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Characterising diel activity patterns to design conservation measures: case study of European bat species

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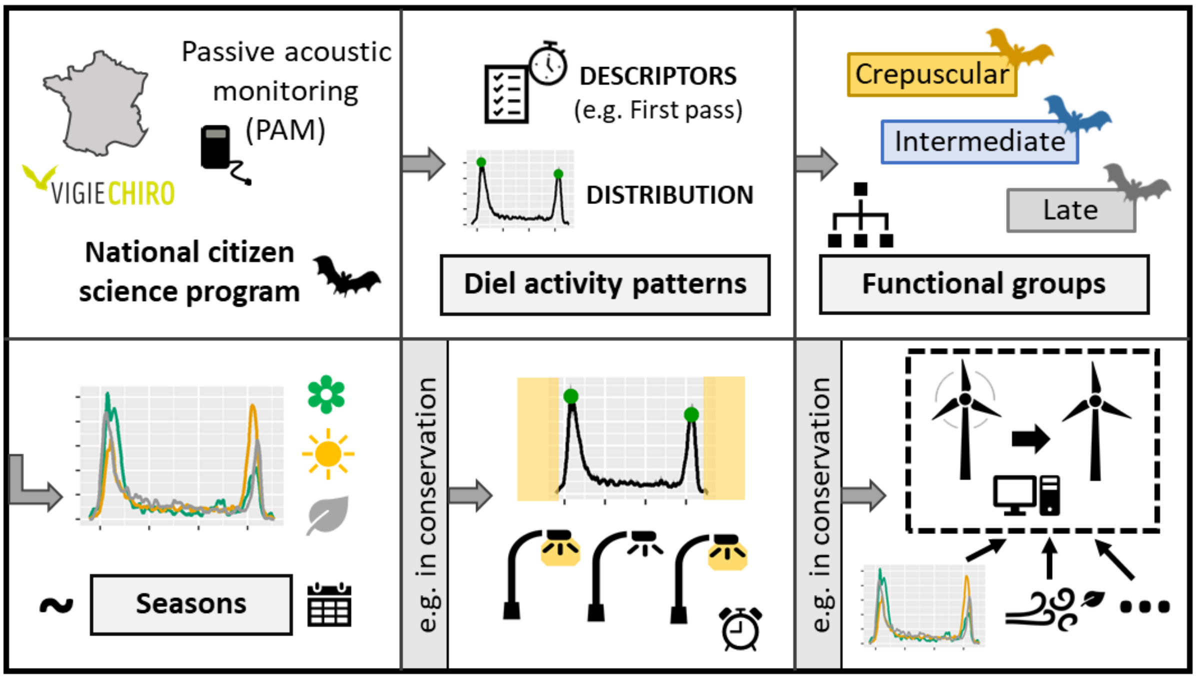

Graphical abstract

Highlights

Conservation should include species temporal distribution besides their spatial one.

Citizen science programs enable to study bat diel activity patterns at wide scales.

Similarities in diel activity patterns of bats enable to define functional groups.

Seasons can interact with the time of night to determine diel activity patterns.

Diel activity patterns should be considered to design efficient mitigation measures.

Abstract

Although diel activity time is a major axis of species' niche space, very few conservation measures focus on preserving daily periods free of anthropogenic pressures. While the spatial ecology of bats has received much attention, less is known about their temporal ecology, the knowledge being dispersed in studies of limited taxonomical, spatial and temporal range. We used data from the French bat monitoring program based on citizen science and standardised acoustic recordings (4409 sites monitored and 9807 nights monitored from 2014 to 2020) to characterise the diel activity patterns of 20 bat species so that their consideration in mitigation measures can help conservation. We designed a method to extract times of key descriptors and describe bat activity distribution throughout the night. We found that bat species could be separated in three functional groups characterised by a crepuscular activity, an activity that occurs when it is completely dark or an intermediate activity. We showed variations of diel activity patterns depending on season. We argue that accounting for these complex diel activity patterns would help design efficient mitigation measures, for instance to reduce the exposure of bats to light pollution or wind turbines. Overall, we advocate multi-taxa approaches to design conservation policies adapted to both the temporal and spatial distributions of species.

Keywords

Bats, Chiroptera, Citizen science, Diel activity pattern, Mitigation measures, Passive acoustic monitoring

Data availability

The estimated densities of bat diel activity are available at https://doi.org/10.5281/zenodo.7458476.

1. Introduction

To address conservation issues, biological conservation must be holistic, considering multiple spatial and temporal scales (Lindenmayer and Hunter, 2010). Spatial ecology has developed to meet this challenge and guide conservation measures from local to global scales (e.g. from the designation of local reserves to the rationalised designation of networks of protected areas and corridors). Space protection has fit in (inter)national regulations and global discussions (e.g. National park designation, Natura 2000 network, Aichi biodiversity target of 17 % of terrestrial surfaces protected by 2020). Conversely, and despite the importance of time in shaping ecosystems, temporal ecology has received much less attention (Wolkovich et al., 2014).

Since anthropogenic changes can alter temporal dynamics of ecosystems at various scales, protecting time should be as important a concern as protecting space. However, conservation measures explicitly based on the temporal ecology of species are mainly implemented at local spatial scales, most are incentives rather than regulations and they generally focus on the annual scale (e.g. changing timing of building work to avoid bat hibernation and maternity season, delaying mowing in pastures to protect chicks and nests of ground-nesting birds, prohibiting hunting of species during reproduction, etc.) (Sutherland et al., 2021). In contrast, finer temporal scales are more rarely accounted for in conservation measures.

Although diel activity time is a major axis of species’ niche space (Schoener, 1974), very few conservation measures focus on preserving daily periods free of anthropogenic pressures. In response to the 24-h periodicity of their environment, living organisms have developed endogenous circadian rhythms entertained by exogeneous influences (e.g. temperature and light-dark cycles) (Aschoff, 1989; Erkert, 1982). These mechanisms allow them to occupy a given temporal niche and coordinate their activity with that of other organisms with which they interact (e.g. conspecifics, predators, prey) (Aschoff, 1989; Erkert, 1982). Time of high species activity should hence be protected to preserve biodiversity at multiple scales, from individual fitness to ecosystem functions.

