ORIGINAL ARTICLE

The duration of acoustic bat passes as a proxy of foraging activity

Charlotte Roemer^{1, 2}, Sarah Chayrigues¹, Romain E. Lacoste³, Yves Bas^{1,4}

¹Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France.

²CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.

³LAMA, UMR 8050, Université Gustave Eiffel.

⁴PatriNat (OFB, MNHN), 75005 Paris, France.

*Corresponding author: charlotte.roemer1@mnhn.fr

DOI: https://doi.org/10.14709/ BarbJ.17.1.2024.08

Keywords: behaviour, bioacoustics, Chiroptera, island species, social call, social communication

received: April, 5th 2024 accepted: December, 12nd 2024

ABSTRACT

The feeding activity of bats can be quantified by counting the number of feeding buzzes, which are a specific series of short calls emitted in an attempt to capture prey. However, identifying them in large amounts of recordings is very time-consuming. With the availability of automated identification tools, it is now possible to automatically identify feeding buzzes and associate this with the identity of the bat species. Yet, this process is still consuming in terms of time and computational resources. In this study, our objective was to find a simple metric to predict the occurrence of feeding buzzes.

For our demonstration, we used acoustic data from the citizen science program Vigie-Chiro, France. We first automatically classified species with a species classifier, and then feeding buzzes with a sonotype classifier. We then associated the buzzes with the species identity and evaluated the performance of this pair of classifications. We calculated two candidate metrics, namely the mean bat pass duration and the standard deviation of the inter-pass duration over the night. We then compared their performance to predict the number of feeding buzzes per hour of the common pipistrelle (*Pipistrellus pipistrellus*).

The automatic association process between species and feeding buzzes had a sensitivity of 96 % and a specificity of 84%. Both assessed metrics significantly predicted the number of feeding buzzes per hour. However, the mean duration of bat passes per night was a better predictor than the standard deviation of the interpass duration.

We conclude that the mean duration of bat passes per night can be used to study the foraging activity of the common pipistrelle. This metric is probably usable for other species using similar foraging strategies. It could also be very convenient to monitor the foraging activity of species that do not produce feeding buzzes, although additional investigations must be done to confirm this hypothesis.

INTRODUCTION

Many animals need to move around the landscape periodically to satisfy needs, such as fleeing predators and reaching grounds suited for foraging, drinking, resting, reproducing or hibernating (Alcock 2009). While small-distance movements are often studied by visual observations or external sensors such as video recordings or acoustic tracking, long-distance movements are usually followed by animal-borne sensors such as radio-telemetry, GPS, or ARGOS (Demšar et al. 2015, Koblitz 2018, Williams et al. 2020, Morrant et al. 2022). Each one of these methods has pros and cons, and should be chosen according to the specific goals of the study. For example, studying the success rate of lions when attacking their prey is best done using visual observations rather than radio-telemetry.

The differentiation of movement functions (e.g. foraging vs. commuting) is a challenge that is tackled in each of

these methods differently. For instance, in GPS tracking, a stronger sinuosity of the track or clusters of locations are associated with a higher probability of foraging than commuting, because the animal will spend more time at the same location (Saldanha et al. 2023). Classifying animal movements has applications in countless disciplines, including ethology, evolutionary ecology, conservation ecology, virology, and statistics and mathematics applied to ecology (Smouse et al. 2010, Doherty & Driscoll 2018, Riotte-Lambert & Matthiopoulos 2020, Abrahms et al. 2021, Schloesing et al. 2023). However, when the classification of animal movements at a large spatio-temporal scale is desired, e.g. classifying the use of habitats across a country, air-borne sensors are not always an option because some animals are too small, too rare or too elusive to be equipped. Even at a small scale, e.g. to study how a few hectares are used by a species, equipping a lot of individuals is very timeconsuming and costly.

Acoustic monitoring is a relatively recent method that notably allows one to detect and quantify the activity of vocal species, while providing the identity of the species in many cases (Browning et al. 2017). Acoustic activity is usually quantified by counting the number of bat passes, which are either defined as individual calls, more calls within a time interval, or any series of calls before a silence (Britzke et al. 2013). With a single microphone, additional information on movement, such as foraging activity, can also be measured, e.g. the feeding buzzes of bats; these feeding buzzes are series of more than five very short echolocation calls emitted with very short time intervals (<10 ms) and a large bandwidth, best suited to locate prey at a very short distance from the bat (Griffin et al. 1960).

