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# Potential of bat pass duration measures for studies of bat activity

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**ABSTRACT**

Acoustic detectors have become increasingly used by bat workers to investigate bat ecology and assess the impacts of anthropogenic pressures. Within these studies, the metric used, 'bat activity', is based on the number of bat passes, without considering the bat pass duration (i.e. each event of a bat detected within the range of an ultrasonic detector). We expected that bat pass duration may contain information about site quality in terms of foraging potential. Because bats are expected to have a more sinuous trajectory and slower velocity when they exhibit foraging behaviour, as opposed to commuting behaviour, we hypothesize a longer bat pass duration in favourable habitats; during seasons with important energetic demands; or during night peak activity. We used datasets from a large-scale acoustic bat survey ($n = 2890$ sites), with a total of 24,597 bat pass measures from 6 taxa, and performed GLMM modelling. We detected a significant effect of habitat type on bat pass duration for five taxa. Shorter bat pass durations were detected at the beginning of the night. We detected longer pass durations during the lactation period or just before hibernating, while weather conditions or ageing and wear of the detector rarely influenced bat pass duration. Bat pass duration appears to be a simple and easy measure for position calls on a gradient between commuting vs. foraging behaviour. We suggest that the traditional measure of bat activity may be weighted by bat pass duration by giving more weight to events with potentially stronger links to foraging behaviour.

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Bats calls; bat pass duration; bat community; intra species variation

## Introduction

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

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We have witnessed an exponential increase in the knowledge of the acoustic identification of bat species (Russo and Jones 2002; Obrist et al. 2004; Barataud 2015). In addition to this taxonomic knowledge, the cost of ultrasonic recorders has reduced and has resulted in the development of passive acoustic sensors that are able to record throughout the night. Acoustic detectors have been used to increase inventory completeness in bat assemblage studies (MacSwiney et al. 2008), and these methods have been proposed to form part of a single standardized monitoring protocol (Stahlschmidt and Brühl 2012). In addition, contrary to capture methods, radio tracking methods, roost surveys and the use of ultrasonic detectors, all non-intrusive methods, are often the only logistically feasible methods (Stahlschmidt and Brühl 2012). Thus, since the two last decades, these approaches have been widely used by researchers working for environmental consulting firms or government agencies (Adams et al. 2012), for example, during the evaluation of development projects. Acoustic detectors have become increasingly used by academic researchers to investigate the differential use of habitats by bats (Sherwin et al. 2000; Russo and Jones 2003) or to test various anthropogenic pressures such as the following: (i) agricultural intensification based on high levels of agrochemicals (Wickramasinghe et al. 2003); (ii) non-lethal impacts of wind turbines, such as the disturbance of commuting and migration routes and local habitat loss (Hötker et al. 2006; Millon et al. 2015); or (iii) artificial light at night (Stone et al. 2009; Azam et al. 2016). Finally, monitoring of bat populations based on nocturnal acoustic standardized recordings are under development in an increasing number of countries, including the UK (Russ et al. 2008), USA (Herzog and Britzke 2009), Ireland (Roche et al. 2011) and France (Kerbiriou et al. 2010).

In all these studies, the measure used, ‘bat activity’, is based on the number of bat passes. The metrics used for assessing bat activity vary among studies; for example, Hayes (1997) used the number of files recorded by bat detectors that include echolocation calls, while Tibbels and Kurta (2003) used the number of pulses in all files that were recorded in one night. In acoustic studies using time expansion bat detectors, a bat pass is defined as one or more bat echolocation call during a record of sound at a × 10 time expansion (Regnery et al. 2013). In these cases, the duration of the record is predefined by the ultra-sound detector (e.g. 0.32 s for the Tranquility Transect (David Bale, Courtpan. Design Ltd, Cheltenham, UK), see Roche et al. 2011; Regnery et al. 2013; Lacoeuilhe et al. 2014). Other studies calculated bat activity as the number of bat passes per night, and a bat pass was defined as a single or several bat calls emitted during a fixed interval (e.g. 5 s in Millon et al. (2015) study). Relative feeding activity is sometimes measured using a ‘buzz ratio’ (Rowse et al. 2016), which is the proportion of call sequences that included ‘feeding buzzes’ (buzzes are signals emitted by bats just before they try to catch insects, or when they drink or before landing). However, the ratio of feeding buzzes in a sample is regularly very low (~1% of whole contacts in the data-set of the French bat-monitoring programme).

