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Winter activity of bats in a peri-urban forest: how do climatic conditions matter?

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Bat activity during winter is perhaps the least documented aspect of their annual behaviour, with few observations of bats leaving their hibernation sites. In this study, we report on bat activity outside hibernacula in a peri-urban forest in France over a period of 52 nights in 2023. We considered 13 climatic variables encompassing temperature, wind, rain, and natural light variations during the night. Five bat species were detected using automatic recorders and identified manually: *Myotis brandtii*, *Nyctalus noctula*, *Pipistrellus pipistrellus*, *P. kuhlii*, and *Plecotus auritus*. The most active species was *P. pipistrellus*, accounting for 95.6% of the total number of contacts, and was therefore the sole species analyzed in detail. The main peaks of activity were observed on warmer nights; however, bat calls were also recorded during colder nights, with activity detected at a minimum temperature of -3.4°C and a mean of -1.9°C. Temperature emerged as the most significant climatic variable positively influencing bat activity, while rain had a notably negative impact. Other variables, such as wind and luminosity, appeared to have minimal or no effect. We also compared our climatic data (temperature and precipitation) with historical records from 1991–2020. This comparison revealed an increase in extreme temperature events and fluctuations, which are known to negatively impact bat populations. Nevertheless, *P. pipistrellus* in northern France may be less affected by these changes due to its tolerance of climate variability and its use of diverse roosting sites. Further research across different locations and time periods would help validate and refine these findings, providing a clearer understanding of the effects of global warming on bat ecology and populations.

Key words: *Pipistrellus pipistrellus*, winter activity, winter climatic conditions, European bats, degree day, climate change

INTRODUCTION

In a large part of the Palearctic and Nearctic regions, bats are subject to strong seasonal climatic variations. To cope with these constraints, during colder and prey-free periods, they may enter a hibernation stage, including periods of torpor (Ransome, 1968, 1971; Mitchell-Jones *et al*., 1999; Ransome and Hutson, 2000; Arthur and Lemaire, 2015). Differing from summer torpor, lasting up to 24 hours, those occurring in winter are generally longer, lasting from 1 to over 40 days. The timing of arousals is quite similar for both seasons, with a tendency to occur near dusk (Ransome and Hutson, 2000). Throughout the hibernation period, individuals, alone or in monospecific or multispecific groups, use a variety of shelters to protect themselves from winter climatic conditions. A variety of sites can be used by these species, such as tree holes, caves, or buildings with little or no human activity (Kervyn *et al*., 1997; Rodrigues *et al*., 2003; Lavillaugouët, 2008; Arthur and Lemaire, 2015). The hibernation period, which lasts from late autumn to spring, is characterized by periods of torpor separated by periodic awakenings, which may have different purposes: changing the hibernation site (when the temperature inside has become either too low or too high); to regulate hydration and/or excretion; or for copulation or foraging (Ransome and Hutson, 2000; Hope and Jones, 2012). These phases are generally short and tend to occur every few days and up to three weeks on a cyclical basis (Arthur and Lemaire, 2015). Many of these activities take place within hibernacula, but some require individuals to move among hibernacula to perform them. Such movements depend on the ecology of the species, its distribution, and the local environment (Hope and Jones, 2012).

Change in climatic conditions plays an important role in winter bat activity (Hayes, 1997), with important roles of climatic factors including temperature level and variation (Ransome, 1968; Wolbert *et al*., 2014) and wind power (Kunz *et al*., 2007; Amorim *et al*., 2012). Higher temperatures favour bat activity, while strong winds and high rainfall have a moderate but significant negative effect

(Avery, 1985; Power *et al*., 2023). In combination, strong wind and rainfall have a strong negative impact on bat activity during the swarming period (Erickson and West, 2002; Parsons *et al*., 2003); we therefore can expect the same for the winter period. According to a few studies carried out in Western Europe, bat activity from hibernation sites mainly represents movement, without taking into account changes in location due to poor conditions or foraging during nights with temperatures of at least 6–7°C (Ransome, 1968, 1971; Avery, 1985; Ransome and Hutson, 2000; Zahn and Kriner, 2016; Laboure *et al*., 2020; Reber, 2022). In winter, these temperatures allow bats to forage for prey, such as insects that emerge in mild climatic conditions (Ransome, 1968, Hope and Jones, 2012), as low as 6–10°C (Jones *et al*., 1995). Emergence timing of adult insect is mostly related to pond mud and ambient temperature (Andrews *et al*., 2016), winter climatic conditions and air temperature (Marshall *et al*., 2020). As arousal presents an important cost for individuals, mild winter temperatures are almost vital to prevent depletion of fat reserves and possible death (Ransome, 1968, 1971; Ransome and Hutson, 2000). Moreover, temperatures of late winter affect the gestational length of species and consequently the reproduction of a population, as demonstrated for *Pipistrellus* species by Racey and Swift (1981), and *Rhinolophus ferrumequinum* by Ransome and McOwat (1994). Early phenological emergence of insect prey species leads to increased foraging frequency and length, and influences pregnancy length (Ransome and McOwat, 1994; Andrews *et al*., 2016). The availability of prey is critical for female bats, as it controls gestational length.

