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► To cite this version:

Léa Mariton, Isabelle Le Viol, Yves Bas, Christian Kerbiriou. Characterising diel activity patterns to design conservation measures: Case study of European bat species. *Biological Conservation*, 2023, 277, pp.109852. 10.1016/j.biocon.2022.109852 . hal-03910292v1

HAL Id: hal-03910292

<https://hal.sorbonne-universite.fr/hal-03910292v1>

Submitted on 22 Dec 2022 (v1), last revised 6 Feb 2023 (v2)

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

8

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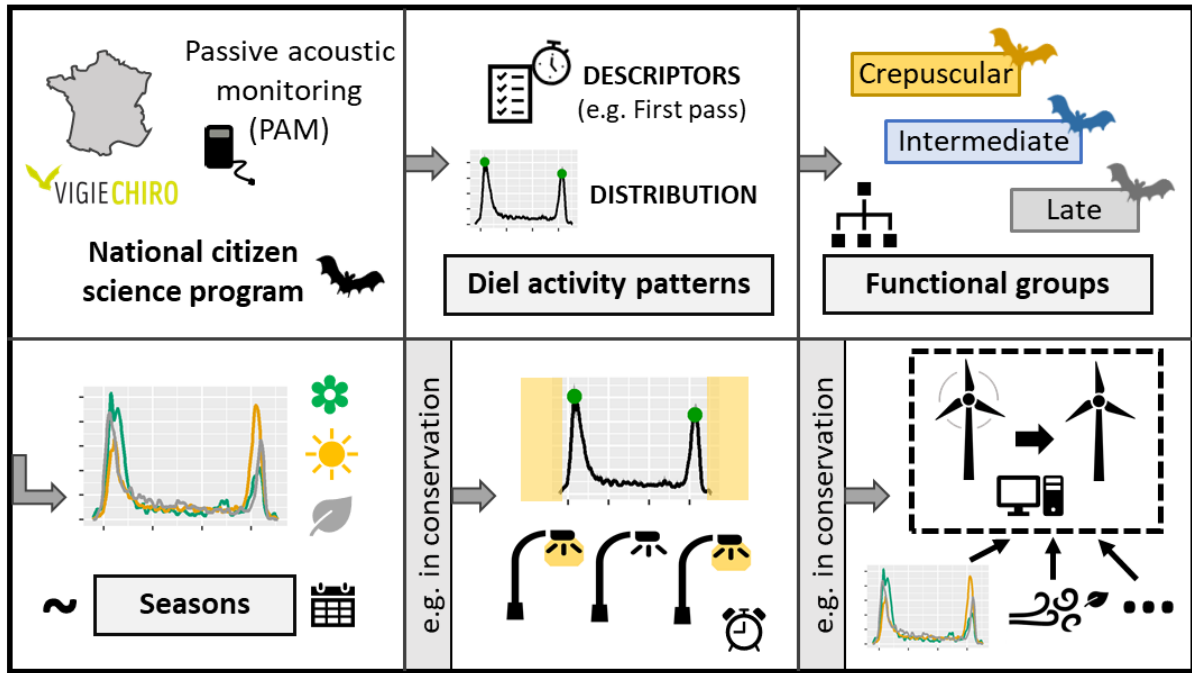
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Graphical abstract

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.

53 **Abstract**

54

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

70

71 **Keywords**

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

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76 **Data availability**

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78 The estimated densities of bat diel activity are available at

79 <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

105 with which they interact (e.g. conspecifics, predators, prey) (Aschoff, 1989; Erkert, 1982). Time
106 of high species activity should hence be protected to preserve biodiversity at multiple scales,
107 from individual fitness to ecosystem functions.

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

124 As European bats are a diversified group mainly composed of long-lived insectivorous
125 species occupying high trophic levels, it has been suggested that they can be good bioindicators
126 of the effects of anthropogenic pressures and mitigation measures on biodiversity (Jones et al.,
127 2009; Russo et al., 2021). However, while the spatial ecology of bats has received much
128 attention (e.g. Laforge et al., 2021) less is known about their diel activity patterns, knowledge
129 being dispersed in literature. Most studies informing on diel activity patterns are monospecific

130 and the activity patterns of many European species have received little to no attention (e.g.
131 *Myotis emarginatus*, *Tadarida teniotis*) (see Appendix A for an overview of the scientific
132 literature). Existing studies have almost all been conducted at local spatial scales (however, at
133 large scales see Day et al., 2015; Mariton et al., 2022; Newson et al., 2015) and they tend to be
134 biased toward monitoring emergence at roosts. Some authors showed that diel activity patterns
135 can vary throughout the year, rising the need for studies conducted at large temporal scales (e.g.
136 Robinson and Stebbings, 1997; Swift, 1980).

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

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

154 activity distribution throughout the night. These methods appear to be complementary by
155 providing different information on the temporal ecology of bats.

156 We used data from a citizen science bat monitoring program – based on standardised
157 acoustic monitoring throughout France (4409 sites monitored and 9807 nights monitored from
158 2014 to 2020) – to characterise the diel activity patterns of 20 bat species. Through the
159 calculation of the times of key descriptors and the representation of the activity distribution
160 throughout the night, we aimed to provide a synthetic and general knowledge on bat diel activity
161 patterns. This knowledge could be used in conservation, for instance, to distinguish functional
162 groups of species that could inspire multi-taxa approaches or to pave the way for the
163 consideration of variation of diel activity patterns throughout the year to design efficient
164 conservation measures. In particular, we predicted that (1) the overall diel activity patterns of
165 bat species will be driven by their diet and foraging strategies along with their ability to avoid
166 predation, (2) that bat diel activity patterns will vary throughout the year according to their
167 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.