Curiously, at the time of writing, it appears that the measure of bat pass duration, (i.e. each event (expressed in seconds) of a bat detected within the detection range of the ultrasonic detector, Figure 1) has never been used. We expected this measure may contain information about site quality in terms of foraging potential. Because bats are expected to have a more sinuous trajectory and slower velocity when they exhibit foraging behaviour, as opposed to commuting behaviour, between their roost and foraging areas or between two patch of foraging areas (Figure 2), we thus hypothesize the following: (i) that sites or habitats with high levels of food resources may be characterized by sequences with longer bat pass

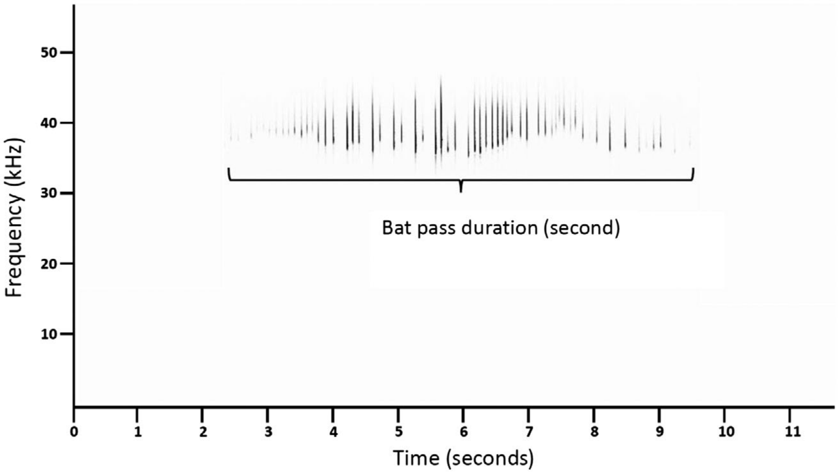

**Figure 1.** Bat pass duration.

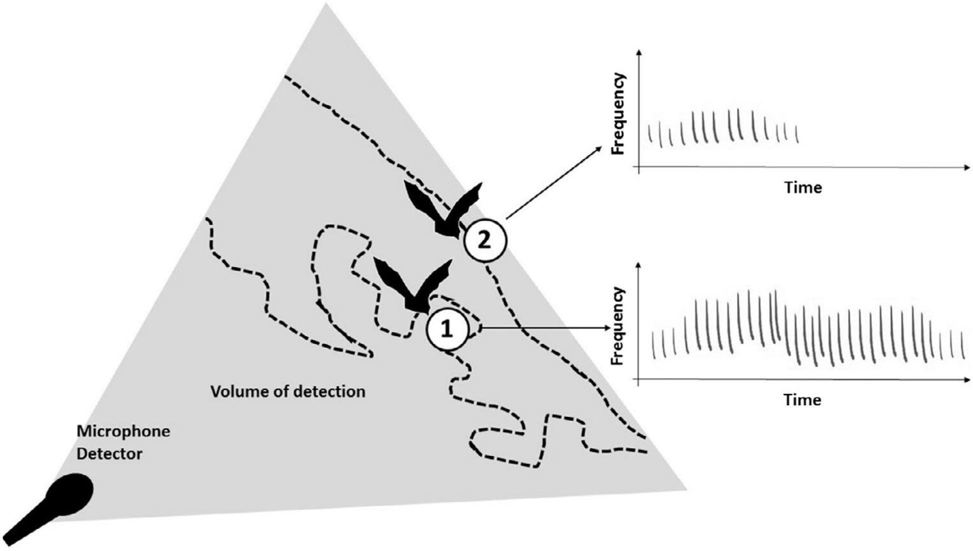

**Figure 2.** Differences in bat pass duration according to the type of trajectory: (1) a sinuous trajectory when a bat forages; and (2) a straight trajectory when a bat is in a commuting flight.

duration on average than sites with low foraging resources; (ii) that bat pass duration may be lower in the first minutes after sunset when bats commute between their roost to their foraging areas; and (iii) that the pass duration may vary, with a longer pass duration on average during the spring when important energetic demands are imposed by pregnancy (Swift 1980; Anthony et al. 1981; Ruedi 1993) or in the autumn period when bats accumulate fat before hibernation.