The very few conservation measures focusing on sharing daily time between human activities and biodiversity tend to be based on the times when human needs are lowest rather than on the diel activity patterns of species. For instance, part-night lighting (PNL, i.e. switching off public lighting during the middle of the night) aims to reduce light pollution impacts on biodiversity (Gaston et al., 2012). However, current PNL schemes are not efficient enough as they do not encompass the range of activity of nocturnal species such as bats (Azam et al., 2015; Day et al., 2015; Hooker et al., 2022). Similarly, algorithm-based curtailment of wind turbines aims to reduce bat fatalities while minimising energy production losses. The most widespread curtailment strategy is only based on a windspeed threshold below which the turbine is curtailed due to expected high bat activity. While curtailment has been shown to be efficient, its results remain variable and it does not fully reduce fatalities (Adams et al., 2021; Whitby et al., 2021). Its efficacy would benefit from considering other variables impacting bat activity such as diel activity time (Behr et al., 2017; Friedenberg and Frick, 2021). To include diel activity patterns in conservation measures, a general knowledge on species' temporal distribution, based on standardised and comparable metrics, should be available, which is not the case so far for taxa like bats.

As European bats are a diversified group mainly composed of long-lived insectivorous species occupying high trophic levels, it has been suggested that they can be good bioindicators of the effects of anthropogenic pressures and mitigation measures on biodiversity (Jones et al., 2009; Russo et al., 2021). However, while the spatial ecology of bats has received much attention (e.g. Laforge et al., 2021) less is known about their diel activity patterns, knowledge being dispersed in literature. Most studies informing on diel activity patterns are monospecific and the activity patterns of many European species have received little to no attention (e.g. *Myotis emarginatus*, *Tadarida teniotis*) (see Appendix A for an overview of the scientific literature). Existing studies have almost all been conducted at local spatial scales (however, at large scales see Day et al., 2015; Mariton et al., 2022; Newson et al., 2015) and they tend to be biased toward monitoring emergence at roosts. Some authors showed that diel activity patterns can vary throughout the year, rising the need for studies conducted at large temporal scales (e.g. Robinson and Stebbings, 1997; Swift, 1980).

The dispersed knowledge on bat diel activity pattern could be synthesised in a review as Jones and Rydell (1994) did for the time of emergence. However, it would be based on a small number of papers with limited taxonomical, spatial and temporal scope. It would not encompass environmental gradients within species' range and would not provide comparable data between species. In comparison, citizen science coupled with technological developments (e.g. acoustic monitoring, computer vision) offers great opportunities to monitor biodiversity at unprecedented spatiotemporal scales (Newson et al., 2015; van Klink et al., 2022). Newson et al. (2015) showed, at a regional scale, the potential for public contribution to provide new insights into the temporal ecology of bats.

Ecologists lack a unified method to describe bat diel activity patterns. In some studies (e.g. Day et al., 2015; Hooker et al., 2022; Newson et al., 2015), they were characterised by a level of activity during time periods (e.g. every hour). While this method can provide an overview of the activity distribution throughout the night, it discretises continuous time series and implies to choose a time period that maximize precision (i.e. shortest periods possible) without flattening activity patterns (i.e. enough activity per period). Other authors focused on times of "key descriptors", such as the time of first or median emergence (Bullock et al., 1987; Jones and Rydell, 1994). It enables to not discretise time series, but it does not describe the activity distribution throughout the night. These methods appear to be complementary by providing different information on the temporal ecology of bats.

We used data from a citizen science bat monitoring program – based on standardised acoustic monitoring throughout France (4409 sites monitored and 9807 nights monitored from 2014 to 2020) – to characterise the diel activity patterns of 20 bat species. Through the calculation of the times of key descriptors and the representation of the activity distribution throughout the night, we aimed to provide a synthetic and general knowledge on bat diel activity patterns. This knowledge could be used in conservation, for instance, to distinguish functional groups of species that could inspire multi-taxa approaches or to pave the way for the consideration of variation of diel activity patterns throughout the year to design efficient conservation measures. In particular, we predicted that (1) the overall diel activity patterns of bat species will be driven by their diet and foraging strategies along with their ability to avoid predation, (2) that bat diel activity patterns will vary throughout the year according to their reproduction phenology.

2. Materials and methods

2.1. Biological data

We used data from the “stationary points protocol” of the French citizen science bat monitoring program Vigie-Chiro (coordinated since 2014 by the French National Museum of Natural History, https://www.vigienature.fr/fr/chauves-souris) (see Appendix B for details on data acquisition and curation). Volunteers were asked to set up ultrasonic recorders on potential bat commuting/foraging sites for at least one full-night. We used data from 9807 monitored nights on 4409 sites. Preliminary analyses ensured that the monitored sites covered similar land-use gradients as randomly selected sites in France.

We considered bat passes, defined as the occurrence of a single or several bat calls during a 5-s interval (Millon et al., 2015) as a proxy for activity. Species identification was performed with the Tadarida software which classifies bat passes into classes according to a confidence index value (Bas et al., 2017). We only kept passes with a confidence index value greater than 0.5, to obtain, for each species, a maximum error rate tolerance (MERT) of 0.5. *Myotis blythii* and *Myotis myotis* were grouped in a complex named Great *Myotis* because of their high acoustic similarity (Barataud, 2020). Species for which there were not enough data (i.e. in less than 200 sites after data curation) and species for which we considered that automatic identification was not robust enough were discarded. Eventually, we studied 20 species. To ensure result robustness against automated identification errors that could persist despite the precautions we took when filtering and analysing the data, we chose to follow the approach of Barré et al. (2019) (Appendix C). We showed that our results were not sensitive to the error rates considered and were robust against automated identification errors.

2.2. Characterisation of the diel activity patterns

2.2.1. Key descriptors

First, we characterised diel activity patterns by defining “key descriptors” within nights. Indeed, descriptors such as the time of emergence has been related to reproduction success (Boldogh et al., 2007; Duvergé et al., 2000). We considered the percentage of the night elapsed (R 4.2.0 (R Core Team, 2022), R package *StreamMetabolism* (Sefick, 2016)). Indeed, we could not use raw time to characterise diel activity patterns as bat activity tends to be parallel to sunset and sunrise times (Erkert, 1982) and as, in our large-scale dataset these times are variable according to the period of the year, latitude and longitude. Hours after sunset have been used in some studies (e.g. Day et al., 2015; Jones and Rydell, 1994; Newson et al., 2015). However, considering hours after sunset as a measure of time does not correct for the variable time of sunrise. In comparison, the percentage of the night elapsed allows the sunset time to always be equal to zero and the sunrise time to 100.