194 2.2. Characterisation of the diel activity patterns

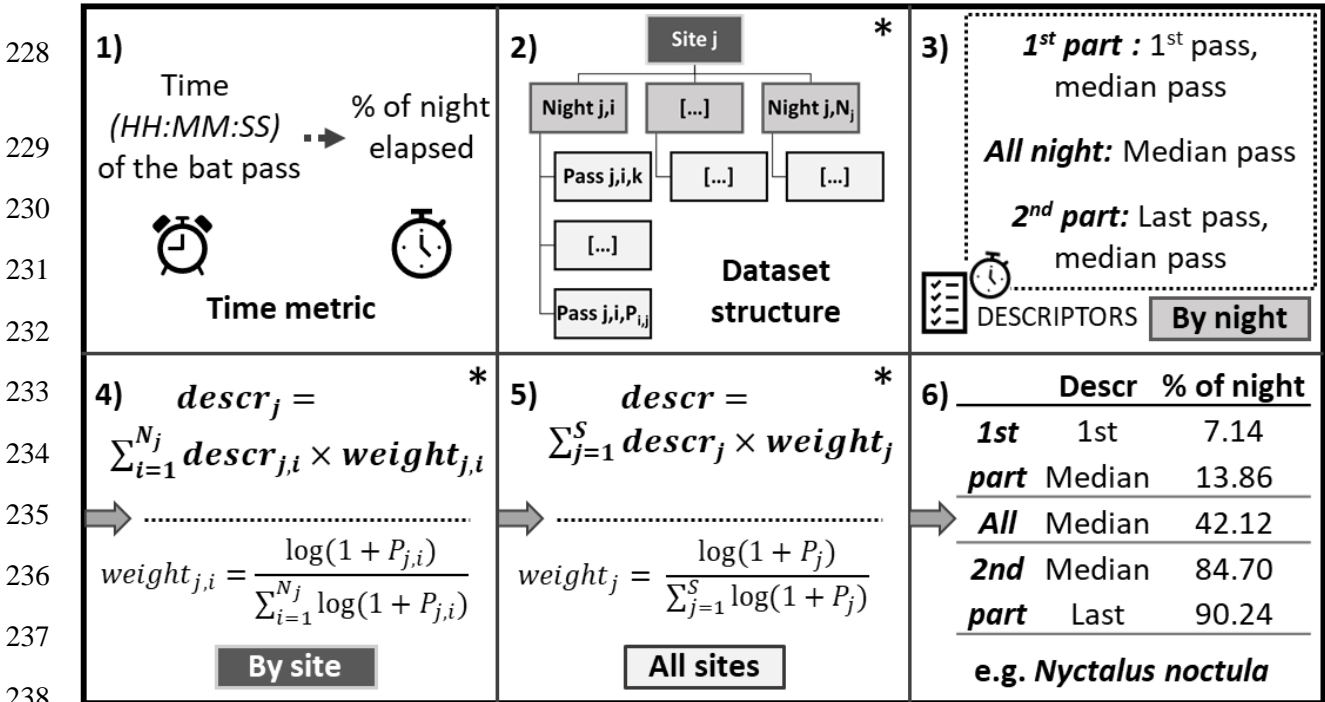
196 2.2.1. Key descriptors

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

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

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

227



239

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

243 * j = site ID; i = i^{th} night of a site; k = k^{th} pass in a night; S = number of sites; N_j = number
 244 of surveyed nights at the site, $P_{j,i}$ = number of passes of the night j,i ;
 245 $descr$ = time of the descriptor; P_j = “mean” number of passes of the site; =

246
$$\left[\sum_{i=1}^{N_j} P_{j,i} \times \log(1 + P_{j,i}) \right] / \left[\sum_{i=1}^{N_j} \log(1 + P_{j,i}) \right]$$