With the development of cheaper, more available acoustic monitoring hardware, there is increasing demand for automated tools to process the large volumes of sound recordings collected, such as automated acoustic classifiers (Bas et al. 2017, Fraser et al. 2020). Once species classification is done, another classifier is necessary to distinguish feeding buzzes from the other echolocation calls. Although feeding buzzes can be classified with a success rate above 93 % (Roemer et al. 2021), classification requires significant computational resources. If possible, it would therefore be more efficient to directly rely on information that is already contained in sound detection (e.g. frequency, duration, inter-call intervals) to describe foraging activity with acoustic recordings. In addition, some bats such as gleaners (e.g. Plecotus auritus or Myotis myotis) will very rarely emit feeding buzzes because they often rely on the acoustic cues emitted by their prey to forage (Dietz et al 2009). Thus, using feeding buzzes to classify bat behaviour will fail for these species.

The results of Kerbiriou et al. (2018) suggest that the duration of a bat pass (i.e. the duration between the first and the last call without silence) is a proxy of its foraging behaviour, as foraging flights should be associated with a stronger sinuosity and thus trigger longer recordings than commuting flights. Another good candidate is the standard deviation of the time between bat passes, because we expect foraging bats to fly back and forth in front of the microphone (i.e. short standard deviation), while we expect commuting bats to demonstrate no particular pattern (i.e. large standard deviation).

Thus, our goal was to test whether the mean duration of bat passes and the standard deviation of the time between bat passes would be good predictors of the number of feeding buzzes emitted per hour, as determined using automated tools. For these purposes, we used the common pipistrelle (*Pipistrellus pipistrellus*) as a model species, which is considered one of the most abundant and widespread species in Europe (Mathews et al. 2023). It is a good candidate for acoustic monitoring because it is easily detectable and frequently emits feeding buzzes.

MATERIAL AND METHODS

Dataset

We used the dataset of the citizen science program Vigie-Chiro (French National Museum of Natural History), in which citizens sample bat acoustic activity with full-spectrum ultrasonic recorders for the whole night in fixed locations in France mainland, where 36 bat species are extant (Arthur & Lemaire 2021). To make sure that the recordings are comparable across the different recorders, different settings are applied according to the material used and they are available in Supplementary Material (SM) 1. Recordings were performed mostly during meteorological conditions known to be selected by bats, i.e. no rain, temperature not too low according to the normal conditions of the geographical area, and low wind speed.

This database contains 370 Terabytes of WAV data. We thus performed a random sampling of this database so to obtain 1000 study sites (approximately equivalent to 12 Terabytes), that we considered to be a satisfying amount for our demonstration. Before that, incomplete nights were removed. We then sampled the 1000 study sites without replacement, which contained one or several nights per site. The study sites were sampled between 2010 and 2021, each site being surveyed for a minimum of one night (mean = 3.5 nights, max = 32 nights).

Sound detection, species and feeding buzz classification

We used the Tadarida software (Bas et al. 2017) to detect sound events and measure their features such as frequencies, amplitude and duration. Following the software recommendations, the recordings were cut in sequences of a maximum of five seconds in length. We used the species classifier built with Tadarida and used in the Vigie-Chiro program (version 03-03-2018) to classify species. We also used the sonotypes classifier built with Tadarida and published by Roemer et al. (2021) to classify feeding buzzes. After classification, each 5-second long sequence is thus given a species classification (e.g. probability of *P. pipistrellus*: 0.5) and also a likelihood that this sequence contains a feeding buzz (e.g. 0.2).

Since a sequence can contain more than one species, we developed a script to match the species identification with the feeding buzzes. This script verifies that the start and end times of the calls identified as buzzes are between the start and end times of calls identified as the species. If there are still several species in this match, the script keeps only the species with the lowest frequency difference with the buzz. Once this match was done, we only kept species with a confidence index for the species identification greater than 0.5 (see Barré et al. 2019). This step is called "species/buzz classification and association".

If the species classifier did not identify any bat in the 5-second sequence, then we used this information to modify the result of the buzz classifier. More precisely, if a buzz was identified by the buzz classifier, while no bat was identified by the species classifier, then we changed the result of the buzz classifier to "absence of buzz" because bush-crickets, birds and noise do not produce bat feeding buzzes. This step is called "bat buzzes only".

Evaluation of the classification performance

To evaluate the classification of feeding buzzes and species, one 5-second sequence was chosen per night for 50 random nights. Only sequences for which a buzz was initially identified by the buzz classifier (before we changed the result during the "bat buzzes only step, see previous section) were randomly selected. For each sequence, we performed a validation for the buzz classifier (buzz or absence of buzz), and we performed a validation for the species classifier (e.g. *Pipistrellus pipistrellus, Eptesicus serotinus*, noise, *Tessellana tessellata*). The WAV file was checked on the spectrogram issued with Syrinx (John Burt, USA). Manual species identification and verification were done using shape, frequency, time and amplitude criteria (Barataud 2015, Russ 2021).