We calculated the time of five “key descriptors” for each species: (i) the time of the median pass (TMedian), (ii) the time of the first pass (TFirst) and the median pass (TMedianP1) during the first part of the night, (iii) the time of the last pass (TLast) and the median pass (TMedianP2) during the second part. TFirst and TLast rely on a single pass and are vulnerable to extreme values, however they provide information on the start and the end of activity independently of the overall activity pattern. Conversely, TMedian, TMedianP1 and TMedianP2 are less influenced by extreme values and provide information on the overall activity pattern. We considered the medians during each night half because previous studies showed that diel activity patterns of insectivorous bats tend to be bimodal with a first activity peak after sunset and a second, weaker, before sunrise (Erkert, 1982).

We calculated an overall value for the time of each key descriptor (hereafter called the “mean” value) following the workflow presented in Fig. 1. To account for the hierarchical structure of the dataset, we calculated (i) the times of the key descriptors by night, then (ii) the mean times by site (we applied a weight based on the number of passes by night as we postulated that the more passes there are during a night, the more robust the estimation of the times of the key descriptors), eventually (iii) the mean times over the whole dataset using the mean times by site (we applied a weight based on the mean number of passes by sites) (Appendix D).

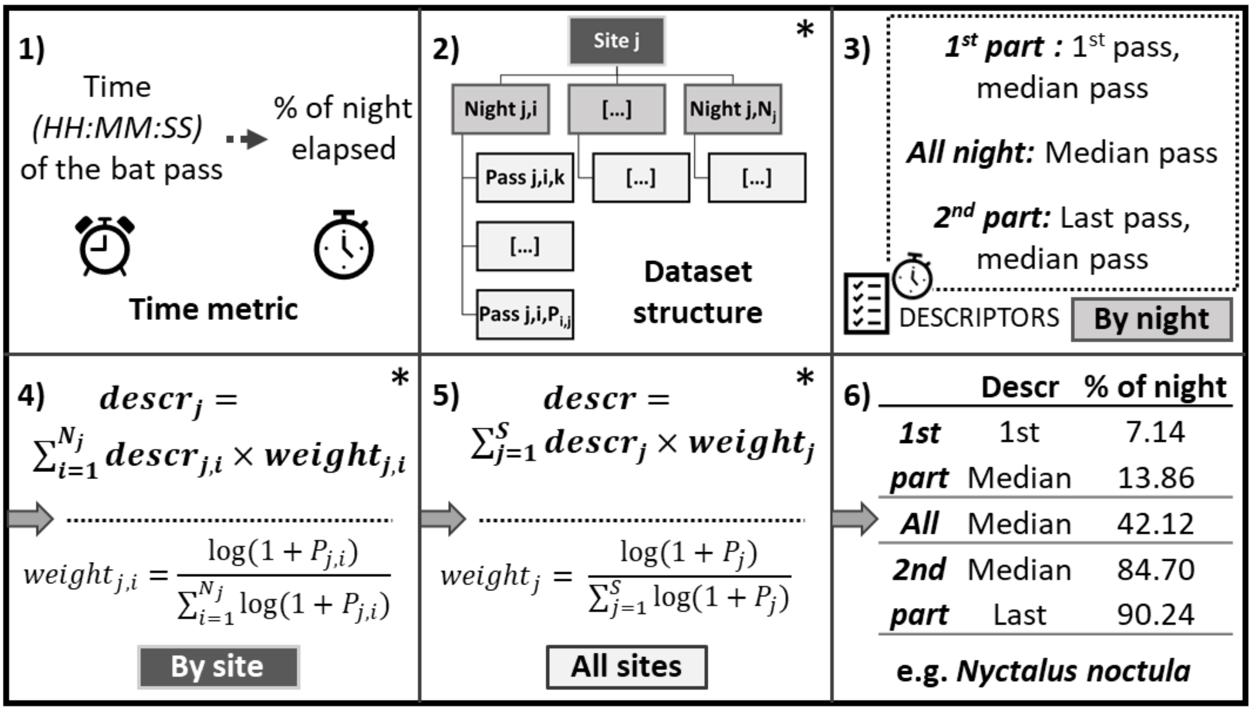

Fig. 1: **Schematic process for the calculation of the times of key descriptors: preliminary information (1-2), method implemented (3-5), example of the mean values for *Nyctalus noctula* (6).**

**** j = site ID; i = i^{th} night of a site; k = k^{th} pass in a night; S = number of sites; N_j = number of surveyed nights at the $site_j$, $P_{j,i}$ = number of passes of the $night_{j,i}$;***

descr = time of the descriptor; P_j = “mean” number of passes of the $site_j$ =

$$[\sum_{i=1}^{N_j} P_{j,i} \times log(1 + P_{j,i})] / [\sum_{i=1}^{N_j} log(1 + P_{j,i})]$$

2.2.2. Activity distribution throughout the night

Secondly, we assessed the activity distribution throughout the night by calculating an estimated density of activity (R function *density*) (see Appendix D). In previous studies (e.g. Day et al., 2015; Newson et al., 2015), some authors considered the number of bat passes during given time periods (e.g. every hour). In comparison, density estimation allowed to better account for the continuous aspect of our data.

We followed the workflow presented in Fig 2. We used all the passes of each species as, for rare species particularly, there were not enough passes to characterise the activity distribution by night. We accounted for the hierarchical structure of our dataset by assigning a weight to each pass so that (i) the weight of a site in the density calculation was based on the mean number of passes of this site, (ii) the weight of a night within a site was based on the number of passes of this night, (iii) each pass of a night within a site had the same weight. We calculated 95 % confidence bands for the estimated densities using bootstrap (1000 resamples). We defined the times of activity peaks (TPeakP1 and TPeakP2 for peaks occurring during the first part and the second part of the night respectively) as the times of local density maxima with a high peak score (a high peak score meaning that the distance between the density value at a time point was high compared the density values surrounding it) (R package *scorepeak* (Ochi, 2019)).

We calculated a cumulative curve of weighted bat activity throughout the night using the cumulative weight of all passes ranked by increasing percentage of the night elapsed. To assess whether the weighted activity of a species was concentrated around activity peaks or more evenly distributed throughout the night, we searched for the 15 % interval of the night during which its weighted activity was maximum and we calculated this maximum.