We conducted a two-month bat-detector study of the winter activity of bats in a peri-urban forest in France. Our aim was to understand and quantify bat activity during this period. We simultaneously recorded climatic variables to investigate their effects on bat activity variation. In view of the impact of climate change on bat populations (Festa *et al*., 2023) and the near actual and global evolution of 1.5°C (Wartenburger *et al*., 2017; Scafetta, 2024), we considered temperature variations by comparing our data with 20-year-old data. We hypothesised that winter bat activity would be positively correlated with increasing temperatures and negatively with strong winds and rainfall.

MATERIALS AND METHODS

Study Site

We conducted our study in 'Trou Berger', a 3.5 ha forest located in Guyancourt (78 – Yvelines, France) (Fig. 1) and

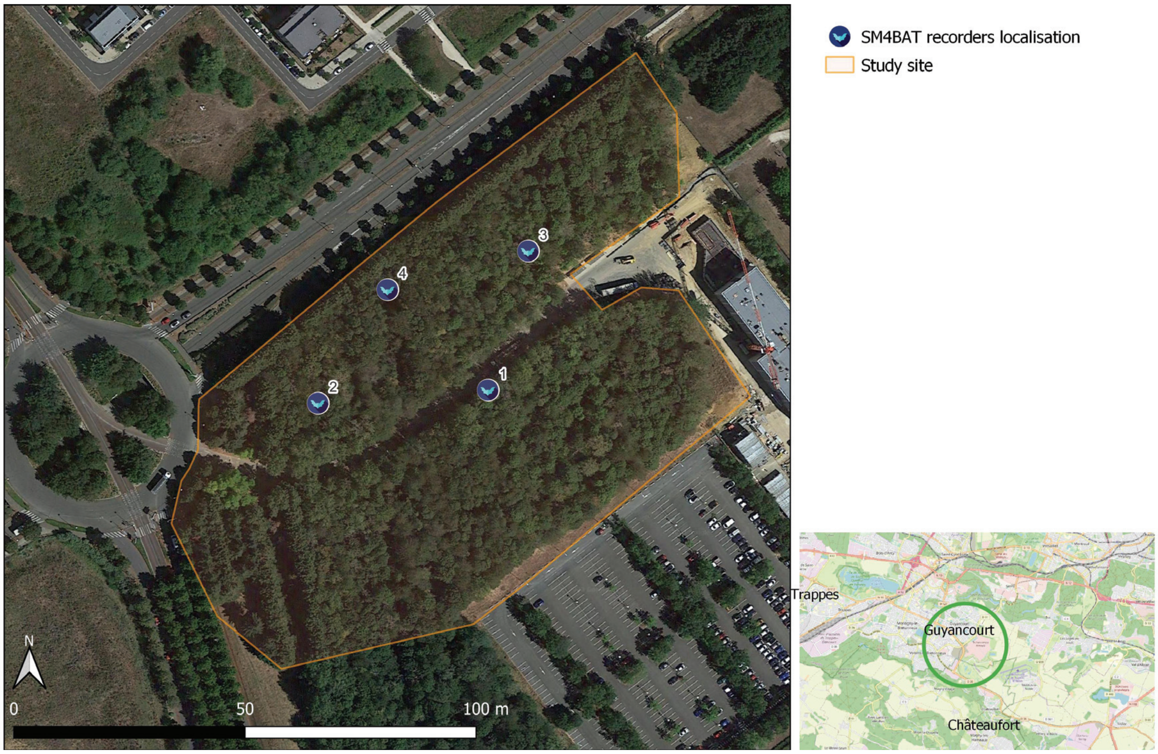

FIG. 1. Location of the study site and SM4BAT recorders

surrounded by French secondary and tertiary sector infrastructures. The forest was originally a native hardwood plantation, divided into two parts by a road. Relatively young (> 40 years), it has been able to grow freely and is now dominated by sycamore maple trees (*Acer pseudoplatanus*). In this peri-urban context, this forest is an important support for biodiversity and is part of a fragmented ecological continuum on a local and regional scale. The site is subject to a modified oceanic climate with an average annual temperature of 11°C and an annual rainfall of 660 mm (Joly *et al*., 2010).

Data Acquisition

Bat activity was recorded using four 'SM4BAT FS' automatic recorders (©Wildlife Acoustics, Inc.) placed at a minimum distance of 50 meters from each other. They were installed in different microhabitats to capture the variability of the study site, localised in Fig. 1: SM4 n°1 located at the edge created by the road (< 3 m high); SM4 n°2 located within a dense part of the forest (< 3 m high); SM4 n°3 located within a sparse part of the forest (< 3 m high); SM4 n°4 located in the canopy stage of the forest (> 5 m high).

Two periods were recorded, from the 12th to the 24th of January 2023, and from the 3rd of February 2023 to the 15th of March 2023, for a total of 52 nights. The start and end times of the recordings vary according to the evolution of the duration of the nights (Table 1), ranging from 5:59 pm for the start of the first night to 7:18 pm for the last, and from 9:25 am for the end of the first night to 8:26 am for the last. The duration of each night ranges from 926 minutes at the beginning of the study to 788 minutes at the end. This part was programmed with the software 'SM4 Configurator' (version 1.0.7, ©2016 Wildlife Acoustics, Inc.), which automated these variations.