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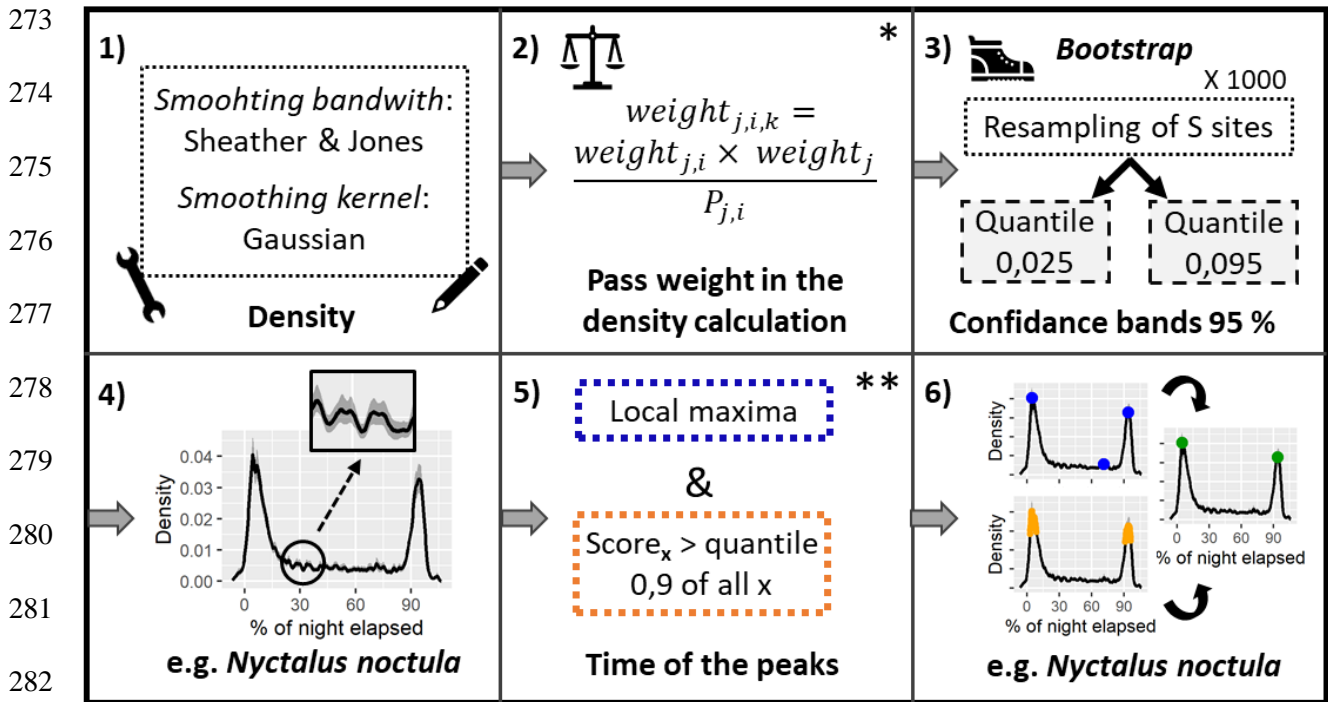
2.2.2. Activity distribution throughout the night

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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.



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

288 * see legend Fig.1

289 ** For local maxima and score calculation, window of temporal neighbours = 129 (i.e. 1/4
 290 of the night); x = percentage of night elapsed discretised;
 291 score_x = density_x – mean (density of the temporal neighbours)
 292

294 2.3. Examples of comparison of diel activity patterns inter- and intra-species

296 2.3.1. Activity distribution throughout the night according to the season

298 To assess variations of activity distribution throughout the night according to the season, we
 299 estimated the densities of activity on subsets of our datasets. Indeed, some authors showed that
 300 bat diel activity patterns could change according to their reproductive states (e.g. Robinson and
 301 Stebbings, 1997; Swift, 1980). We applied the density calculation method to three temporal

302 subsets: spring (1 March to 21 June, 1447 sites, 2762 nights), summer (22 June to 21 August,
303 2448 sites, 4373 nights) and autumn (22 August to 31 October, 1342 sites, 2642 nights). In
304 France, for most species, these periods corresponded approximately to the hibernation
305 ending/gestation, lactation and dispersion/reproduction (Arthur and Lemaire, 2015).

306

307 **2.3.2. Clustering of the species**

308

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

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317 **3. Results**

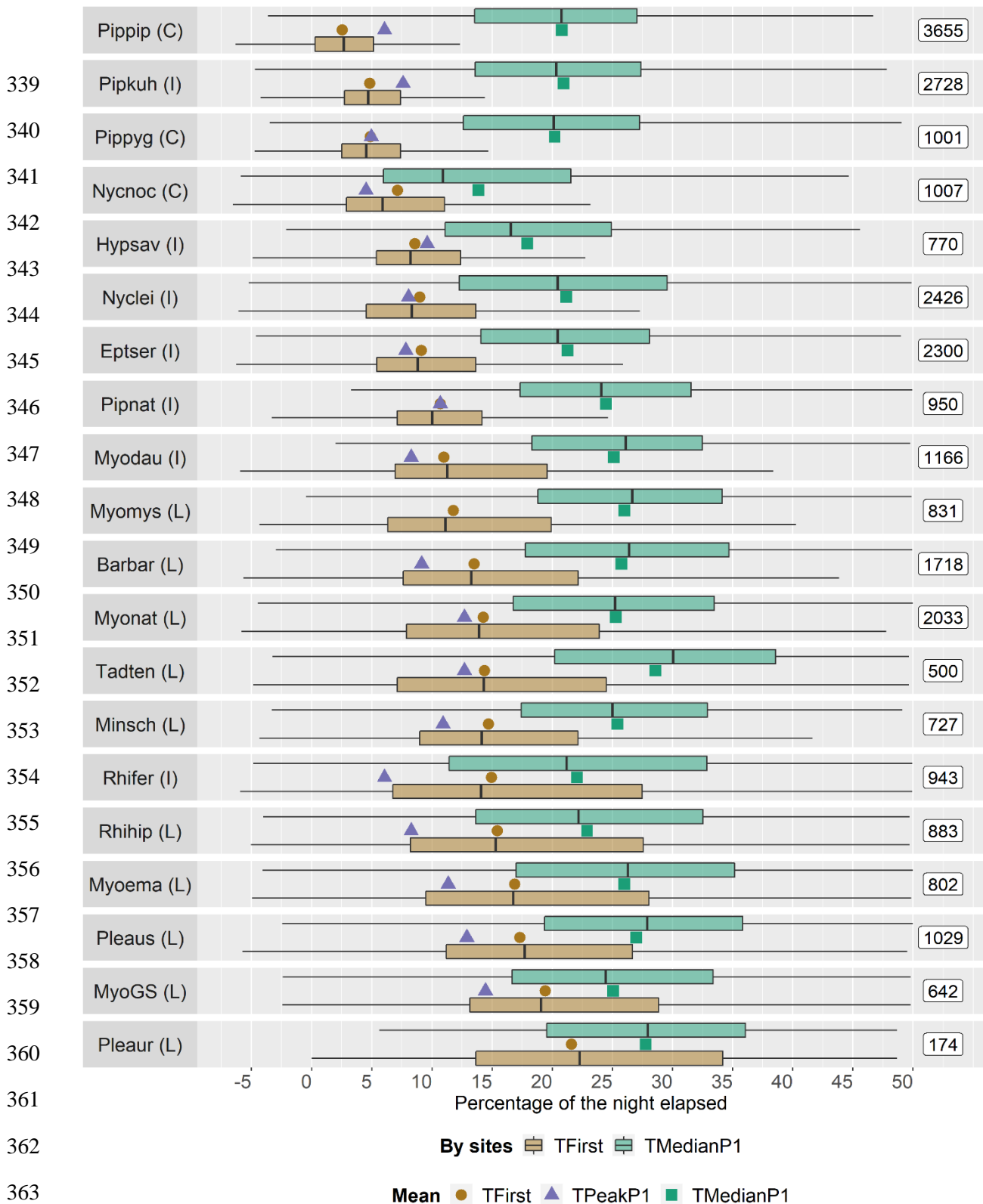
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319 **3.1. Diel activity pattern description**