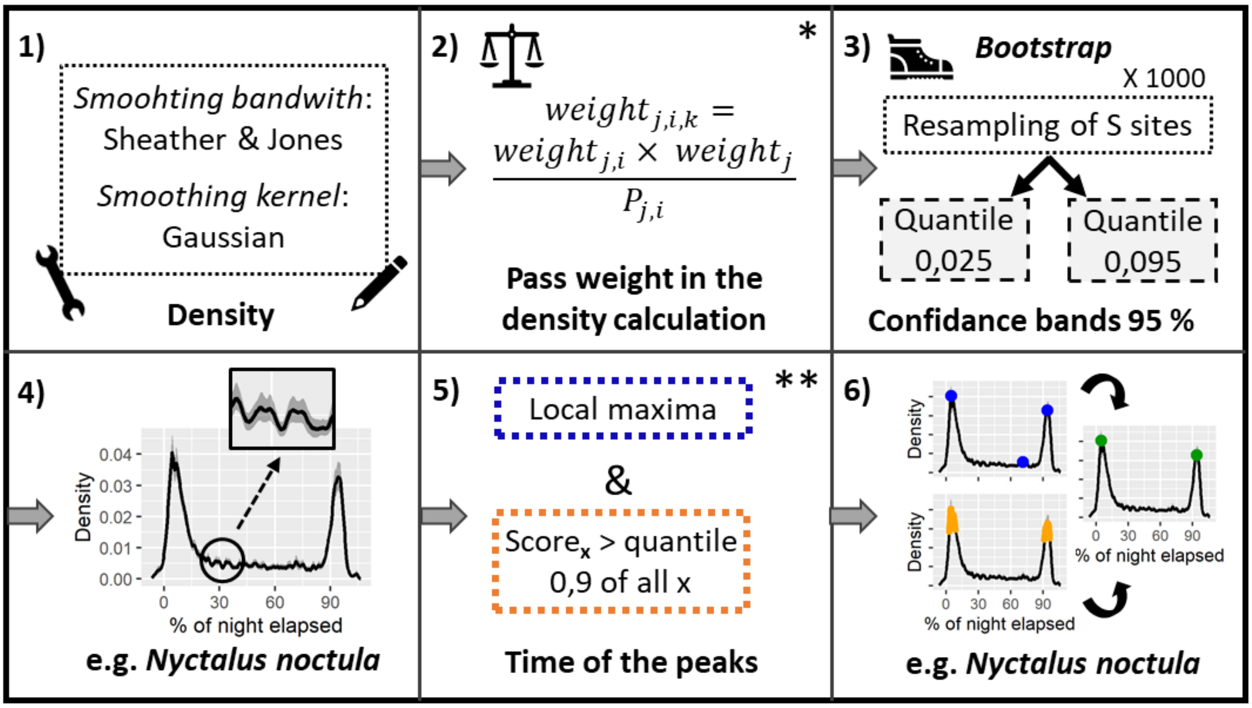

Fig. 2: Schematic process of the characterisation of the activity distribution throughout the night: calculation of a density (1-2), calculation of the confidence bands (S being the number of sites in the dataset for the species considered), (3) example: activity pattern *of Nyctalus noctula* (4), extraction of the time of the activity peaks (5), example: peak detection *for N. noctula* (6).

**** see legend Fig.1***

***** For local maxima and score calculation, window of temporal neighbours = 129 (i.e. 1/4 of the night); x = percentage of night elapsed discretised;***

$score_x = density_x$ – mean (density of the temporal neighbours)

2.3. Examples of comparison of diel activity patterns inter- and intra-species

2.3.1. Activity distribution throughout the night according to the season

To assess variations of activity distribution throughout the night according to the season, we estimated the densities of activity on subsets of our datasets. Indeed, some authors showed that bat diel activity patterns could change according to their reproductive states (e.g. Robinson and Stebbings, 1997; Swift, 1980). We applied the density calculation method to three temporal subsets: spring (1 March to 21 June, 1447 sites, 2762 nights), summer (22 June to 21 August, 2448 sites, 4373 nights) and autumn (22 August to 31 October, 1342 sites, 2642 nights). In France, for most species, these periods corresponded approximately to the hibernation ending/gestation, lactation and dispersion/reproduction (Arthur and Lemaire, 2015).

2.3.2. Clustering of the species

To determine whether species could be clustered in functional groups according to similarities in their diel activity patterns, we performed a Hierarchical Clustering on the Principal Components (HCPC) of a Principal Component Analysis (PCA) (R package *FactoMineR* (Lê et al., 2008)), the variables used being the times of the keys descriptors and the times of the activity peaks. For each variable, we calculated the difference between the average for the species in a cluster and the overall average (i.e. the average for all species studied). We tested whether the average in each cluster was equal to the overall average (Husson et al., 2010, 2009).

3. Results

3.1. Diel activity pattern description

The mean time of the key descriptors and the time of the activity peaks varied greatly according to the species (Fig. 3, Table E and Fig. G). We did not detect any activity peak for *Myotis mystacinus* and *Plecotus auritus*. For six species, we detected a unimodal activity pattern with a single activity peak in the first part of the night (*Barbastella barbastellus Eptesicus serotinus*, the Great *Myotis*, *Myotis daubentonii, Pipistrellus nathusii* and *Plecotus austriacus*). For the remaining 12 species, we detected a bimodal activity pattern with one peak during the first part of the night and another during the second. As the times of the peaks were extracted from the estimated density using all weighted passes they are not directly comparable to the times of the key descriptors calculated as successive weighted means by night and site.

The activity distribution throughout the night varied substantially according to the species (Fig. 4 and Fig. H). For instance, the 15 % interval of the night with the most activity occurred at the beginning of the night and included the TFPeak for all species for which we detected an activity peak (except for *T. teniotis*). However, the percentage of weighted activity during this interval varied from 17.4 % for *M. emaginatus* – whose activity is almost uniformly distributed – to 43.1 % for *Hypsugo savii* – whose activity is strongly condensed into peaks (Table I). Some species were more crepuscular than others: for instance, 54 % of the weighted activity of *Nyctalus noctula* occurred before 10 % of the night had elapsed and after 90 % of the night had elapsed, compared to only 7.7 % of the weighted activity of *P. auritus*.

