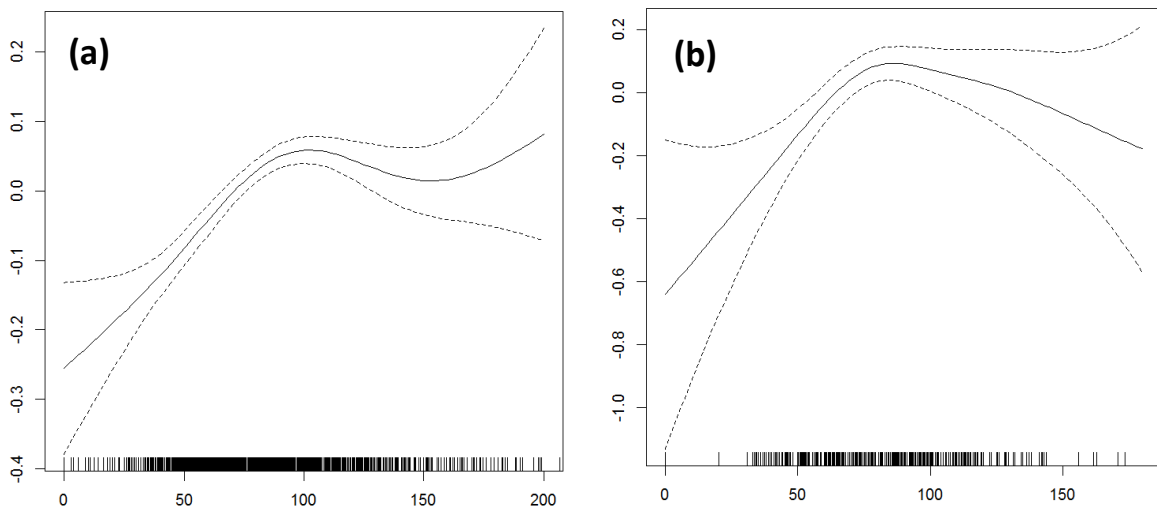
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713 **Figure 3.** Variation of bat pass duration (scaled values) within early night (expressed as  
714 minutes after sunset): (a) *P. pipistrellus*, and (b) *E. serotinus*. For GAMM modelling on data  
715 from the car transect survey. See the supplementary material for analyses from the count  
716 point survey. Rugs on the X-axis indicate values present at least once in the data set.

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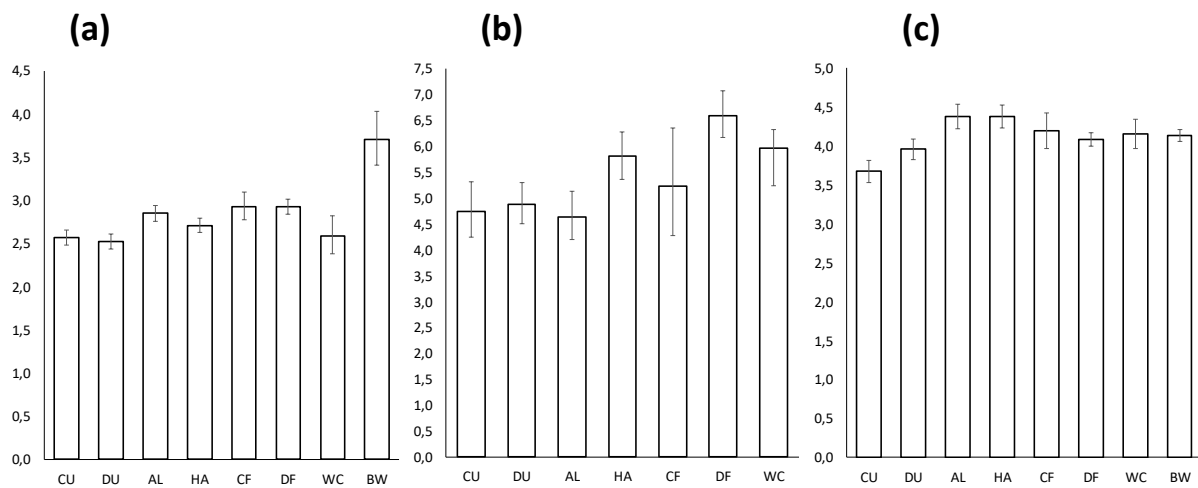
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722 **Figure 4.** Variation in bat pass duration (for adjusted to other co-variables included in the  
723 model, see supplementary material ESM 4.4) across habitat type: (a) *P. pipistrellus* car  
724 transect survey; (b) *E. serotinus* car transect survey; and (c) *P. kuhlii* count point survey.

725 Habitat type: continuous urban areas (CU), discontinuous urban areas (DU), arable land (AL),  
726 heterogeneous agricultural areas (HA), coniferous forest (CF), deciduous forest (DF), water  
727 courses (WC), and bodies of water (BW).

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