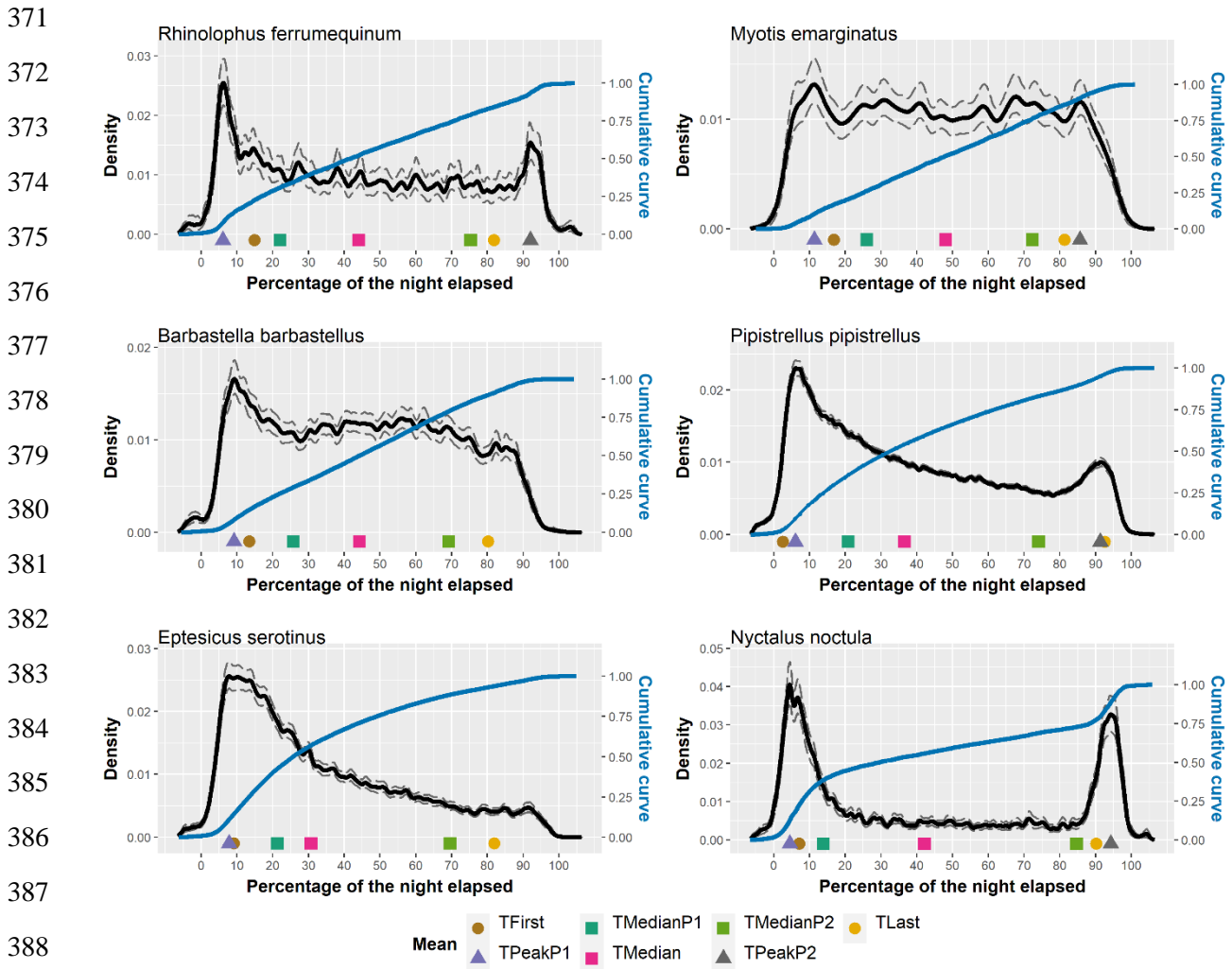
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321 The mean time of the key descriptors and the time of the activity peaks varied greatly
322 according to the species (Fig. 3, Table E and Fig. G). We did not detect any activity peak for
323 *Myotis mystacinus* and *Plecotus auritus*. For six species,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