We evaluated the performance of the classifiers using a sensitivity and specificity analysis. The specificity (Sp) and the sensitivity (Se) were calculated as such:

Specificity:
$$Sp = \frac{TN}{TN + FP}$$

Sensitivity: $Se = \frac{TP}{TP + FN}$

Where TN = True Negative, TP = True Positive, FN = False Negative and FP = False Positive.

A confusion matrix was then calculated to obtain the rate of true/false positives and negatives.

We first evaluated the performance of the species classifier. Since our target are bat feeding buzzes, we focused our evaluation on the capacity of the species classifier to correctly identify bat species, and it was not important whether the classifier could correctly identify other sound categories (e.g. noise, bush-crickets, birds). In this framework, a true positive is a sequence in which a bat species was correctly identified by the classifier. A false positive is a sequence in which a sound was falsely identified by the classifier as a bat species. A true negative is a sequence in which there was no bat and the classifier did not identify a bat. A false negative is a sequence in which there was a bat that was not identified as a bat by the classifier. See Table 1 for examples.

For sequences in which a buzz was identified by the buzz classifier, we checked whether it was a true positive (a real buzz) or a false positive (not a buzz). We did not check true negatives (a sequence that was correctly identified as not containing a buzz) and false negatives (a sequence that was incorrectly determined as not containing a buzz) because our final workflow processes bat buzzes only.

We finally evaluated the performance of the full process, i.e. the species/buzz classification and association, using the sensitivity and specificity analysis. Here again, since our target are bat feeding buzzes, we focused our evaluation on the capacity of the species classifier to correctly identify bat species, and it was not important whether the classifier could correctly identify other sound categories (e.g. noise, bush-crickets, birds). In this framework, a true positive is a buzz correctly identified and associated to a bat species correctly identified. A false positive can be either (1) a sequence in which a feeding buzz was present and correctly identified, but the bat species producing it was falsely identified, or (2) a sequence in which a species was correctly identified, but the buzz classifier identified a buzz when in fact there was no buzz. A true negative is a sequence that was, after the "bat buzzes only" step, correctly determined as not containing any buzz or bat echolocation call. A false negative is a sequence that was, after the "bat buzzes only" step, falsely determined as not containing any buzz while the bat species was either correct or incorrect. See Table 1 for examples.

Calculation of metrics: Number of feeding buzzes/hour, mean bat pass duration and standard deviation of the inter-pass duration

The metrics were only calculated for *P. pipistrellus*. For each night, we calculated the number of bat passes and removed the night from the dataset if there were less than 20 bat passes to make sure that the calculation of the metrics was sufficiently accurate. Indeed, to compute the relative number of feeding buzzes per hour (see below), we divide the number of buzzes by the cumulated duration of bat passes during the night; in the case of a night with, e.g., only one buzz and one minute of cumulated activity, the result would thus be an abnormal high amount of relative feeding buzzes per hour. We thus avoided these abnormal cases.

Mean bat pass duration. We defined bat pass duration as the time between the start time of the first call and the start time of the last call of a species detected and identified by the species classifier without silence, where silence is defined as no bat call for at least two seconds. This metric is calculated by considering the possibility that bat passes can occur across consecutive sequences of 5 seconds. The mean bat pass duration is calculated over the entire night. The minimum length of a sequence was 0.1 s.

Standard deviation of the inter-pass duration. This metric is the standard deviation of the time separating the bat passes of the same species during the night (see Fig. 1).

Relative number of feeding buzzes per hour. A medium rate of feeding buzzes per hour could be the result of a high activity associated with few feeding buzzes, but it could also be the result of a moderate activity associated with a moderate amount of feeding buzzes. Therefore, to account for the amount of activity, we included the duration of the cumulated passes during the night (representing the activity level) to calculate the relative number of feeding buzzes per hour:

Relative n° feeding buzzes per hour :

$$\mathrm{buzz_{hour}} = rac{\sum \mathrm{buzzes \ during \ the \ night}}{\sum \mathrm{duration \ bat \ passes \ (hour)}}$$

Table 1 – Examples for the determination of true positives, false positives, true negatives and false negatives for the different steps of classification.