Climatic variables were collected from two sources. Temperature data were recorded every hour by two temperature loggers 'HOBO® MX2300 Series Data Loggers' placed in the forest, at an altitude of approximately 1.5 m. The average of these two loggers was recorded. Precipitation, wind, rain and night-time luminosity variables were obtained from the climate 'Météociel' database using the nearest measuring station (Toussus-le-Noble; located 2.5 km from the study site). In order to focus on the nocturnal variables recorded hourly, we defined an effective period close to the recording period: from the 12th to the 24th of January 2023 and the 3rd to the 16th of February 2023, we defined night duration from 6pm to 9 am; from the 17th of February 2023 to the 15th of March 2023, the selected period was from 7 pm to 9 am.

Thirteen variables were chosen to cover a wide range of climatic variations: 1) Mean night temperature (Temp_mean); 2) Mean temperature of the night before (Temp_mean-1); 3) Minimum night temperature (Temp_min); 4) Maximum night temperature (Temp_max); 5) Temperature of the recorded hour (Temp_h); 6) Temperature of the day before the recorded night (Temp_dmean-1); 7) Temperature of the second day before the recording night (Temp_dmean-2); 8) Mean precipitation of the night (Preci_mean); 9) Mean wind speed of the night (Wind_mean); 10) Minimum wind speed of the night (Wind_min); 11) Maximum wind speed of the night (Wind_max); 12) Moon phase (Moon_phase); Mean nebulosity of the night (Nebulosity_mean); 13) Nebulosity of the recorded hour (Nebulosity). Due to incomplete access to absolute humidity data, the relative humidity variable was not included to avoid bias (Kurta, 2014).

We made a comparison of our recorded temperature and precipitation data, with regard to climatic evolution and divergence, from the period 1991–2020, using the same climate database 'Météociel' and the same observation station. By using minimum and maximum temperatures to calculate a daily

TABLE 1. Duration of night-time records (duration in hours) from January to March 2023

Night	Start	End	Night duration
12/13 Jan.	17h59	9h25	15.433
13/14 Jan.	18h01	9h24	15.383
14/15 Jan.	18h02	9h23	15.350
15/16 Jan.	18h03	9h22	15.317
16/17 Jan.	18h04	9h21	15.283
17/18 Jan.	18h05	9h20	15.250
18/19 Jan.	18h06	9h19	15.217
19/20 Jan.	18h08	9h19	15.183
20/21 Jan.	18h09	9h18	15.150
21/22 Jan.	18h10	9h17	15.117
22/23 Jan.	18h11	9h16	15.083
23/24 Jan.	18h13	9h15	15.033
03/04 Feb.	18h27	9h15	14.800
04/05 Feb.	18h29	9h14	14.750
05/06 Feb.	18h30	9h13	14.717
06/07 Feb.	18h31	9h12	14.683
07/08 Feb.	18h33	9h11	14.633
08/09 Feb.	18h34	9h10	14.583
09/10 Feb.	18h35	9h10	14.567
10/11 Feb.	18h37	9h09	14.517
11/12 Feb.	18h38	9h08	14.483
12/13 Feb.	18h39	9h07	14.450
13/14 Feb.	18h41	9h06	14.400
14/15 Feb.	18h42	9h05	14.367
15/16 Feb.	18h44	9h05	14.333
16/17 Feb.	18h45	9h05	14.333
17/18 Feb.	18h46	9h05	14.317
18/19 Feb.	18h48	9h04	14.267
19/20 Feb.	18h49	9h03	14.233
20/21 Feb.	18h50	9h02	14.200
21/22 Feb.	18h51	9h01	14.167
22/23 Feb.	18h53	9h00	14.117
23/24 Feb.	18h54	8h59	14.083
24/25 Feb.	18h55	8h58	14.050
25/26 Feb.	18h57	8h57	14.000
26/27 Feb.	18h57	8h55	13.967
27/28 Feb.	18h58	8h53	13.917
28/01 Feb.	18h59	8h51	13.867
01/02 Mar.	19h02	8h50	13.800
02/03 Mar.	19h03	8h48	13.750
03/04 Mar.	19h04	8h46	13.700
04/05 Mar.	19h05	8h44	13.650
05/06 Mar.	19h07	8h42	13.583
06/07 Mar.	19h08	8h40	13.533
07/08 Mar.	19h09	8h38	13.483
08/09 Mar.	19h10	8h36	13.433
09/10 Mar.	19h12	8h34	13.367
10/11 Mar.	19h13	8h33	13.333
11/12 Mar.	19h14	8h31	13.283
12/13 Mar.	19h15	8h30	13.250
13/14 Mar.	19h17	8h28	13.183
14/15 Mar.	19h18	8h26	13.133
Total			744.1

average, we also determine the degree-day coefficient with the following equation (McMaster and Wilhelm, 1997; Andrews *et al*., 2016, 2024):