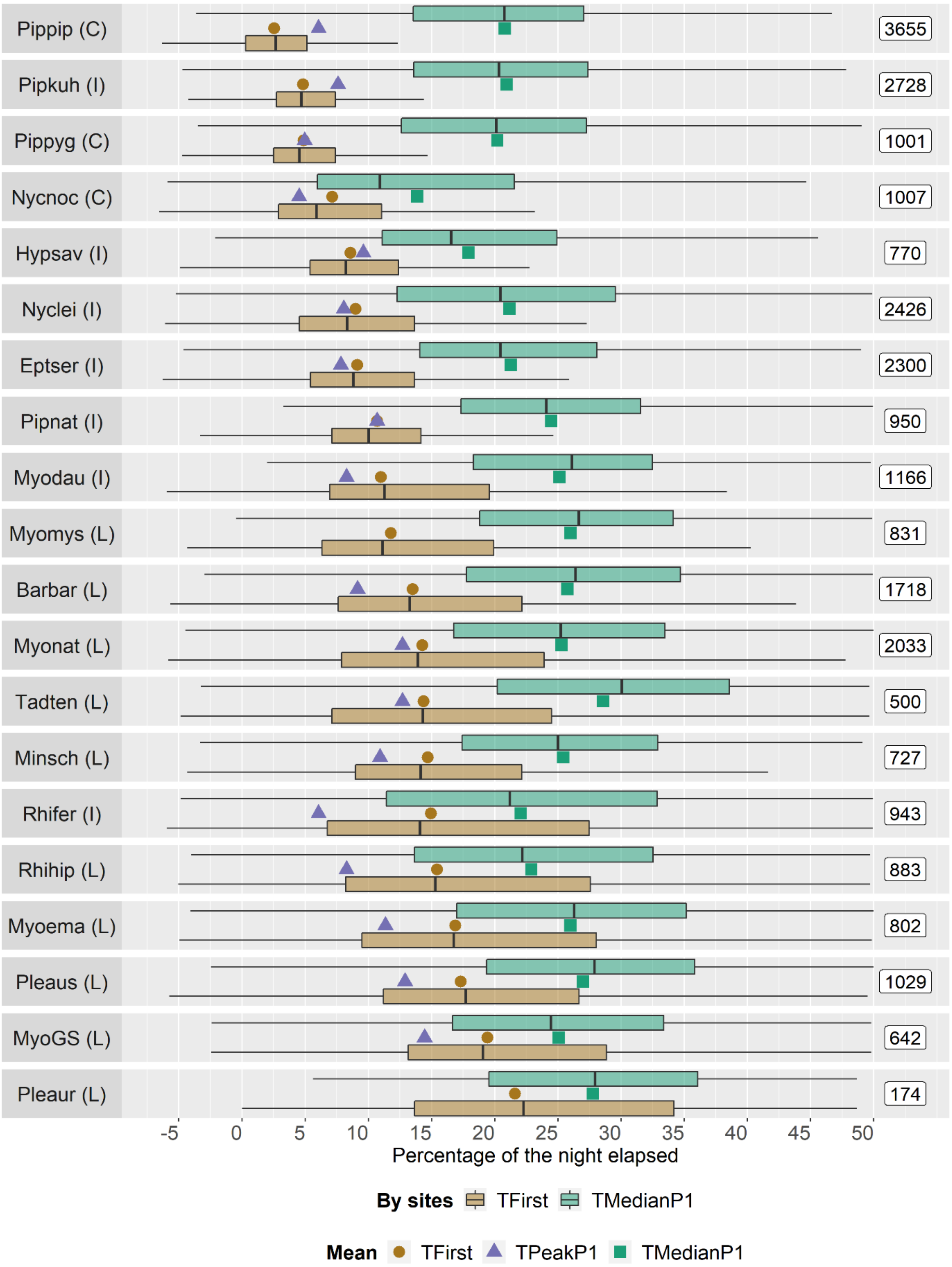

Fig. 3: *TFirst, TPeakP1 and TMedianP1 for each bat species. On the left are the codes of the species studied (correspondence between the codes and the full Latin and English names in Table F), followed by the cluster in which they were classified according to the HCPC (C: crepuscular species, I: intermediate species, L: late species). On the right is the number of sites monitored by species. Species are ranked by increasing value of mean TFirst. For Pipistrellus pygmaeus (Pippyg) and Pipistrellus nathusii (Pipnat) the mean TPeakP1 and TFirst were almost equal.*