| Category | Result of classifier | Result of manual checking | | |
|------------------------|-------------------------------|---------------------------|--|--|
| Species classifier | | | | |
| True positive | P. pipistrellus | P. pipistrellus | | |
| | | P. pygmaeus | | |
| Faise positive | P. pipistrenus | Noise | | |
| True negative | Bush-cricket | Bush-cricket | | |
| | noise | 0 ministrallus | | |
| Faise negative | Bush-cricket | P. pipistrellus | | |
| Buzz classifier | | | | |
| True positive | Buzz | Buzz | | |
| False positive | Buzz | No buzz | | |
| Species/buzz classific | ation and association | | | |
| True positive | P. pipistrellus + buzz | P. pipistrellus + buzz | | |
| e 1 | P. pipistrellus + buzz | P. pygmaeus + buzz | | |
| Faise positive | <i>P. pipistrellus</i> + buzz | P. pipistrellus (no buzz) | | |
| Tura | P. pipistrellus (no buzz) | P. pipistrellus (no buzz) | | |
| irue negative | Bush-cricket | Bush-cricket | | |
| | P. pipistrellus (no buzz) | | | |
| False negative | P. pygmaeus (no buzz) | P. pipistrellus + buzz | | |
| | Bush-cricket | | | |



Fig. 1 – Illustration of the calculation of inter-pass duration. The arrow represents the time elapsing during the night.

It is thus a measure of the relative occurrence of a feeding buzz that is independent of the amount of activity on the site. We therefore expect the value of this measure to be high in the case of foraging only, and to be low in the case of commuting only.

Correlation tests

Pearson correlation tests were done between the different metrics. The Relative number of feeding buzzes per hour and the mean bat pass duration were not normally distributed, and we thus normalised their distribution with the logarithmic function before running the test.

Modelling

Modelling was performed in R (R Core Team 2021) with the glmmTMB package (Brooks et al. 2018). The relative number of buzzes per hour (response variable) was modelled as a function of the mean bat pass duration and the

standard deviation of the inter-pass duration (predictors). We added the site as a random effect to account for the spatial structure of the dataset. We built a null model, a full model with both predictors, and models with either one of the predictors. The full model is described by the following equation:

 $buzz_{hour}$ ~ Mean bat pass duration + Standard deviation of the inter-pass duration + (1|Site)

The distribution of the response variable (i.e. the number of buzzes per hour) was zero-inflated. We thus used three different candidate families to model the response variable: (1) Poisson, (2) negative binomial (nbinom2), and (3) negative binomial with zero inflation. The last model accounts for zero inflation in the distribution of the values in the response variable. We kept only the model with the lowest Akaike Information Criterion (AIC); if there was a tie between models, we would keep the one that had no

variable without a significant effect (e.g. for two models with an AIC difference inferior to 2, if the Mean bat pass duration is significant in the first model, but not in the second model, we would keep the first model). We then analysed the residuals using the simulateResiduals function of the DHARMa package (Hartig 2017). We evaluated the r^2 of the model using the r^2 function of the performance package (Lüdecke et al. 2021). Predictions were made with the ggpredict function of the ggeffects package (Lüdecke et al. 2020).

RESULTS

After the selection of sampling nights with a minimum of 20 bat passes, 831 study sites were retained from the initial set of 1000 study sites. Twenty-five different species were identified with a probability greater than 0.5 by the species classifier (see Table 1 in SM 2). *P. pipistrellus* was identified by the species classifier in 1044 of the 1168 site*nights, which represents 264,893 bat passes in total for a total of 10659.53 hours of recording.

Validation of the automatic association of feeding buzzes with species identifications

Concerning the species classifier, 41 out of 50 files were correctly identified as a bat, a bush-cricket, a bird or noise (SM Table 2). Concerning bats, 28 out of 29 files were correctly identified at the species level (Table 2 and SM Table 2). The only false negative was a *P. pipistrellus* identified as a bush-cricket (*Leptophyes punctatissima*). The species classification had a sensitivity of 96.6 % and a specificity of 100 %.

When the feeding buzz classifier identified a buzz, half of the files did not contain one (Table 3). Among these false positives, 52 % were bush-crickets, 32 % were noise, and 14 % (i.e. four files) were high-pitched (> 90 kHz) echolocation calls of *Rhinolophus ferrumequinum (harmonics), Rhinolophus hipposideros, P. pipistrellus* and *Myotis emarginatus*. Concerning the species/buzz classification and association (Table 4), the false positives remain the same ones as those identified during the previous step (Table 3). The only false negative was due to the error of the species classier mentioned before (Table 2): the feeding buzz emitted by a *P. pipistrellus* was classified by the species classifier as a bush-cricket (*Leptophyes punctatissima*). The species/buzz classification and association had a sensitivity of 96 % and a specificity of 99.1 %.