$$D = (T_{\max} + T_{\min})/2 - T_{\mathrm{thr}} \quad \text{(Equation 1)}$$

With D = degree day, $T_{\max}$ and $T_{\min}$ being, respectively, daily maximum and minimum air temperatures, and with T_{thr} = the minimum temperature for the growth of midge larvae. This variable is assumed to be equal to 5°C, following the Marziali and Rossaro (2013) study on the thermal response of aquatic larvae of *Chironomus* spp. within lakes and rivers from Europe, where adults mostly emerge in spring and summer. For each year, we cumulated positive results of degree day of each day of the three studied months (McMaster and Wilhelm, 1997). These sums of annual degrees per day allow comparisons of temperature between years, in the context of climate change, with respect to the timing of bat prey emergence.

Data Analysis

The 'Sonochiro' software (©Biotope, Recherche and Développement, 2013) was used to automatically filter all data files containing ultrasonic sounds not associated with bat calls. We then used the 'BatSound' software (© Wildlife Acoustics, Inc., 2016) to identify species and determine the number of contacts file by file (Barataud, 2020). Within a unique file, we discriminated between individuals to take into account all contacts. Contacts were defined as follows (Bas *et al*., 2020): i) One isolated call = one contact; ii) A sequence of calls for a period of less than five seconds = one contact; iii) A sequence of calls for a period of more than five seconds = one contact every five seconds.

Due to a difference in detectability for each species, we used a multiplication coefficient to allow comparison between them. This detectability coefficient was applied to the number of contacts to reduce the bias caused by differences in ultrasound signal intensity. The corrected number of contacts, called the activity index, allowed a better comparison between species activity and species habitat use. For this study, we used a detectability coefficient associated with the forest, presented in Supplementary Table S1, for each species found in Ile-de-France. After using the ratio, the indices obtained were grouped by hour to facilitate comparison.

A second treatment was applied to the data to compare site activity with the referential activity of Bas *et al*. (2020). This reference system enables a determination of the activity level of the site, represented by the average bat activity per night, by comparing it with an activity threshold (quantile). In their study, they defined these thresholds based on the study of a large panel of data, separating four quantiles representing low to very high activity levels (Supplementary Table S2). We used the national reference for its robustness as the basis for our comparison (Supplementary Table S3). Detectability coefficients were not used in this treatment.

After analysing the data files, we were able to add variables about the bats and their environment: i) Species (Esp); ii) Number of calls (Nb_Contacts); iii) Type of habitat in which the data were recorded (Micro-Habitat); iv) Night of recording (Night); v) The exact day of recording, e.g. 12th when recorded during the night from 12th to 13th (Day); vi) Hour of recording (Hour). Only the first three variables on this list were retained for statistical analysis, sufficient to describe each individual. Others were used to describe the global distribution of data during the study period.

Statistical analyses were performed to investigate in detail the effects of climatic variables on bat activity. They were carried out using RStudio 3.6.2 (RStudio Team, 2015). The Shapiro test was used to evaluate the normality of the quantitative data. All variables did not follow a normal distribution (Shapiro test: P-value < 0.05). Following the non-normality of the variables, we calculated the correlation between the number of calls and each climatic variable using the Kendall rank correlation coefficient (Kendall's τ). This gives an idea of the correlation between variables ranked from 0 to 1.

To investigate the relationships more deeply between variables on bat activity, we performed regression models as presented in Zeileis *et al*. (2008). To better fit our data, which are characterised by count data with the presence of zero observations, we chose the Hurdle regression model. Besides other less fitted models that we tested, this is associated with a more fitted likelihood and a great consideration of zero counts (Table 2). This model is also presented by Muoka *et al*. (2016) as more suitable for a large number of null counts. The count data represented by the number of contacts were tested as before with climatic variables supplemented by habitat type variables.

RESULTS

A total of 904 call sequences were recorded during the 52 nights of sampling, representing a total of 1,280 bat calls. A total of five species were identified during the study. The common pipistrelle (*Pipistrellus pipistrellus*) was the most frequent species with more than 95.6% of the total number of contacts (864 contacts), followed by the common noctule (*Nyctalus noctula*) with 2.1% (19 contacts), Kuhl's pipistrelle (*Pipistrellus kuhlii*) with 1.2% (11 contacts), Brandt's bat (*Myotis brandtii*) with 1% (nine contacts) and brown long-eared bat (*Plecotus auritus*) with 0.1% of total contacts (one contact) (Table 3).