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



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



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

397 3.2. Clustering of species according to their temporal niche

398
 399 The species clustering resulted in three clusters (Table 1, Appendix J). The first cluster,
 400 composed of *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *N. noctula* was characterised
 401 by an earlier activity at the beginning of the night and a later activity at the end, we called the
 402 species in this group “crepuscular” species. The second cluster was composed of ten species:

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

411

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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

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415

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

425

426 **3.3. Variations of the activity distribution throughout the night according to** 427 **the seasons**

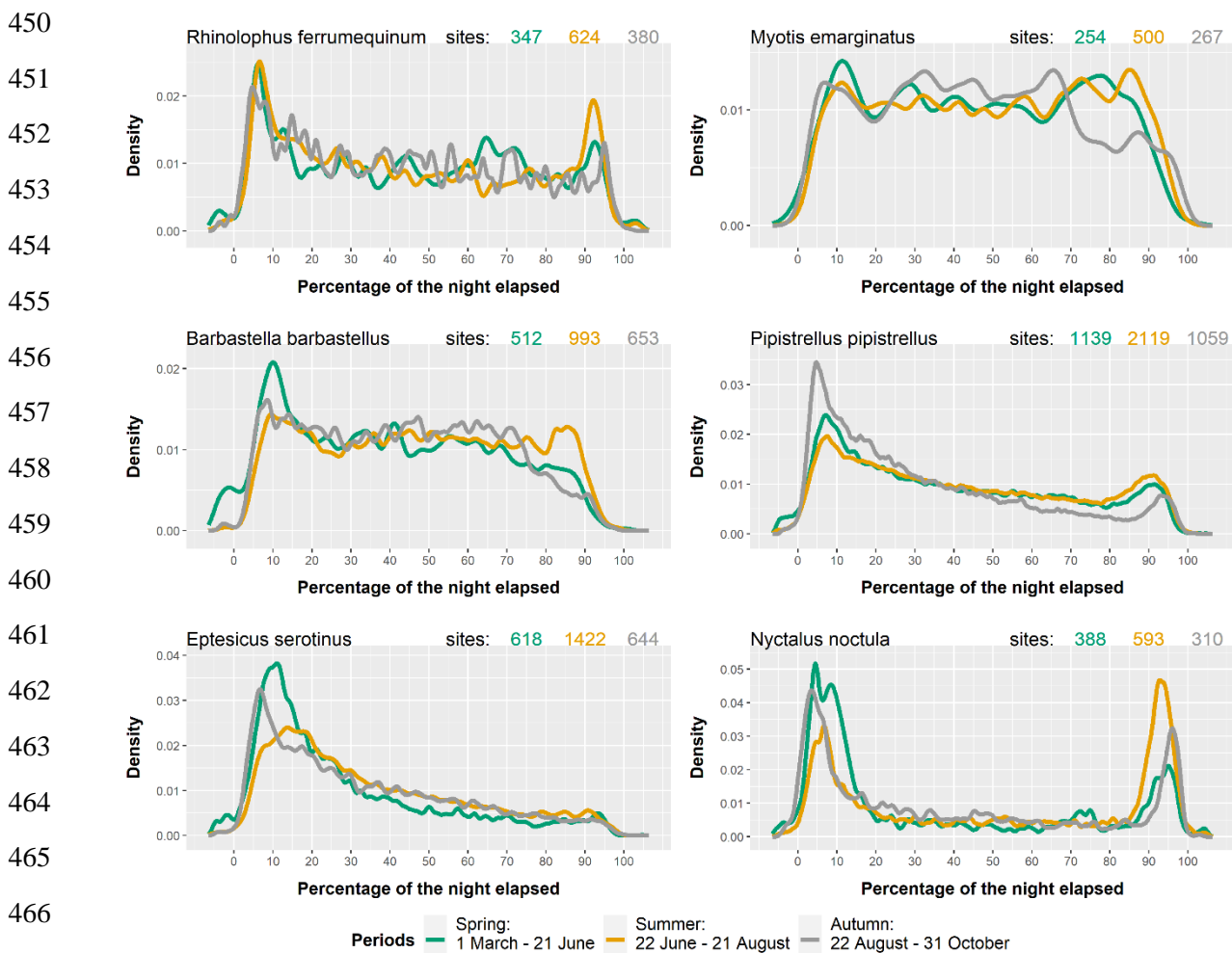
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429 Despite slight variations, the times of the activity peak and the activity distributions throughout
430 the night remained generally similar across all seasons (Fig 5, Fig. K). However, for some
431 species, the amplitudes of the activity peaks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

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

441 elapsed was also greater in spring than in autumn for 15 species out of 20 (mean difference of
 442 weighted activity between spring and autumn: 1.6 %).