Distribution of the predictors

The mean bat pass duration has a right-skewed distribution with a median value of 5 seconds and the standard deviation of the inter-pass duration has a normal distribution with a median value of 13.6 seconds (Fig. 2).

Correlation between the different metrics

All metrics were significantly correlated: the number of buzzes per hour increased with the mean bat pass duration and decreased with the standard deviation of the inter-pass duration (Table 5).

Modelling the relative number of feeding buzzes per hour

All models were significantly better than the null models, including models for each family types (Table 6). The lowest AlC values correspond to models with a negative binomial family with zero-inflation. The mean bat pass duration always had a significant effect, but the standard deviation of the inter-pass duration only had a significant effect in the negative binomial family if it was the only predictor. The retained model is thus the negative binomial family with zero-inflation with mean bat pass duration as a predictor. The analysis of the residuals detected no major problem (SM Fig. A1). The conditional r^2 was 0.982 and the marginal r^2 was 0.1.

As expected, the longer the bat pass duration, the more feeding buzzes per hour were recorded (Fig. 3).

Table 2 – Confusion matrix for the species classification. TN = True Negative, TP = True Positive, FN = False Negative and FP = False Positive. The meaning of species abbreviations is shown in SM Table 3.

| | | Validation | | | | | | | | | | |
|------|---------|------------|--------|--------|--------|--------|--------|--------|--------|--------|------------------|--------|
| | | barbar | eptser | myodau | туоета | pipkuh | pippip | pippyg | rhifer | rhihip | bush- cricket | noise |
| | barbar | 1 TP | | | | | | | | | | |
| | eptser | | 2 TP | | | | | | | | | |
| | myodau | | | 2 TP | | | | | | | | |
| | myoema | | | | 1 TP | | | | | | | |
| | pipkuh | | | | | 3 TP | | | | | | |
| fier | pippip | | | | | | 15 TP | | | | | |
| ssi | pippyg | | | | | | | 2 TP | | | | |
| G | rhifer | | | | | | | | 1 TP | | | |
| | rhihip | | | | | | | | | 1 TP | | |
| - | bush- | | | | | | 1 EN | | | | 11 TN | 2 TN |
| _ | cricket | | | | | | 1 FIN | | | | TT IN | 2 1 11 |
| | bird | | | | | | | | | | | 1 TN |
| | noise | | | | | | | | | | 2 TN | 5 TN |

Table 3 – Confusion matrix for the feeding buzz classification. TP = True Positive and FP = False Positive.

| | | Validation | | |
|------------|------|------------|---------|--|
| | | buzz | no buzz | |
| Classifier | buzz | 25 TP | 25 FP | |

Table 4 – Confusion matrix for the species/buzz classification and association. TN = True Negative, TP = True Positive, FN = False Negative and FP = False Positive. The meaning of species abbreviations is shown in Table A3.



Fig. 2 – Distribution of the mean bat pass duration and the standard deviation of the inter-pass duration over the night for the common pipistrelle (*Pipistrellus pipistrellus*).

Journal of Bat Research & Conservation

DISCUSSION

Our study provides the simplest proxy to describe bat foraging behaviour at a study site: the mean bat pass duration. It is a continuous variable, meaning that it cannot be used to differentiate a feeding site from a commuting site based on a threshold. However, it can be very conveniently used as a continuous predictor of the probability that a site is used for foraging.

Automated matching between feeding buzzes and species identification

Our study is the first to provide a workflow to automatically match the identification of feeding buzzes with species identifications using automated classifiers. Although



Fig. 3 – Prediction of the relative number of feeding buzzes per hour as a function of mean bat pass duration (logarithmic scale). 95% confidence intervals are shown in grey. The ticks on the x axis show the sampled data.

the number of files checked was relatively low (i.e. 50), the sensitivity (96%) and specificity (84%) were satisfactory to conduct our analyses. The only false negative was due to misidentifying a feeding buzz as a bush-cricket. Both sounds are indeed particularly similar and this confusion might be quite common. According to Roemer et al. (2021), feeding buzzes are less often identified as bush-crickets (1 out of 183 cases) than bush-crickets are identified as feeding buzzes (26 out of 183 cases). As bush-crickets have a low mobility, it is usually easy to detect study sites with potential problems because the validation of at least one file with a bush-cricket increases the probability to find it throughout the rest of the night. In many cases, it is indeed advised to check manually a subset of files when using automatic classifiers to correct their identification errors (López-Baucells et al. 2019).