However, acoustic recordings (here, the bat pass duration) depend not only on the specificity of the transmitter (here the bats) but also on the receiver (here, the detector) and the medium (here, the air). For example, the speed of sound is influenced by the density of the medium and temperature. However, temperature and humidity could also indirectly influence the behaviour of bats due to their impact on feeding prey (O'Donnell 2000; Ciechanowski et al. 2007). In addition, acoustic recordings are expected to be influenced by technical choices such as the following: the detector microphone (Waters and Walsh 1994; Adams et al. 2012), bat detector height (Weller and Zabel 2002; Baerwald and Barclay 2009; Collins and Jones 2009; Jones et al. 2009), detector orientation (Weller and Zabel 2002) and distance of the signal from the detector (Adams et al. 2012). Moreover, long-term acoustic monitoring involves also considering the wear of the microphones. Finally, methods to survey bat activity (mainly, line transects and stationary measurement) are expected to influence acoustic recordings (Stahlschmidt and Brühl 2012).

With the aim to test if bat pass duration was longer in favourable habitats, during seasons with high energetic constraints or during night peak activity, we used two independent data sets (i.e. two recording protocols along line transects or stationary recordings) from the French bat-monitoring programme, a large scale acoustic bat survey that has involved numerous volunteers since 2006. These data sets offer the opportunity to simultaneously test multiple factors, such as habitat, season, hour of the night, weather condition, detector characteristics and ageing of the detector, that are expected to influence acoustic recordings and more particularly, the bat pass duration of various species of bats. In addition, the protocol of this large survey avoids extreme weather conditions (i.e. lower temperatures, strong winds and rain). Thus, the conditions of the recordings of these data are close to the conditions often selected for comparative studies (see Lacoeuilhe et al. 2014; Azam et al. 2016)

## Material and methods

### Bat sampling

The data were provided by the French bat-monitoring programme (FBMP) (http://vigie-nature.mnhn.fr/page/vigie-chiro), a citizen-science programme running since 2006 and coordinated by the French Museum of Natural History (MNHN). The FBMP is based on standardized echolocation recordings (Stahlschmidt and Brühl 2012), where bat calls are detected using 2 types of bat detectors (Tranquility Transect Bat detector, Courtpan Design Ltd, UK; and D240x, Pettersson Elektronik AB) and were recorded on a Zoom H2 digital recorder (Samson Technologies, USA) at a sampling rate of 96 ks/s. Sound was stored on a Secured Card in Waveform Audio File Format, more commonly known as the WAV format. Each site was monitored twice: once during the period of 15 June to 31 July, when females are expected to give birth and feed their offspring; and second, during the period 15 August to 31 September, when the young bats are flying, and individuals are expected to be less dependent on their reproductive roost. The observers begin their sampling at thirty minutes after sunset, from season to season and year to year. Thus, this sampling occurred during the bat activity peak that begins 30 min after sunset and spans less than 3 h (Roche et al. 2005). Observers sampled bats only when weather conditions were considered favourable, i.e. no rain, temperature higher than 12 °C, 30 min after sunset and without strong winds (<20 km/h). Two different versions were used: road survey by car and count point.

### Car transect survey

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

### Count point survey

The protocol consists of a 2 × 2 km square randomly chosen (by the Museum) in a radius of 10 km from the observer's home, within which a minimum of ten points are chosen by the observer, with at least five points being representative of the habitats of the square, the others being located in 'favourable' places for bats, such as riverbanks and wood edges. The ten points of a site were sampled (continuous recording during 6 min/point) during the same night. Currently, data were gathered on 120 squares representing 1272 different points (see ESM 1). The count point survey is the second protocols used by the FBMP in order to monitor common bat population (for more details see Kerbiriou et al. 2018b, and ESM 1

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

### Species identification

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

### Variables expected to influence bat passes duration

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

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

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

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

Fourth, sound propagation is proportional to temperature, air composition (i.e. humidity, see Griffin 1971) and pressure. However, in the Earth's atmosphere, the chief factor affecting sound propagation is the temperature, a variable previously selected for our analyses according to its potential impact on bat prey.