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



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

470 **4. Discussion**

471
472 The use of a seven-year nationwide citizen science project gave us the opportunity to
473 characterise the diel activity patterns of 20 insectivorous bat species at broad spatial and
474 temporal scales. We showed that, although these patterns varied substantially between species,
475 species could be grouped according to similarities in their temporal niches. Diel activity patterns
476 also varied according to the season. We argue that this knowledge can be used to inform
477 conservation measures to better preserve key times of bat diel activity.

478 479 **4.1. Characterisation of diel activity patterns**

480
481 We developed a methodology that can be applied to all taxa, whether abundant or rare, and at
482 different spatial scales. This allowed us to go further than an hourly representation of bat passes
483 by providing the times of key diel descriptors and a representation of activity distribution
484 throughout the night, while accounting for the hierarchical structure of the dataset. The
485 representativity and the large number of sites of the Vigie-Chiro dataset allowed to provide
486 robust results that could be a first step toward further statistical analyses on the impacts of
487 environmental (e.g. reproductive status, weather) and/or anthropogenic stressors (e.g. land-use
488 change, pollution) on bat diel activity patterns while controlling for possible spatiotemporal
489 autocorrelation issues (e.g. Mariton et al., 2022).

490 A strength of this study is to describe the diel activity patterns of many species using a
491 single dataset, allowing direct comparisons between them. As diel activity patterns influence
492 species' performance in a given environment, they can be considered as functional traits
493 (Bennie et al., 2014) and we can thus distinguish functional groups based on similarities in their
494 temporal niches. We distinguished: (1) "crepuscular" species with a marked bimodal activity
495 starting shortly after sunset and ending shortly before sunrise, (2) "late" species with an overall

496 well distributed activity throughout the night (i.e. no activity peak or a weak unimodal or
497 bimodal activity pattern), starting late at night and ending earlier than the activity of the other
498 species, (3) “intermediate” species with a unimodal or bimodal activity pattern and an overall
499 activity that, while fairly early in the night, had intermediate start and end times compared to
500 the other groups.

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

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

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

533

534 **4.2. Diel activity patterns in conservation policies**

535

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

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

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

568 Similarly, including bat diel activity patterns in algorithm-based curtailments of wind
569 turbines would be of utmost interest (Behr et al., 2017; Friedenber and Frick, 2021). This
570 would allow a stricter cut-in speed to be implemented when fatality risks are susceptible to be

571 the highest (e.g. dusk and dawn) than during the rest of the night. However, the curtailment
572 algorithm of Behr et al. (2017), which is now the standard method for mitigating bat collision
573 risks of at wind farms in Germany, is one of the only algorithms we know of that consider bat
574 diel activity patterns (Adams et al., 2021; Whitby et al., 2021). Adding an interaction between
575 the time of the year and the time of the night could even increase the performance of such
576 algorithms. For instance, in the dataset of Behr et al. (2017), *N. noctula* and *P. pipistrellus* were
577 the species that accounted for most of the recordings. According to our results, the times of the
578 two activity peaks of these species remain quite similar throughout the year but their amplitude
579 change with, for instance, a proportionally greater activity at dawn in summer than during the
580 rest of the year. These results hence raise the need for stronger curtailment efforts at dawn
581 during summer.

582

583 **4.3. Conclusions**

584

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

594

595

596

597 **CRedit authorship contribution statement**

598

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

604

605 **Declaration of competing interest**

606

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

609

610 **Acknowledgements**

611

612 L.M. was funded by the Institut de la Transition Environnementale de l'Alliance Sorbonne
613 Université (SU-ITE). Y.B. was funded by the French Biodiversity Agency (OFB). We thank
614 Brigitte Zanda for supporting this project and for her involvement in funding acquisition. We
615 thank Kévin Barré for the insightful discussion on algorithm-based curtailments. We thank
616 CC-IN2P3 and PCIA-MNHN for providing computing and storage facilities, and Didier Bas
617 for his help in this process. The success of such a large-scale study relies on the continuous
618 participation of the volunteers of the Vigie-Chiro program, who we warmly thank. We also
619 thank the two anonymous reviewers for their insightful comments on the manuscript.

620

621 **References**

622

623 Adams, E.M., Gulka, J., Williams, K.A., 2021. A review of the effectiveness of operational curtailment
624 for reducing bat fatalities at terrestrial wind farms in North America. PLoS ONE 16, e0256382.
625 <https://doi.org/10.1371/journal.pone.0256382>

626 Arthur, L., Lemaire, M., 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ;
627 Muséum national d'Histoire Naturelle, Mèze; Paris.

628 Aschoff, J., 1989. Temporal orientation: circadian clocks in animals and humans. Animal Behaviour 37,
629 881–896. [https://doi.org/10.1016/0003-3472\(89\)90132-2](https://doi.org/10.1016/0003-3472(89)90132-2)

630 Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J., Le Viol, I., 2015.
631 Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? Glob Change
632 Biol 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>

633 Barataud, M., 2020. Acoustic ecology of European bats: species identification, study of their habitats
634 and foraging behaviour, 2nd ed. ed, Inventaires & biodiversité series. Biotope Muséum national
635 d'histoire naturelle, Mèze Paris.