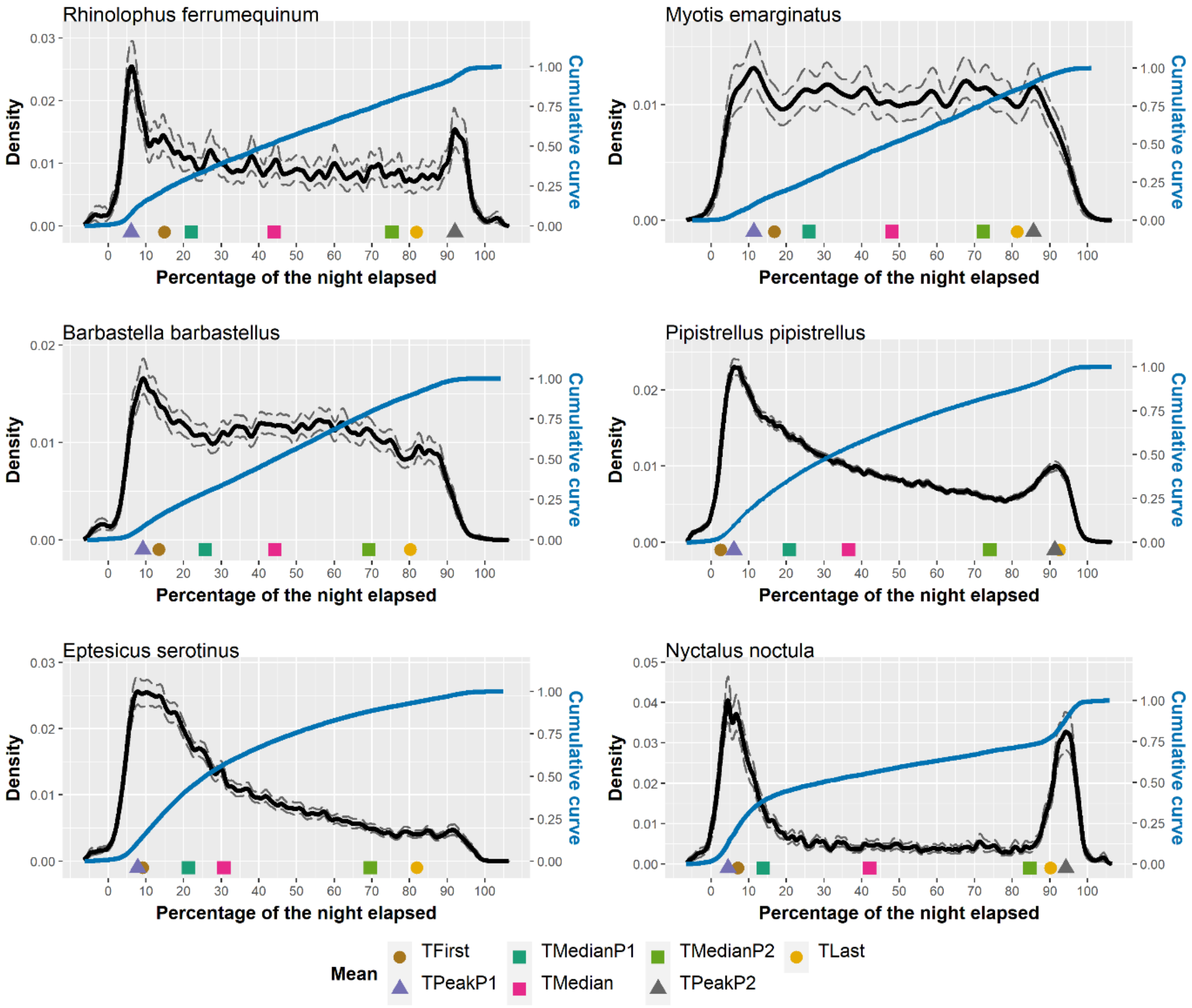

***Fig*. 4: Activity distribution throughout the night for six species: in black, estimated density of activity according to the percentage of the night elapsed. In blue, cumulative curve of weighted bat activity. The dashed lines represent the 95 % confidence bands for the estimated density. Symbols represent the mean times of the key descriptors and the times of the activity peaks detected.**

3.2. Clustering of species according to their temporal niche

The species clustering resulted in three clusters (Table 1, Appendix J). The first cluster, composed of *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *N. noctula* was characterised by an earlier activity at the beginning of the night and a later activity at the end, we called the species in this group “crepuscular” species. The second cluster was composed of ten species:

Table 1: Description of the clusters: "*Average cluster*" and "*Overall average*" correspond to the average of the variables (mean times of the key descriptors or times of the activity peaks) for the species in the cluster and for all species respectively. "*p.value*" is the p-value obtained by testing the hypothesis: "*the average of the cluster is equal to the overall average*". Only variables for which the p-value was lower than 0.05 for the cluster are shown. "*Diff in %*" is the difference between the average in the cluster and the overall average in percentage of the night elapsed. "*Diff in min*" is the difference in minutes for a nine-hour night.

Cluster	**Key descriptors**	**Average cluster**	**Overall average**	**Diff in %**	**Diff in min**	**p.value**
Crepuscular	TLast	91.5	83.7	7.8	42.2	0.0016
	TMedianP2	78.2	72.7	5.5	30.0	0.0034
	TPeakP2	92.7	85.8	6.9	37.2	0.0368
	TPeakP1	5.2	9.7	-4.5	-24.2	0.0097
	TMedianP1	18.3	23.4	-5.1	-27.5	0.0081
	TFirst	4.9	12.1	-7.2	-39.1	0.0072
Intermediate	TMedian	37.0	41.7	-4.7	-25.3	0.0078
Late	TFirst	15.9	12.1	3.8	20.7	0.0007
	TMedianP1	26.0	23.4	2.6	14.0	0.0013
	TPeakP1	12.0	9.7	2.3	12.4	0.0016
	TMedian	45.6	41.7	3.9	21.3	0.0023
	TLast	80.8	83.7	-3.0	-15.9	0.0046
	TPeakP2	81.5	85.8	-4.4	-23.6	0.0016

the Great *Myotis*, *P. auritus*, *M. emarginatus*, *Myotis nattereri*, *P. austriacus*, *Rhinolophus hipposideros*, *M. mystacinus*, *T. teniotis*, *B. barbastellus* and *Miniopterus schreibersii*. It was characterised by a later activity at the beginning of the night and a sooner end of activity at the end, we called species in this group "late" species. The last cluster was composed of seven species: *Pipistrellus kuhlii*, *H. savii*, *E. serotinus*, *M. daubentonii*, *P. nathusii*, *Nyctalus leisleri* and *Rhinolophus ferrumequinum*. These species had an activity at the beginning and the end of the night intermediate between those of the "crepuscular" and "late" species, with an average TMedian that was significantly earlier than the average considering all species. We called species in this group "intermediate" species.

3.3. Variations of the activity distribution throughout the night according to the seasons

Despite slight variations, the times of the activity peak and the activity distributions throughout the night remained generally similar across all seasons (Fig 5, Fig. K). However, for some species, the amplitudes of the activity peaks changed between seasons (e.g. weak and widespread activity peak at the beginning of the night for *E. serotinus* in summer, compared to thinner and stronger peaks during other seasons). For some species, activity peaks were not even detectable during some periods (e.g. strong activity peak at the beginning of the night for *B. barbastellus* in spring, compared to weak or even non-detectable peaks during other seasons).

Bats tended to be proportionally more active at the end of the night in summer. For all species (except for the Great *Myotis*), the percentage of weighted activity occurring after 80 % of the night had elapsed was greater in summer than in other seasons (considering all species, mean difference of weighted activity between summer and spring: 4.6 %, between summer and autumn: 6.3%). The percentage of weighted activity occurring after 80 % of the night had elapsed was also greater in spring than in autumn for 15 species out of 20 (mean difference of weighted activity between spring and autumn: 1.6 %).

Conversely, bats tended to be proportionally less active at the beginning of the night in summer. For all species (except for both *Rhinolophus*), the percentage of weighted activity occurring before 20 % of the night had elapsed was weaker in summer than in other periods (mean difference of weighted activity between summer and spring: -7.7 %, between summer and autumn: -5.4 %). The percentage of weighted activity occurring before 20 % of the night had elapsed was also greater in spring than in autumn for 13 species out of 20 (mean difference of weighted activity between spring and autumn: 2.3 %).