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

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

## Statistical analysis

### Influence of variables on the measure of bat pass duration

For each taxa and method used to survey bat activity (i.e. car transect and point count), we performed general linear mixed models (GLMM function *glmmPQL*, package R: MASS) using the duration of bat passes as a response variable with a Poisson error distribution according to the long tail pattern of bat passes duration (see ESM 3). The variables potentially influencing bat pass duration, such as habitat (habitat type or clutter index), date, time after sunset, weather conditions (temperature, humidity, cloud cover and wind), receiver (detector model, age of detector and the car speed for the car transect survey) were used as fixed effects. We included a quadratic effect for the date and time after sunset, and we used general additive mixed models (GAMM function *gamm*, package R: mgcv) for visualizing these potentially non-linear effects. To account for possible spatial pseudo-replication involving several measurements taken from the same individual or environment, we included a group effect (named 'date-point') for identifying bat passes recorded within the same site at the same date as a random effect. In addition, to taking temporal pseudo-replication into account, involving repeated measurements from the same volunteers, we included volunteer identity as one supplementary independent random effect. The fixed effects, except detector model and habitat type (categorical variable), were standardized so that the regression coefficients were comparable in magnitude (Schielzeth 2010). Before running each GLMM, we systematically evaluated the correlations among explanatory variables using Spearman's rho for quantitative variables (Crawley 2009) to detect obvious correlation (See ESM 2). Second, we performed variance-inflation factors (VIF) on each model (Fox and Monette 1992); all variables had a VIF < 3, indicating no problem of multicollinearity in the explanatory variables of our models. Thus, we ran 12 models, one for each bat taxa (n = 6) and for each protocol (car transect or point count), structured in the following way:

> [bat passes duration] ~ date + date$^2$ + time after sunset + time after sunset$^2$ + temperature + wind speed + humidity + cloud cover + detector model * age of detector + clutter index or habitat type + 1|volunteer + 1| date-point

For the six models running on data from the car survey protocol, we added car speed as a fixed effect. Clutter index or habitat type is intrinsically correlated variables and could not be simultaneously included in the modelling; thus, we performed separate modelling.

## Results

The most common taxa (5 bats species: *P. kuhlii, P. pipistrellus E. serotinus, N. leisleri, N. noctula* and one genus: *Myotis*) accounted for 24,597 bat passes (Table 1).

We detected relatively few effects of the clutter index: just a significant positive effect on bat pass duration for *N. leisleri* with data from the car survey (Table 2) and for *E. serotinus* with data from the count point survey (Table 3). Habitat type was slightly more significant, with two effects detected with data from the car survey (*P. pipistrellus* and *E. serotinus*) and three effects with data from the count point survey (*P. kuhlii*, *E. serotinus* and *N. leisleri*) (Table 4).

For *P. pipistrellus,* we detected longer bat pass durations recorded over bodies of water (Figure 3). For *P. kuhlii,* shorter bat pass durations were recorded in urban areas. For *E. serotinus,* longer bat pass durations were recorded in heterogeneous agricultural areas, deciduous forests and water courses, and shorter bat pass durations in continuous urban areas, discontinuous urban areas and arable land (Figure 3).

We detected a significant effect of time after sunset for three species (*P. pipistrellus, E. serotinus* and *N. noctula*, for the latter species, only in the car transect survey). The observed pattern is congruent with our hypothesis: shorter bat pass duration was found at the beginning of the night (Tables 2 & 3; Figure 4; ESM 4.2 & ESM 4.5), and in addition, a quadric effect was detected for *P. pipistrellus* and *E. serotinus* (for the latter species, only in the car transect survey), indicating an optimum of approximately 1 h and a half after sunset (Tables 2 & 3; Figure 4; ESM 4.2 & ESM 4.5).