The temperature data for each recorded period are synthetised in Table 4. The mean precipitation at the recorded nights was between 0 ml and 0.7 ml ($\bar{x}$ = 0.1 ml); the mean night-time wind speed was between 2 km/h to 35 km/h ($\bar{x}$ = 14 km/h); the minimum between 0 km/h to 25 km/h ($\bar{x}$ = 8.2 km/h) and the maximum between 6 km/h to 47 km/h

TABLE 2. Full likelihood and observed zero counts compared to the expected number of zero counts for each tested models

Models	Maximized log-likelihood	Data frame size	Zero counts (138 obs.)
Poisson regression	-665	13	138
Negative binomial regression	-653	17	147
Hurdle regression	-607	30	138
Zero-inflated regression	-593	33	159

TABLE 3. Number of contacts, mean activity per night and number of contacts per hour associated with each species

Micro-habitat	*Myotis brandtii*			*Nyctalus noctula*			*Pipistrellus kuhlii*			*Pipistrellus pipistrellus*			*Plecotus auritus*		
	No. of contacts	Mean activity/ night	No. of contacts/ hour	No. of contacts	Mean activity/ night	No. of contacts/ hour	No. of contacts	Mean activity/ night	No. of contacts/ hour	No. of contacts	Mean activity/ night	No. of contacts/ hour	No. of contacts	Mean activity/ night	No. of contacts/ hour
Dense forest	3	0.29	4.03E-04	16	0.08	2.15E-03	1	0.02	1.34E-04	72	1.38	9.68E-03	–	–	–
Sparse forest	–	–	–	2	0.01	2.69E-04	5	0.10	6.72E-04	278	5.35	3.74E-02	–	–	–
Edge	4	0.38	5.38E-04	–	–	–	4	0.08	5.38E-04	406	7.81	5.46E-02	–	–	–
Canopy	2	0.19	2.69E-04	–	–	–	1	0.02	1.34E-04	108	2.08	1.45E-02	1	0.10	1.34E-04

TABLE 4. Mean, maximum and minimum of temperature variables in January and February–March 2023. Abbreviations are explained in Materials and Methods

Period	Temp_h		Temp_mean		Temp_mean-1		Temp_min		Temp_max		Temp_dmean-1		Temp_dmean-2	
	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max	Mean	Min–Max
January	6.4	5.0–7.9	3.1	-0.3–9.3	3.7	-0.3–9.3	1.3	-2.9–6.9	4.6	0.9–11.8	4.7	1.0–10.5	5.3	1.0–10.5
February–March	8.6	0.9–13.4	4.4	-1.9–11.2	4.5	-1.9–11.2	2.6	-3.7–10.5	7.2	2.0–13.4	8.0	2.0–13.4	8.0	2.0–13.4

(x̄ = 20 km/h); the moon phase was between 0% to 100% (x̄ = 55%); the mean nebulosity of the night was between 0 okta to 8 oktas (x̄ = 5.7 oktas); the nebulosity of the recorded hour was between 0 okta to 8.5 oktas (x̄ = 5.2 oktas).

A comparison of recorded climate data with normal operational data for January, February, and March during the period 1991–2020 is presented in Table 5 (see Supplementary Table S4 for a comparison with detailed monthly recorded climate data for this period). This first brings us a vision of the evolution of temperature and precipitation. We noticed an increase in temperature for the three months, with the greatest increase in maximum temperature observed in February (+2°C) and the greatest increase in minimum temperature for both January (+1.6°C) and March (+1.4°C). Precipitation appears to be more fluctuating, with a low to moderate increase in January (+2.9 mm) and March (+24.6 mm), and an important decrease in February (-47 mm). When detailed, the evolution of the variables seems more fluctuating with the warm and cold years, bringing different levels of variation. For example, the greatest variation in maximum temperature for February was present in 1991, but the one for March was observed in 2013. Even if the amplitudes of the variations are yearly dependant, the positive variations of minimum and maximum temperatures (i.e., when maximum temperatures in 2023 are more important than those of the year tested) are more presented at the beginning of the period than at the end, resulting in colder temperatures in the 1990s than in late 2020.

Yearly degree day sums (Table 6) complete this observation with presence of negative variations only after year 2000, with records in 2002, 2007, 2014, and 2020. Even so, degree variation is still fluctuating from one year to another. We noted that the greatest negative difference took place in 2020 (total degree day = 255, variation from 2023 = -19.8) and the greatest positive one in 2013 (total degree day = 79.4, variation from 2023 = +155.9), reflecting, respectively, a warm and a cold climate. As presented by Andrews *et al*. (2024), warm springs are linked with integrated air temperatures above 200 degree days; at the opposite, cold springs are associated with less than 125 degree days. As the oscillation from warm to cold climate seems to accelerate in 2007 (Fig. 3), we separate the period of studies into two, 1991–2006 and 2007–2020. Four days were > 200 degrees day and two day < 125 for the period 1991–2006; period 2007–2020 presents seven days with > 200 degrees day and three day < 125. The mean integrated air temperatures increased between those periods, with 176.2 ± 42.3 degree days for 1991–2006 and 180.9 ± 59 degree days for 2007–2020; in comparison, the value for the entire period was 178.4 ± 49.9 degree days. Two observations are made for those results: warmer springs are recorded after 2007, and an increase in the oscillation from warm to cold periods is observed due to the greatest number of extreme within the second period.