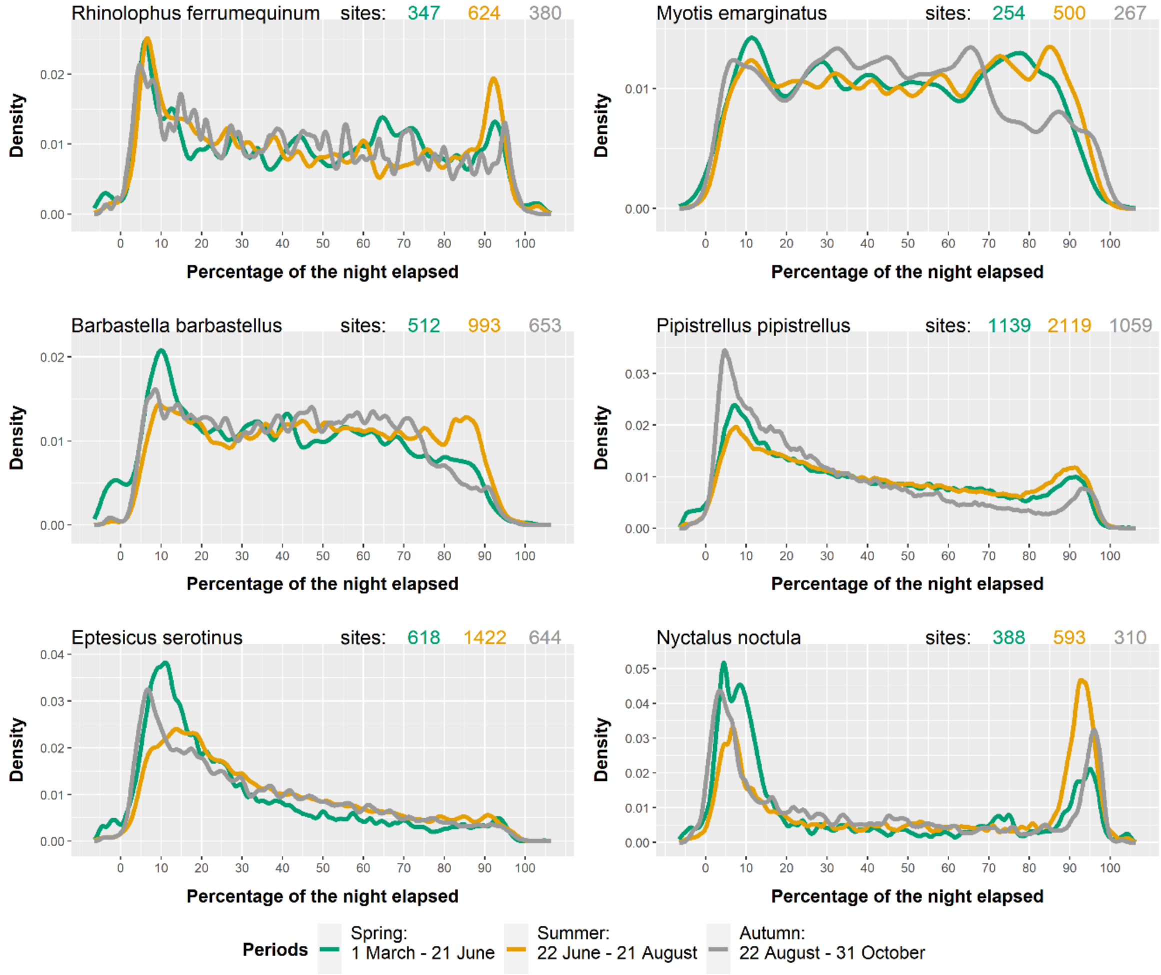

Fig. 5: Activity distribution throughout the night for six species according to season, in percentage of the night elapsed. Top right, number of sites considered for each season.

4. Discussion

The use of a seven-year nationwide citizen science project gave us the opportunity to characterise the diel activity patterns of 20 insectivorous bat species at broad spatial and temporal scales. We showed that, although these patterns varied substantially between species, species could be grouped according to similarities in their temporal niches. Diel activity patterns also varied according to the season. We argue that this knowledge can be used to inform conservation measures to better preserve key times of bat diel activity.

4.1. Characterisation of diel activity patterns

We developed a methodology that can be applied to all taxa, whether abundant or rare, and at different spatial scales. This allowed us to go further than an hourly representation of bat passes by providing the times of key diel descriptors and a representation of activity distribution throughout the night, while accounting for the hierarchical structure of the dataset. The representativity and the large number of sites of the Vigie-Chiro dataset allowed to provide robust results that could be a first step toward further statistical analyses on the impacts of environmental (e.g. reproductive status, weather) and/or anthropogenic stressors (e.g. land-use change, pollution) on bat diel activity patterns while controlling for possible spatiotemporal autocorrelation issues (e.g. Mariton et al., 2022).

A strength of this study is to describe the diel activity patterns of many species using a single dataset, allowing direct comparisons between them. As diel activity patterns influence species' performance in a given environment, they can be considered as functional traits (Bennie et al., 2014) and we can thus distinguish functional groups based on similarities in their temporal niches. We distinguished: (1) "crepuscular" species with a marked bimodal activity starting shortly after sunset and ending shortly before sunrise, (2) "late" species with an overall well distributed activity throughout the night (i.e. no activity peak or a weak unimodal or bimodal activity pattern), starting late at night and ending earlier than the activity of the other species, (3) “intermediate” species with a unimodal or bimodal activity pattern and an overall activity that, while fairly early in the night, had intermediate start and end times compared to the other groups.

Such differences in the diel activity patterns of these functional groups can be explained by a trade-off between energy needs and predation risks. Almost all the “crepuscular” and “intermediate” species are known to forage mainly on Diptera (Arthur and Lemaire, 2015; Jones and Rydell, 1994; Ware et al., 2020). It has been suggested that the unimodal to bimodal activity pattern of these species, with peaks at dusk and dawn, resulted from the need to match the abundance peaks of these small insects (Dietz and Kalko, 2007; Jones and Rydell, 1994; Newson et al., 2015; Rydell et al., 1996; Swift, 1980). Almost all the species in these two groups are aerial edge- or open-space-foraging species that are usually considered to have a fast and agile flight, they are then less vulnerable to predation risks when exposed to light, allowing them to be active earlier than other species (Jones and Rydell, 1994; Voigt et al., 2021).