Candidate metrics to predict foraging activity

Both mean bat pass duration and the standard deviation of inter-pass duration were correlated with the relative number of feeding buzzes per hour. However, the comparison of the different generalised linear mixed models demonstrated that the mean bat pass duration is the best predictor. The longer the mean bat pass duration, the more feeding buzzes per hour are recorded. This result validates the hypothesis of Kerbiriou et al. (2018) according to which a foraging bat will display a flight trajectory with a stronger sinuosity than a commuting bat, and thus trigger longer acoustic recordings.

Limitations

Our study used *P. pipistrellus* as a model species. Completing this analysis for other species would be needed to generalise the results. Furthermore, we expect the amount of feeding buzzes emitted by one individual during

Table 5 – Pearson correlation coefficients between the different metrics for the common pipistrelle (Pipistrellus pipistrellus).

| Variable 1 | Variable 2 | ρ | p-value |
|--|---|--------|---------|
| Number of buzzes per hour | Mean bat pass duration | 0.46 | < 0.001 |
| Number of buzzes per hour | Standard deviation of the inter-pass duration | - 0.16 | < 0.001 |
| Standard deviation of the inter-pass duration | Mean bat pass duration | - 0.30 | < 0.001 |

Table 6 – AIC values of the different models built to model the number of buzzes per hour for the common pipistrelle (*P. pipistrellus*). *: the effect of the standard deviation of the inter-pass duration was not significant. The values in bold represent the lowest values.

| | Model family | | | | |
|--|--------------|----------------------|--------------------------------------|--|--|
| Variables | Poisson | Negative binomial | Negative binomial and zero-inflation | | |
| (null model) | 17749.8 | 9878.3 | 9526.6 | | |
| Mean bat pass duration | 17348.4 | 9801.5 | 9473.9 | | |
| Standard deviation of the inter-pass duration | 17676.8 | 9862.4 | 9521.1 | | |
| Mean bat pass duration + Standard deviation of the inter-pass duration | 17331.3 | 9803.3* | 9475.2* | | |

the night to be correlated with the biomass of insects preyed upon. This means that for the same number of prey and the same number of bats, we expect to record fewer buzzes on a study site containing bigger prey on average than another study site, because bats will obtain more calories from bigger prey and be satiated sooner.

In addition, buzzes are not only emitted for foraging; they can be emitted for drinking and to land (Russ 2021), although we expect these non-feeding buzzes to be much less frequent. Some social calls (e.g. *Vespertilio murinus*) may resemble feeding buzzes, and Roemer et al. (2021) indeed show that social calls resembling buzzes will be classified as such by the sonotypes classifier. Moreover, we expect the performance of the species/buzz classification and association process to drop in the case of multiple species because the automatic assignation of the buzz to the right species is a very complex task.

Pipistrellus pipistrellus has a relatively small home range (Laforge et al. 2021), and it is therefore expected that it will spend a relatively small amount of time commuting; this could limit our capacity to disentangle the commuting activity from the foraging activity. Yet, our analysis captured enough signal to find a relationship between mean bat pass duration and the relative number of feeding buzzes per hour. It would be interesting to reproduce this analysis with species with larger home ranges such as *Myotis daubentonii*, *Barbastellus* or *Nyctalus* species.

Additional investigations should be done to test whether the mean bat pass duration can be used directly to compare foraging activity between habitat types. Indeed, the clutter could be a confounding variable to explain the mean pass bat duration, i.e. cluttered habitats could lead to shorter bat pass durations than open habitats. In addition, it is likely that mean bat pass duration is a poor metric to qualify foraging activity close to roosting and swarming sites, since bats will spend an unusual amount of time at these sites to perform social activity.

Finally, in some situations, damaged microphones continue to record with a lower amplitude, which will consequently reduce bat pass durations. Defective microphones may be identified thanks to abnormal distributions of bat pass duration.

CONCLUSION

The mean bat pass duration over the night can be used to predict foraging grounds of *P. pipistrellus*. This proxy likely works well for other species using similar foraging strategies. Using mean bat pass duration as a proxy for foraging activity would be particularly useful for monitoring species that produce few or no feeding buzzes. However, more focused research is needed to test the effectiveness of our method for these species. This proxy also saves important computational resources as it does not require the use of a classifier dedicated to feeding buzzes.

AVAILABILITY OF DATA

The dataset used to build models is available in Supplementary_material_3.csv.