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

Weather conditions (humidity, temperature, cloud cover and wind) rarely influence bat pass duration, with less than 10% of significant effects. An effect of the bat detector is

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

| | Count point survey | Car transect survey |
|---|---|---|
| *Pipistrellus kuhlii* | 805 | 981 |
| *Pipistrellus pipistrellus* | 8,117 | 11,132 |
| *Eptesicus serotinus* | 130 | 713 |
| *Nyctalus leisleri* | 226 | 531 |
| *Nyctalus noctula* | 143 | 414 |
| *Myotis ssp.* | 1,131 | 274 |

**Table 2.** Averaged partial regression coefficient and *p*-value from GLMM of the fixed effects included in the analysis performed on data from the car transect survey.

| | *P. pipistrellus* | *P. kuhli* | *E. serotinus* | *N. leisleri* | *N. noctula* | *Myotis ssp* |
|---|---|---|---|---|---|---|
| Clutter index | $p = 0.102$ | $p = 0.183$ | $p = 0.311$ | **$p = 0.024$**<br>**$\beta = 0.063$** | $p = 0.089$ | $p = 0.967$ |
| Time after sunset | **$p < 0.001$**<br>**$\beta = 0.074$** | $p = 0.151$ | **$p = 0.001$**<br>**$\beta = 0.111$** | $p = 0.426$ | $p = 0.198$ | $p = 0.582$ |
| Time after sunset$^2$ | **$p = 0.006$**<br>**$\beta = -0.046$** | **$p = 0.004$**<br>**$\beta = -0.066$** | **$p = 0.002$**<br>**$\beta = -0.061$** | $p = 0.910$ | $p = 0.702$ | $p = 0.908$ |
| Date | **$p < 0.001$**<br>**$\beta = 0.033$** | $p = 0.775$ | **$p = 0.031$**<br>**$\beta = -0.082$** | $p = 0.281$ | $p = 0.439$ | $p = 0.071$ |
| Date$^2$ | **$p < 0.001$**<br>**$\beta = 0.081$** | $p = 0.652$ | $p = 0.043$ | $p = 0.226$ | $p = 0.401$ | $p = 0.572$ |
| Temperature | $p = 0.599$ | $p = 0.722$ | **$p = 0.001$**<br>**$\beta = 0.095$** | $p = 0.059$ | $p = 0.179$ | $p = 0.625$ |
| 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 | **$p < 0.001$**<br>***D240x > TT*** | $p = 0.751$ | $p = 0.177$ | $p = 0.163$ | $p = 0.468$ | $p = 0.851$ |
| Age | **$p = 0.018$**<br>**$\beta = 0.012$** | $p = 0.055$ | $p = 0.436$ | $p = 0.068$ | **$p = 0.007$**<br>**$\beta = -0.211$** | **$p = 0.019$**<br>**$\beta = -0.026$** |
| Bat detector: Age | **$p = 0.004$**<br>**$\beta TT = -0.366$** | $p = 0.460$ | **$p = 0.023$**<br>**$\beta TT = 0.225$** | $p = 0.455$ | **$p = 0.039$**<br>**$\beta TT = 0.285$** | $p = 0.161$ |
| Car speed | **$p < 0.001$**<br>**$\beta = -0.145$** | $p = 0.280$ | $p = 0.857$ | $p = 0.275$ | $p = 0.051$ | $p = 0.905$ |

Note: Bold indicates a *P*-value < 0.05.

**Table 3.** Averaged partial regression coefficient and *p*-value from GLMM of the fixed effects included in the analysis performed on data from the count point survey.