Due to the important differences in activity between species, only data from *P. pipistrellus* were retained for analysis. *Pipistrellus pipistrellus* activity can be illustrated by plotting the contacts of this species in correlation with changes in temperature throughout the period studied (Fig. 2). It showed a recovery of activity at the beginning of February associated with the stabilisation of higher temperatures, mostly present from the night of 09/10 February to the night of 17/18 February. After a period of lower temperatures, a renewal of activity was noticed mid-March with an important peak of activity the 12/13 of March. In addition, we noticed interesting observations on the second most common species, *N. noctula*, which was mainly represented by social calls. We assumed that these calls were made by individuals roosting in the area, supported by the absence of other types of call, such as echolocation, bringing a supposed absence of movement at least during the night.

By comparing the average activity per night with the national reference, we observed a low level of activity throughout the session. However, we highlight six nights where the activity of one species, *P. pipistrellus*, exceeded the first level of the benchmark and can be considered as moderate activity.

TABLE 5. Monthly variation in maximum/minimum temperatures and precipitation for January, February, and March, based on recorded monthly data, followed by observed fluctuations for 2023 (shown in parentheses) within the global recorded climate data from 1991–2020

Month	Precipitation (mm)	Maximum temperature (°C)	Minimum temperature (°C)
January	58.0 (+2.9)	7.6 (+0.9)	3.2 (+1.6)
February	3.0 (-47.0)	10.0 (+2.0)	1.7 (+0.3)
March	68.4 (+24.6)	12.7 (+0.6)	4.9 (+1.4)

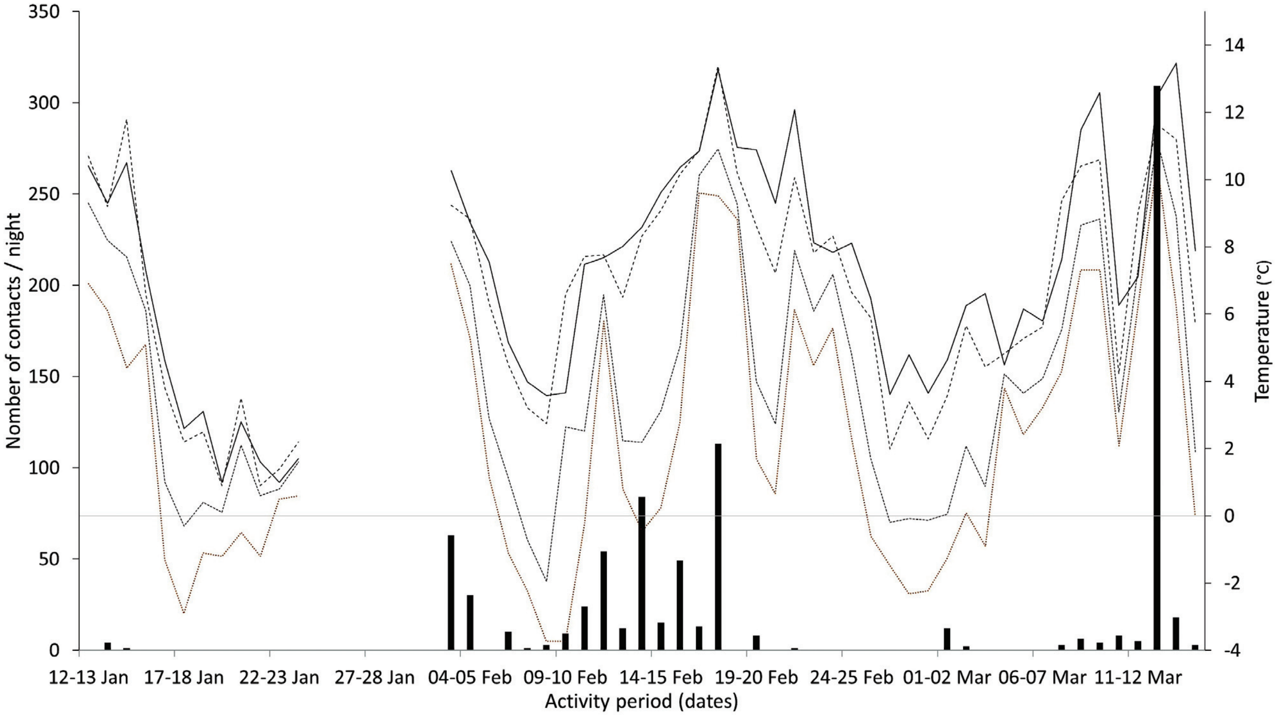

FIG. 2. Evolution of *P. pipistrellus* activity correlated with temperature variables throughout the study period. Black histograms represent *P. pipistrellus* activity as the number of contacts per night. The grey dotted line represents the mean nocturnal temperature (°C); the brown dotted line represents the minimum nocturnal temperature (°C); the light grey dotted line represents the maximum nocturnal temperature (°C); and the black continuous line represents the temperature of the day prior to the recording night (°C)

These are the nights of 03/04, 11/12, 13/14, 15/16 and 17/18 February, followed by 12/13 March. Another species, *N. noctula*, reached a moderate level of activity on 17/18 February and 01/02 March. These nights were among the warmest, and most of them showed activity levels above the mean of the variables or above the third quartile. Bat activity seems to really increase in February, but