Conversely, most of the “late” species are gleaning or flutter-detecting narrow-space-foraging species that have a low and slow flight, making them more vulnerable to predation when exposed to light (Jones and Rydell, 1994; Voigt et al., 2021). The diet of the “late” species is composed of a large number of Lepidoptera (whose abundance remains quite high throughout the night) and/or flightless prey (Jones and Rydell, 1994; Ware et al., 2020). They can hence forage outside the dusk and dawn activity peaks of Diptera (Entwistle et al., 1996; Jones and Rydell, 1994; Marques et al., 2004; Rydell et al., 1996; Swift, 1997). Thus, it has been suggested that they can remain active throughout the night and avoid higher predation risks by emerging from their roost later than other species, when light levels are low (Entwistle et al., 1996; Jones and Rydell, 1994).

We observed variations in bat diel activity patterns according to the season. The overall patterns remained similar throughout the year, but the amplitude of the activity peaks varied. This is consistent with studies showing that the reproductive status of bats influences their diel activity pattern (Catto et al., 1995; Dietz and Kalko, 2007; Maier, 1992; Swift, 1997, 1980). We observed that there was a greater concentration of bat activity at the end of the night during early summer. The short duration of the night at this time may force bats to exploit the whole night. Besides, early summer matches the lactation period of most species, during which energy requirements are the highest for reproductive females (Racey and Speakman, 1987) and during which they must return to the roost at night to suckle their young. Hence, a greater concentration of activity before sunrise could also be due to the need to forage longer and/or more efficiently (as some insects are abundant at dawn) to reach their high energy requirements while suckling their young after one or more activity bouts.

4.2. Diel activity patterns in conservation policies

We showed that bat diel activity patterns are highly variable according to the species, with variations between seasons. We advocate that this complexity be better accounted for in conservation policies aimed at reducing species' exposure to pressures. This would pave the way for the design of conservation policies that would include both the spatial and the temporal distributions of species, for example, with stronger efforts to spare key diel times of species activity where conservation stakes are highest and to share time where human needs are highest. We illustrated below how conservation measures could better account for diel activity patterns through the example of two pre-existing but still developing measures focusing on pressures that have been recognised as potential drivers of changes in bat population: wind turbines and light pollution (Browning et al., 2021).

Part-night lighting (PNL) is increasingly implemented in Europe (Bennie et al., 2014). Only a few studies have focused on this mitigation measure against light pollution, however they agree on the need to encompass the range of activity of bats, by switching off streetlights earlier, for PNL to be efficient (Azam et al., 2015; Day et al., 2015; Hooker et al., 2022). Our method and results would allow for the possibility of defining a threshold based on a multi-taxa approach, including all bat species targeted by PNL. For instance, Azam et al. (2015) study was conducted in summer in a French regional park. They did not detect a significant effect of PNL on five out of the eight bat species studied, likely because the PNL scheme did not cover their key times of activity. According to our results, at this time and place, implementing a PNL scheme that would start before the mean time of the first pass of the “late” species (i.e. the group of species whose activity starts the latest and which is mainly composed of light-intolerant species) would result in switching off lights on average at 22:33, whereas at the studied sites streetlights were switched off around midnight.

Local people would probably object to the implementation of such a PNL scheme, as streetlights would be switched off when human needs for lighting are likely the highest (Gaston et al., 2012). Finding compromises between the light needs of humans and the dark needs of bats is therefore of importance, one solution being the consideration of both the spatial and the temporal distribution of bats. For instance, streetlights could be switched off early near key sites for bats (e.g. roosts, ecological corridors) while working on other mitigation measures – at least during key times for bat activity – where light is needed by humans and cannot be switched off as early as needed (e.g. changing the light spectrum, reducing light intensity and trespass or installing motion detectors).

Similarly, including bat diel activity patterns in algorithm-based curtailments of wind turbines would be of utmost interest (Behr et al., 2017; Friedenberg and Frick, 2021). This would allow a stricter cut-in speed to be implemented when fatality risks are susceptible to be the highest (e.g. dusk and dawn) than during the rest of the night. However, the curtailment algorithm of Behr et al. (2017), which is now the standard method for mitigating bat collision risks of at wind farms in Germany, is one of the only algorithms we know of that consider bat diel activity patterns (Adams et al., 2021; Whitby et al., 2021). Adding an interaction between the time of the year and the time of the night could even increase the performance of such algorithms. For instance, in the dataset of Behr et al. (2017), *N. noctula* and *P. pipistrellus* were the species that accounted for most of the recordings. According to our results, the times of the two activity peaks of these species remain quite similar throughout the year but their amplitude change with, for instance, a proportionally greater activity at dawn in summer than during the rest of the year. These results hence raise the need for stronger curtailment efforts at dawn during summer.

4.3. Conclusions

We characterised the diel activity patterns of 20 bat species using a nationwide citizen science dataset. This new insight into the temporal ecology of bats can pave the way for fundamental analyses. For instance, insectivorous bat communities are diverse and probably highly structured by competition (Jachowski et al., 2014), studying how temporal niche partitioning determined their activity patterns would hence be of interest. From a conversation perspective, all mitigation measures aimed at reducing the impacts of stressors – whose intensity vary throughout the day – on biodiversity would benefit for a better consideration of species' diel activity patterns in addition to their spatial distribution. We strongly advocate multi-taxa approaches covering as many taxa known to be impacted as possible.

CRediT authorship contribution statement

Léa Mariton : Conceptualization, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Isabelle Le Viol** : Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Yves Bas** : Resources, Data curation, Writing – review & editing. **Christian Kerbiriou** : Conceptualization, Methodology, Writing – review & editing, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices

Appendix A: Overview of scientific literature on bat diel activity patterns

Appendix B: Acquisition and curation of the biological data

Appendix C: Robustness of the automated identification

Appendix D: Additional information on the methods designed to characterise and compare bat diel activity patterns

Table E: Mean time of the key descriptors and time of the activity peaks in percentage of the night elapsed

Table F: Correspondence between species codes and Latin and English full names

Fig. G: TLast, TPeakP2 and TMedianP2 for each bat species

Fig. H: Activity distribution throughout the night for the twenty species studied

Table I: Descriptive metrics on bat activity distribution throughout the night

Appendix J: Clustering results

Fig. K: Activity distribution throughout the night for the 20 species studied according to season