All R scripts and example files are available at https:// github.com/Charlotte-Roemer/bat-pass-duration

ACKNOWLEDGMENTS

This study was funded by the French Office of Biodiversity, and the Chair "Modélisation Mathématique et Biodiversité" of Veolia-École polytechnique-Museum national d'Histoire naturelle-Fondation X. We warmly thank the Vigie-Chiro participants for the collection of sounds used in this work. We thank the two anonymous reviewers as well as the editor Adrià Lopez-Baucells for their help in improving the manuscript.

REFERENCES

- ABRAHMS, B., AIKENS, E. O., ARMSTRONG, J. B., DEACY, W. W., KAUFFMAN, M. J. & MERKLE, J. A. (2021). Emerging perspectives on resource tracking and animal movement ecology. *Trends Ecol Evol*, 36(4): 308-320.
- ALCOCK, J. (2009). Animal behavior, ninth edition. ed.: Sinauer Associates. Sunderland, MA, USA, 546 pp.
- ARTHUR, L. & LEMAIRE, M. (2021). Les Chauves-souris de France, Belgique, Luxembourg et Suisse. 3rd edition. ed.: Biotope -Muséum national d'Histoire naturelle. Pairs, France, 592 pp.
- BARATAUD, M. (2015). Acoustic ecology of European bats. Species identification and studies of their habitats and foraging behaviour. ed.: Biotope Muséum national d'Histoire naturelle. Paris, France, 340 pp.
- BAS, Y., BAS, D. & JULIEN, J. -F. (2017). Tadarida: a toolbox for animal detection on acoustic recordings. J Open Res Softw, 5(1): 6. https://doi.org/10.5334/jors.154
- BARRÉ, K., LE VIOL, I., JULLIARD, R., PAUWELS, J., NEWSON, J. E., JULIEN, J. -F., CLAIREAU, F., KERBIRIOU, C. & BAS, Y. (2019). Accounting for automated identification errors in acoustic surveys. *Methods Ecol Evol*, 10(8): 1171-1188. https://doi. org/10.1111/2041-210X.13198
- BRITZKE, E. R., GILLAM, E. H. & MURRAY, K. L. (2013). Current state of understanding of ultrasonic detectors for the study of bat ecology. Acta Theriol, 58: 109-117. https://doi.org/10.1007/ s13364-013-0131-3
- BROOKS, M., KRISTENSEN, K., VAN BENTHEM, K. J., MAGNUSSON, A., BERG, C. W., NIELSEN, A., SKAUG, H. J., MAECHLER, M. & BOLKER, B. M. (2018). glmmTMB: Generalized Linear Mixed Models using Template Model Builder.
- BROWNING, E., GIBB, R., GLOVER-KAPFER, P. & JONES, K. E. (2017). Passive acoustic monitoring in ecology and conservation. ed.: WWF Conservation Technology Series. On-line, 75 pp.
- DEMŠAR, U., BUCHIN, K., CAGNACCI, F., SAFI, K., SPECKMANN, B., VAN DE WEGHE, N., WEISKOPF, D. & WEIBEL, R. (2015). Analysis and visualisation of movement: an interdisciplinary review. *Mov Ecol*, 3: 5. https://doi.org/10.1186/s40462-015-0032-y
- DIETZ, C., VON HELVERSEN, O. & NILL, D. (2009). Bats of Britain, Europe and Northwest Africa. ed.: Black Publishers. London, UK, 400 pp.
- DOHERTY, T. S. & DRISCOLL, D. A. (2018). Coupling movement and landscape ecology for animal conservation in production landscapes. *Philos T R Soc B*, 28520172272. http://doi. org/10.1098/rspb.2017.2272

- FRASER, E. E., SILVIS, A., BRIGHAM, R. M. & CZENZE, Z. J. (2020). Bat echolocation research: a handbook for planning and conducting acoustic studies, second edition. ed.: Bat Conservation International. On-line, 135 pp.
- GRIFFIN, D. R., WEBSTER, F. A. & MICHAEL, C. R. (1960). The echolocation of flying insects by bats. *Anim Behav*, 8(3-4): 141-154. https://doi.org/10.1016/0003-3472(60)90022-1

HARTIG, F. (2017). Package 'DHARMa.' R package.