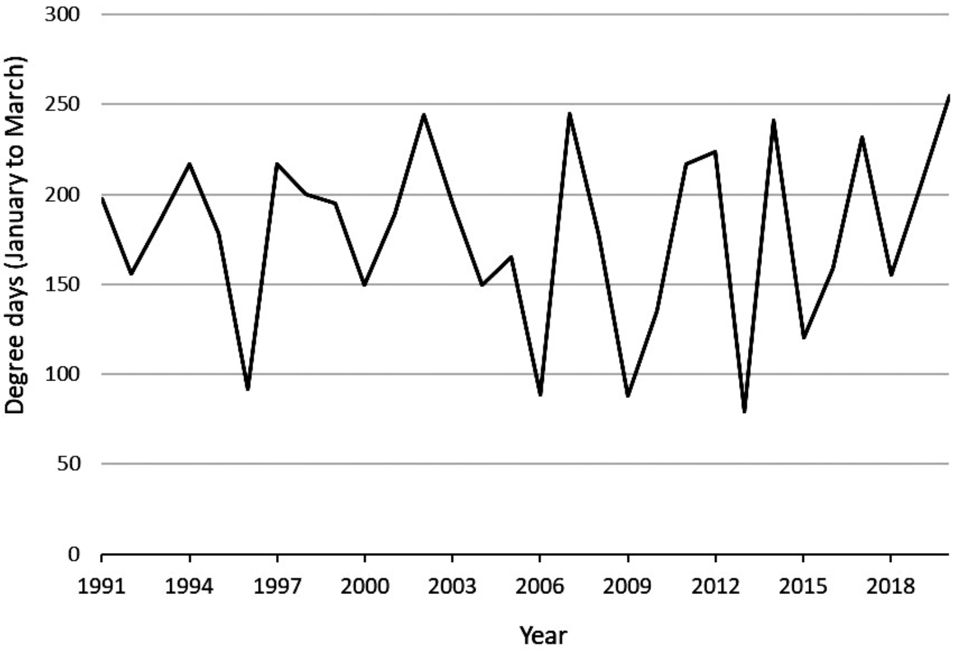

FIG. 3. Integrated air temperature (degree days) from January to March, spanning the period from 1991 to 2020

TABLE 6. Yearly degree day sums for 1991–2020, with observed differences compared to the degree day value for 2023 (D = 235.2 degree days). Degree day values were calculated using a threshold level of 5°C (see Equation 1)

Year	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Degree days (total)	197.5	156.0	186.0	217.0	178.5	91.5	217.0	200.0	195.1	149.4
Degree days (difference)	37.7	79.2	49.2	18.2	56.7	14.7	18.2	35.2	40.1	85.8
Year	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
Degree days (total)	189.1	244.5	194.4	149.5	165.2	88.3	245.1	177.4	88.1	135.4
Degree days (difference)	46.1	-9.3	40.8	85.7	70.1	146.9	-9.9	57.8	147.2	99.8
Year	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
Degree days (total)	217.0	223.6	79.4	241.0	120.5	158.7	231.7	155.2	204.7	255.0
Degree days (difference)	18.2	11.6	155.9	-5.8	114.8	76.6	3.5	80.1	30.6	-19.8

the gap in our records between January 24 and February 3 does not allow us to rule out this conclusion.

We observed three variables that were moderately positively correlated with the number of contacts: maximum temperature of the night (‘Temps_max’: $\tau = 0.355$, $P \ll 0.001$), temperature of the day before the recording night (‘Temp_dmean-1’: $\tau = 0.348$, $P \ll 0.001$) and the mean temperature of the night (‘Temp_mean’: $\tau = 0.338$, $P \ll 0.001$). The minimum night-time temperature (‘Temps_min’: $\tau = 0.321$, $P \ll 0.001$) can also be presented due to its value, but it is less correlated than the first three (Table 7).

Results from the Hurdle regression model present a more precise vision of the link between the number of contacts and the variables. Describing the probability of observing a positive count in relation to each variable, we used the zero hurdle component, leading to three variables having an important impact on the number of contacts: the type of habitat ‘Edge‘’ and the maximum temperature of the night are correlated with a positive count (‘Micro-Habitat=Edge’: est. = 2.053, $P \ll 0.001$ / ‘Temp_ max’: est. = 1.356, $P < 0.001$); at the opposite, the mean precipitation of the night tends to be associated with a negative count (‘Preci_moy’: est. = -8.080, $P \ll 0.001$). Other variables tend to have a negligent impact on the number of counts (Table 8).