636 Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S.E., Julien, J.-F., Claireau, F., Kerbiriou, C.,
637 Bas, Y., 2019. Accounting for automated identification errors in acoustic surveys. Methods Ecol Evol
638 10, 1171–1188. <https://doi.org/10.1111/2041-210X.13198>

639 Bas, Y., Bas, D., Julien, J.-F., 2017. Tadarida: A Toolbox for Animal Detection on Acoustic Recordings.
640 Journal of Open Research Software 5, 6. <https://doi.org/10.5334/jors.154>

641 Behr, O., Brinkmann, R., Hochradel, K., Mages, J., Korner-Nievergelt, F., Niermann, I., Reich, M.,
642 Simon, R., Weber, N., Nagy, M., 2017. Mitigating Bat Mortality with Turbine-Specific Curtailment
643 Algorithms: A Model Based Approach, in: Köppel, J. (Ed.), Wind Energy and Wildlife Interactions.
644 Springer International Publishing, Cham, pp. 135–160. https://doi.org/10.1007/978-3-319-51272-3_8

645 Bennie, J., Davies, T.W., Duffy, J.P., Inger, R., Gaston, K.J., 2014. Contrasting trends in light pollution
646 across Europe based on satellite observed night time lights. Sci Rep 4, 3789.
647 <https://doi.org/10.1038/srep03789>

648 Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling
649 bats and its conservation consequences. Acta Chiropterologica 9, 527–534.
650 [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)

651 Browning, E., Barlow, K.E., Burns, F., Hawkins, C., Boughey, K.L., 2021. Drivers of European bat
652 population change: a review reveals evidence gaps. Mam Rev mam.12239.
653 <https://doi.org/10.1111/mam.12239>

654 Bullock, D.J., Combes, B.A., Eales, L.A., Pritchard, J.S., 1987. Analysis of the timing and pattern of
655 emergence of the pipistrelle bat (*Pipistrellus pipistrettus*). Journal of Zoology 211, 267–274.
656 <https://doi.org/10.1111/j.1469-7998.1987.tb01533.x>

657 Catto, C.M.C., Racey, P.A., Stephenson, P.J., 1995. Activity patterns of the serotine bat (*Eptesicus*
658 *serotinus*) at a roost in southern England. Journal of Zoology 235, 635–644.
659 <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>

660 Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for
661 bat conservation: Part-night lighting and bats. Anim Conserv 18, 512–516.
662 <https://doi.org/10.1111/acv.12200>

663 Dietz, M., Kalko, E.K.V., 2007. Reproduction affects flight activity in female and male Daubenton's
664 bats, *Myotis daubentoni*. *Can. J. Zool.* 85, 653–664. <https://doi.org/10.1139/Z07-045>

665 Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing
666 in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>

667 Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaning bat, *Plecotus*
668 *auritus*. *Phil. Trans. R. Soc. Lond. B* 351, 921–931. <https://doi.org/10.1098/rstb.1996.0085>

669 Erkert, H.G., 1982. Ecological Aspects of Bat Activity Rhythms, in: Kunz, T.H. (Ed.), *Ecology of Bats*.
670 Springer US, Boston, MA, pp. 201–242. https://doi.org/10.1007/978-1-4613-3421-7_5

671 Friedenberg, N.A., Frick, W.F., 2021. Assessing fatality minimization for hoary bats amid continued
672 wind energy development. *Biological Conservation* 262, 109309.
673 <https://doi.org/10.1016/j.biocon.2021.109309>

674 Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. REVIEW: Reducing the ecological
675 consequences of night-time light pollution: options and developments. *J Appl Ecol* 49, 1256–1266.
676 <https://doi.org/10.1111/j.1365-2664.2012.02212.x>

677 Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation
678 strategy on riparian bats. *Environmental Pollution* 307, 119552.
679 <https://doi.org/10.1016/j.envpol.2022.119552>

680 Husson, F., Josse, J., Pagès, J., 2010. Principal component methods-hierarchical clustering-partitional
681 clustering: why would we need to choose for visualizing data? (Technical Report of the Applied
682 Mathematics Department). Agrocampus.

683 Husson, F., Lê, S., Pagès, J., 2009. *Analyse de données avec R*, 1st ed, *Pratique de la statistique*. Presses
684 universitaires de Rennes, Rennes.

685 Jachowski, D.S., Dobony, C.A., Coleman, L.S., Ford, W.M., Britzke, E.R., Rodrigue, J.L., 2014.
686 Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning
687 in sympatric bat species. *Diversity Distrib.* 20, 1002–1015. <https://doi.org/10.1111/ddi.12192>

688 Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of
689 bats as bioindicators. *Endang. Species. Res.* 8, 93–115. <https://doi.org/10.3354/esr00182>

690 Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time
691 in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455. <https://doi.org/10.1098/rstb.1994.0161>

692 Laforge, A., Archaux, F., Coulon, A., Sirami, C., Froidevaux, J.S.P., Gouix, N., Ladet, S., Martin, H.,
693 Barré, K., Roemer, C., Claireau, F., Kerbirou, C., Barbaro, L., Algar, A., 2021. Landscape composition
694 and life-history traits influence bat movement and space use: Analysis of 30 years of published telemetry
695 data. *Global Ecol Biogeogr* 30, 13397. <https://doi.org/10.1111/geb.13397>