- KERBIRIOU, C., BAS, Y., LE VIOL, I., LORRILLIERE, R. MOUGNOT, J. & JULIEN, J. F. (2018). Potential of bat pass duration measures for studies of bat activity. *Bioacoustics*, 28(2): 177-192. https://doi. org/10.1080/09524622.2017.1423517
- KOBLITZ, J. C. (2018). Arrayvolution: using microphone arrays to study bats in the field. *Can J Zool*, 96(9). https://doi. org/10.1139/cjz-2017-0187
- LAFORGE, A., ARCHAUX, F., COULON, A., SIRAMI, C., FROIDEVAUX, J., GOUIX, N., LADET, S., MARTIN, H., BARRÉ, K., ROEMER, C., et al. (2021). Landscape composition and life-history traits influence bat movement and space use: analysis of 30 years of published telemetry data. *Global Ecol Biogeogr*, 30(12): 2442-2454. https://doi.org/10.1111/geb.13397
- LÓPEZ-BAUCELLS, A., TORRENT, L., ROCHA, R., BOBROWIEC, P. E. D., PALMEIRIM, J. M. & MEYER, C. F. L. (2019). Stronger together: combining automated classifiers with manual post-validation optimizes the workload vs reliability trade-off of species identification in bat acoustic surveys. *Ecol Inform*, 49: 45-53. https://doi.org/10.1016/j.ecoinf.2018.11.004
- LÜDECKE, D., AUST, F., CRAWLEY, S. & BEN-SHACHAR, M. (2020). Package 'ggeffects.' Create tidy data frames of marginal effects for "ggplot" from model outputs 23.
- LÜDECKE, D., BEN-SHACHAR, M. S., PATIL, I., WAGGONER, P. & MAKOWSKI, D. (2021). performance: an R package for assessment, comparison and testing of statistical models. *JOSS*, 6(60): 3139. https://doi.org/10.21105/joss.03139
- MATHEWS, F., ANDERSON, M., COOMBER, F., FINCH, D., LE MARQUAND, C., O'MALLEY, K. & WRIGHT, P. (2023). Common Pipistrelle *Pipistrellus pipistrellus* (Schreber, 1774). In: Chiroptera. Handbook of the Mammals of Europe. ed.: Springer, Cham. On-line, p.555-589. https://doi.org/10.1007/978-3-030-44029-9_66

- MORRANT, D. S., TURNER, J. M., JENSEN, M. A., HANSEN, N. A., BOWER, D. S., KÖRTNER, G., MEEK, P. D., PESTELL, A. J., RISMILLER, P. D. & WAUDBY, H. P. (2022). Wildlife tracking methods. In: Wildlife research in Australia: practical and applied methods. ed.: CSIRO Publishing. China, p.180-200. https://doi. org/10.1071/9781486313457
- R CORE TEAM. (2021). R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- RIOTTE-LAMBERT, L. & MATTHIOPOULOS, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends Ecol Evol*, 35(2): 163-174.
- ROEMER, C., JULIEN, J. -F., PATRICE AHOUDJI, P., CHASSOT, J. M., GENTA, M., COLOMBO, R., BOTTO, G., NEGREIRA, C. A., DJOSSA, B. A., ING, R. K., et al. (2021). An automatic classifier of bat sonotypes around the world. *Methods Ecol Evol*, 12(12): 2432-2444. https://doi.org/10.1111/2041-210X.13721
- RUSS, J. (2021). Bat calls of Britain and Europe: a guide to species identification. ed.: Pelagic Publishing. Exeter, UK, 432 pp.
- SALDANHA, S., COX, S. L., MILITÃO, T. & GONZÁLEZ-SOLÍS, J. (2023). Animal behaviour on the move: the use of auxiliary information and semi-supervision to improve behavioural inferences from Hidden Markov Models applied to GPS tracking datasets. *Mov Ecol*, 11: 41. https://doi.org/10.1186/s40462-023-00401-5
- SCHLOESING, E., CARON, A., CHAMBON, R., COURBIN, N., LABADIE, M., NINA, R., MOUITI MBADINGA, F., NGOUBILI, W., SANDIALA, D., TOBI, N., et al. (2023). Foraging and mating behaviors of *Hypsignathus monstrosus* at the bat-human interface in a central African rainforest. *Ecol Evol*, 13(7): e10240. https://doi. org/10.1002/ece3.10240
- SMOUSE, P. E., FOCARDI, S., MOORCROFT, P. R., KIE, J. G., FORESTER, J. D. & MORALES, J. M. (2010). Stochastic modelling of animal movement. *Phil Trans R Soc B*, 365: 2201-2211. http://doi. org/10.1098/rstb.2010.0078
- WILLIAMS, H. J., TAYLOR, L. A., BENHAMOU, S., BIJLEVELD, A. I., CLAY, T. A., DE GRISSAC, S., DEMŠAR, U., ENGLISH, H. M., FRANCONI, N., GÓMEZ-LAICH, A., et al. (2020). Optimizing the use of biologgers for movement ecology research. J Anim Ecol, 89(1): 186-206. https://doi.org/10.1111/1365-2656.13094