| | *P. pipistrellus* | *P. kuhli* | *E. serotinus* | *N. leisleri* | *N. noctula* | *Myotis ssp* |
|---|---|---|---|---|---|---|
| Clutter index | $p = 0.527$ | $p = 0.890$ | **$p = 0.017$**<br>**$\beta = 0.163$** | $p = 0.574$ | $p = 0.389$ | $p = 0.245$ |
| Time after sunset | **$p = 0.010$**<br>**$\beta = 0.059$** | $p = 0.057$ | **$p = 0.003$**<br>**$\beta = 0.391$** | $p = 0.414$ | **$p = 0.006$**<br>**$\beta = -0.312$** | $p = 0.727$ |
| Time after sunset$^2$ | **$p < 0.001$**<br>**$\beta = -0.037$** | $p = 0.079$ | $p = 0.233$ | $p = 0.528$ | $p = 0.798$ | $p = 0.244$ |
| Date | **$p = 0.012$**<br>**$\beta = 0.052$** | **$p = 0.015$**<br>**$\beta = 0.107$** | $p = 0.298$ | $p = 0.748$ | $p = 0.393$ | $p = 0.818$ |
| Date$^2$ | $p = 0.926$ | $p = 0.475$ | $p = 0.636$ | $p = 0.161$ | **$p = 0.001$**<br>**$\beta = -0.538$** | $p = 0.927$ |
| Temperature | $p = 0.214$ | $p = 0.849$ | $p = 0.892$ | $p = 0.858$ | $p = 0.166$ | $p = 0.569$ |
| Humidity | **$p = 0.011$**<br>**$\beta = 0.054$** | $p = 0.063$ | $p = 0.285$ | **$p = 0.022$**<br>**$\beta = -0.200$** | $p = 0.349$ | $p = 0.547$ |
| Cloud cover | **$p = 0.018$**<br>**$\beta = -0.052$** | $p = 0.240$ | $p = 0.269$ | $p = 0.811$ | $p = 0.934$ | $p = 0.013$ |
| Wind | $p = 0.938$ | $p = 0.910$ | $p = 0.452$ | $p = 0.066$ | $p = 0.298$ | **$p = 0.032$**<br>**$\beta = 0.087$** |
| Bat detector | **$p < 0.001$**<br>***D240x > TT*** | $p = 0.214$ | $p = 0.479$ | $p = 0.160$ | $p = 0.597$ | **$p < 0.001$**<br>***D240x > TT*** |
| Age | $p = 0.282$ | $p = 0.657$ | $p = 0.524$ | $p = 0.202$ | $p = 0.563$ | $p = 0.567$ |
| Bat detector: Age | **$p < 0.001$**<br>**$\beta TT = -0.256$** | $p = 0.260$ | $p = 0.986$ | **$p = 0.012$**<br>**$\beta TT = -0.518$** | $p = 0.731$ | **$p = 0.011$**<br>**$\beta TT = -0.208$** |

Note: Bold indicates a *P*-value < 0.05.

**Table 4.** Effects of habitat type on bat call duration.

| | *P. pipistrellus* | *P. kuhli* | *E. serotinus* | *N. leisleri* | *N. noctula* | *Myotis ssp* |
|---|---|---|---|---|---|---|
| Car transect survey | **$p < 0.0001$** | $p = 0.52$ | **$p = 0.027$** | $p = 0.45$ | $p = 0.67$ | $p = 0.25$ |
| Count point survey | $p = 0.81$ | **$p = 0.021$** | **$p = 0.044$** | **$p = 0.002$** | $p = 0.46$ | $p = 0.37$ |

Note: Bold indicates *P*-value < 0.05; for effects of the other variable that were similar to those found with clutter index analysis, see ESM 4.5 for details.

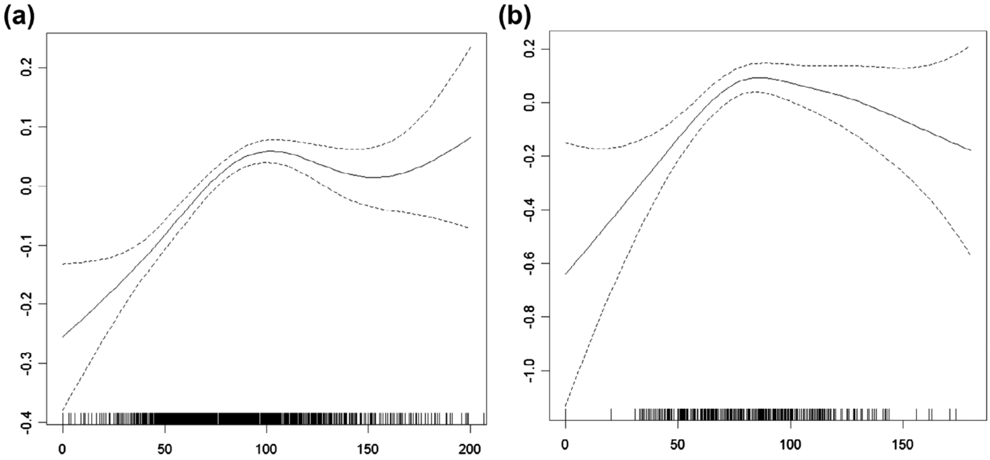

**Figure 3.** Variation of bat pass duration (scaled values) during early night (expressed as minutes after sunset): (a) *P. pipistrellus* and (b) *E. serotinus*. Marks on the X-axis indicate values present at least once in the data-set. For GAMM modelling on data from the car transect survey, see the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