696 Lê, S., Josse, J., Husson, F., 2008. **FactoMineR** : An R Package for Multivariate Analysis. *J. Stat. Soft.*
697 25, 1–18. <https://doi.org/10.18637/jss.v025.i01>

698 Lindenmayer, D., Hunter, M., 2010. Some Guiding Concepts for Conservation Biology. *Conservation*
699 *Biology* 24, 1459–1468. <https://doi.org/10.1111/j.1523-1739.2010.01544.x>

700 Maier, C., 1992. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal*
701 *of Zoology* 228, 69–80. <https://doi.org/10.1111/j.1469-7998.1992.tb04433.x>

702 Mariton, L., Kerbiriou, C., Bas, Y., Zanda, B., Le Viol, I., 2022. Even low light pollution levels affect
703 the spatial distribution and timing of activity of a “light tolerant” bat species. *Environmental Pollution*
704 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>

705 Marques, J.T., Rainho, A., Carapuço, M., Oliveira, P., Palmeirim, J.M., 2004. Foraging Behaviour and
706 Habitat use by the European Free-Tailed Bat *Tadarida teniotis*. *Acta Chiropterologica* 6, 99–110.
707 <https://doi.org/10.3161/001.006.0108>

708 Millon, L., Julien, J.-F., Julliard, R., Kerbiriou, C., 2015. Bat activity in intensively farmed landscapes
709 with wind turbines and offset measures. *Ecological Engineering* 75, 250–257.
710 <https://doi.org/10.1016/j.ecoleng.2014.11.050>

711 Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale
712 standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological*
713 *Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>

714 Ochi, S., 2019. scorepeak: Peak Functions for Peak Detection in Univariate Time Series.

715 R Core Team, 2022. R: A language and environment for statistical computing.

716 Racey, P.A., Speakman, J.R., 1987. The energy costs of pregnancy and lactation in heterothermic bats.
717 *Symp. zool. Soc. Lond.* 107–125.

718 Robinson, M.F., Stebbings, R.E., 1997. Activity of the serotine bat, *Eptesicus serotinus*. *Myotis* 35, 5–
719 16.

720 Russo, D., Salinas-Ramos, V.B., Cistrone, L., Smeraldo, S., Bosso, L., Ancillotto, L., 2021. Do We
721 Need to Use Bats as Bioindicators? *Biology* 10, 693. <https://doi.org/10.3390/biology10080693>

722 Rydell, J., Entwistle, A.C., Racey, P.A., 1996. Timing of Foraging Flights of Three Species of Bats in
723 Relation to Insect Activity and Predation Risk. *Oikos* 76, 243–252. <https://doi.org/10.2307/3546196>

724 Schoener, T.W., 1974. Resource Partitioning in Ecological Communities: Research on how similar
725 species divide resources helps reveal the natural regulation of species diversity. *Science* 185, 27–39.
726 <https://doi.org/10.1126/science.185.4145.27>

727 Sefick, S., 2016. Stream Metabolism-A package for calculating single station metabolism from diurnal
728 Oxygen curves.

729 Sutherland, W.J., Dicks, L.V., Petrovan, S.O., Smith, R.K. (Eds.), 2021. *What Works in Conservation*
730 2021. Open Book Publishers. <https://doi.org/10.11647/obp.0267>

731 Swift, S.M., 1997. Roosting and foraging behaviour of Natterer’s bats (*Myotis nattereri*) close to the
732 northern border of their distribution. *Journal of Zoology* 242, 375–384. <https://doi.org/10.1111/j.1469-7998.1997.tb05809.x>

733

734 Swift, S.M., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland.
735 *Journal of Zoology* 190, 285–295. <https://doi.org/10.1111/j.1469-7998.1980.tb01428.x>

736 van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E.,
737 Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard,
738 J.K., Svenningsen, C., Tschan, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022.
739 Emerging technologies revolutionise insect ecology and monitoring. *Trends in Ecology & Evolution*
740 S0169534722001343. <https://doi.org/10.1016/j.tree.2022.06.001>

741 Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens,
742 H.J.G.A., Mathews, F., Rydell, J., Spoelstra, K., Zagamajster, M., 2021. The Impact Of Light Pollution

- 743 On Bats Varies According To Foraging Guild And Habitat Context. *BioScience* 71, 1103–1109.
744 <https://doi.org/10.1093/biosci/biab087>
- 745 Ware, R.L., Garrod, B., Macdonald, H., Allaby, R.G., 2020. Guano morphology has the potential to
746 inform conservation strategies in British bats. *PLoS ONE* 15, e0230865.
747 <https://doi.org/10.1371/journal.pone.0230865>
- 748 Whitby, M.D., Schirmacher, M.R., Frick, W.F., 2021. The State of the Science on Operational
749 Minimization to Reduce Bat Fatality at Wind Energy Facilities, A report submitted to the National
750 Renewable Energy Laboratory. Bat Conservation International, Austin, Texas.
- 751 Wolkovich, E.M., Cook, B.I., McLauchlan, K.K., Davies, T.J., 2014. Temporal ecology in the
752 Anthropocene. *Ecol Lett* 17, 1365–1379. <https://doi.org/10.1111/ele.12353>
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- 754

755 **Appendices**

756

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

758 **Appendix B:** Acquisition and curation of the biological data

759 **Appendix C:** Robustness of the automated identification

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

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

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

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

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

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

768 **Appendix J:** Clustering results

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

770