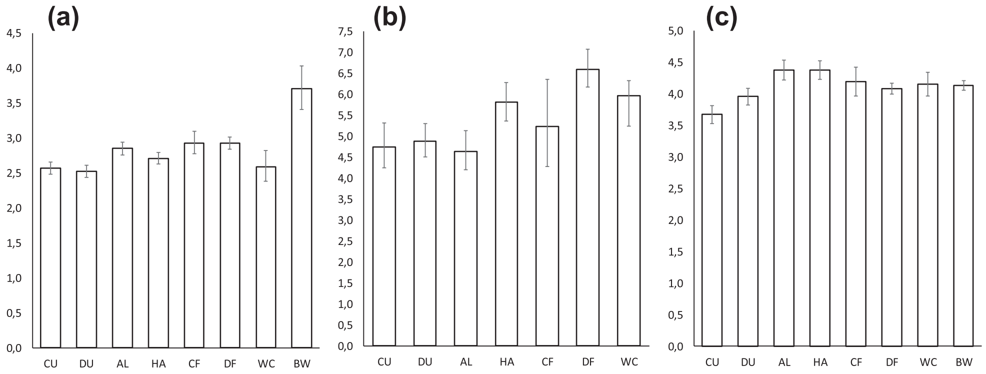

**Figure 4.** Variation in bat pass duration across habitat type: (a) *P. pipistrellus* car transect survey; (b) *E. serotinus* car transect survey; and (c) *P. kuhlii* count point survey. Habitat type: continuous urban areas (CU), discontinuous urban areas (DU), arable land (AL), heterogeneous agricultural areas (HA), coniferous forest (CF), deciduous forest (DF), water courses (WC) and water bodies (BW). Note: for variations adjusted to other co-variables included in the model, see supplementary material ESM 4.4.

detected for *P. pipistrellus* and *Myotis* spp., with the Tranquility Transect detector recording shorter bat pass durations than the D240x. Ageing and wear of detector are only detected for data from the car survey and for some species, but with some opposite effects (Tables 2 & 3), and the interaction between bat detector type and age indicates that when significant, this effect differs among species.

## Discussion

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

As expected, we detected a significant effect of time after sunset in bat pass duration for half of the species studied. When significant, the pattern is congruent with our prediction: shorter bat pass durations are recorded in the beginning of the night due to a greater percentage of individuals leaving the colony to reach foraging sites and then exhibit commuting flight. The maximum bat pass duration is detected approximately 1.5 h after sunset, which matches the activity pattern of individuals outside the roost during the night, as described by Swift (1980) for *P. pipistrellus* or by Catto et al. (1995) for *E. serotinus*.

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

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

We found results that confirm the three main hypotheses that we formulated on bat pass duration: (i) longer bat pass durations within selected habitats for foraging; (ii) shorter bat pass durations in the first minutes after sunset; and (iii) longer bat pass durations during periods with important energetic demands. While we did not detect results that clearly reject our hypotheses, we did, however, not simultaneously detect these effects for each species. For *P. pipistrellus* and *E. serotinus* to a lesser extent, our main predictions were found; note that *P. pipistrellus* is the species for which we have by far the largest number of measures (~8000 and ~10,000 measures, respectively, for the count point survey and the car transect survey). This sample size appears impressive according to the recorded sample of 4–6 min of recording per point, manual identification and manual measure of bat pass duration; however, the recent reduced cost of acoustic recorders has resulted in an exponential development of Passive Acoustic Monitoring (PAM) involving, for example, a third protocol in the FMBP. PAM produces considerable amounts of data, while before we recorded 4–6 min per site in the two previous protocols, now these detectors can record the entire night; so, regularly, several hundred bat passes could be recorded per night, site and species (see e.g. Charbonnier et al. 2014), even in habitats with regularly low bat activity, such as agriculture land (see Millon et al. 2015). In addition to the arrival of a new generation of passive recorders on the market, the development of a software toolbox (Bas et al. 2017) can detect every sound event and extract numerous features, so that sounds may be well characterized during the same process and used to produce species identification and characteristics of the call (buzz, social call, etc.). Thus, in the near future, we expect that analysing bat pass durations will not be limited by the amount of data.

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

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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