DISCUSSION

Severe winter conditions are challenging for small endothermic mammals, such as insectivorous bats. Reduced metabolic activity by torpor use when prey are scarce enables survival in temperate zones (Findley, 1995; Arthur and Lemaire, 2015). Our study confirms that flight activity occurs when the climatic conditions are favourable. As shown by Ransome (1968), temperature is one of the most important factors, with a significant increase in activity linked to an increase in the maximum night-time temperature and the temperature of the day preceding the recording night. During this cold period of the year, these high values are associated with the first hours of darkness, close to dusk, which are the warmest. The dawn temperatures are the coldest on a given night. Higher dusk temperatures may lead to a greater presence of insect prey, but since their peak flight activity generally occurs at both dusk and dawn (Duvergé *et al*., 2000; Pavey *et al*., 2001), it is not the only factor. This has been shown for greater horseshoe bat (*Rhinolophus ferrumequinum*) in the UK as the species feeds all winter during favourable nights (Ransome, 1971; Park *et al*., 2000; Ransome, 2002). Important for European insectivorous bat species, the presence of prey during extended warmer periods could play a role in reducing the cost of arousal. Despite this, we observed bat activity at low temperatures, with a minimum

TABLE 7. Corelation test (Kendall’s τ) between the number of contacts and climatic variables

Variables tested	Kendall’s τ	*P*-value	Variables tested	Kendall’s τ	*P*-value
Nb_Contacts × Temps_mean	0.338	< 2.2e-16	Nb_Contacts × Preci_mean	0.081	4.762e-02
Nb_Contacts × Temp_mean-1	0.170	2.455e-06	Nb_Contacts × Wind_mean	0.008	0.816
Nb_Contacts × Temp_min	0.321	< 2.2e-16	Nb_Contacts × Wind_min	0.004	0.897
Nb_Contacts × Temp_max	0.355	< 2.2e-16	Nb_Contacts × Wind_max	0.019	0.603
Nb_Contacts × Temp_h	0.039	0.371	Nb_Contacts × Moon_phase	0.144	6.314e-5
Nb_Contacts × Temp_dmean-1	0.348	< 2.2e-16	Nb_Contacts × Nebulosity_moy	0.098	0.357
Nb_Contacts × Temp_dmean-2	0.078	3.024e-02	Nb_Contacts × Nebolisity	0.098	8.235e-03

TABLE 8. Results of zero hurdle modelling. Acronyms: Micro_HabitatDense_Forest — dense forest habitat; Micro_HabitatEdge — edge habitat; Micro_HabitatSparse_Forest — sparse Forest habitat. Significant values underlined

Variable	Estimate	Standard error	*z*-value	*P*-value
(Intercept)	-13.327	2.335	-5.708	1.15e-08
Micro.HabitatDense_Forest	-0.062	0.516	-0.121	0.904
Micro.HabitatEdge	2.053	0.534	3.844	1.21e-4
Micro.HabitatSparse_Forest	0.439	0.507	0.867	0.386
Temp_mean	-0.658	0.502	-1.310	0.190
Temp_mean-1	-0.158	0.132	-1.203	0.229
Temp_min	0.249	0.254	0.980	0.327
Temp_max	1.356	0.408	3.324	8.88e-4
Temp_dmean-1	0.318	0.257	1.236	0.216
Temp_dmean-2	0.063	0.143	0.443	0.658
Preci_mean	-8.080	1.962	-4.118	3.83e-05
Wind_mean	0.039	0.179	0.220	0.826
Wind_min	-0.236	0.133	-1.779	0.075
Wind_max	0.024	0.099	0.246	0.805
Moon_phase	0.060	0.010	5.822	5.81e-09
Nebulosity_mean	-0.033	0.122	-0.273	0.787
Log(theta)	-13.327	2.335	-5.708	1.15e-08

temperature of -3.4°C during the hour recorded and a mean of -1.9°C during the night. The lowest average recorded for the temperature for the previous day was 3.6°C. This might indicate that bats move for other physiological needs (Hope and Jones, 2012), but even if less frequent, feeding can also be observed at such low temperatures (Park *et al*., 2000; Ransome, 2002). This type of observations has already been documented, since *P. pipistrellus* and *N. noctula* appear to be among the most common species with winter activity (Zahn and Kriner, 2016), with *N. noctula* recorded at very low temperatures (Cel'uch and Kanuch, 2005).

In addition to the positive impact of warm temperatures, we noted the negative influence of precipitation. As a constraint on echolocation and the energy cost of flies (Voigt *et al*., 2011), our observation is in line with studies on the swarming period (Erickson and West, 2002; Parsons *et al*., 2003), and complements it for the winter period in Western Europe. Our results support the work of Avery (1985) from the late 20th century. Other variables studied here, such as wind or luminosity, linked with moon phase, seem to have few or no significant impact on it.

In the actual context of global warming (Terray and Boé, 2013), an increase in winter temperatures and important events of fluctuation for temperatures as for precipitations might have important impacts on bat communities. As we recorded, the 1991–2020 period presents oscillations in the integrated air temperature between 79.4 and 255 degree days, with more extreme temperature events and fluctuation events from one extreme to another. This increase of integrated air temperature could lead to a reduction in the torpor period by impacting hibernacula intern temperature, leading to less favourable conditions. When considering the work of Andrews *et al*. (2024) conducted on *Pipistrellus pygmaeus* in the UK, they found similar trends in degree days evolution, except for years 2001 and 2017 as warmer integrated air temperature were recorded within our study site. Despite divergent diets, as *P. pygmaeus* is considered as specialist and *P. pipistrellus* as generalist (Barlow, 1997), similarities are pointed between species allowing to transpose their observation on *P. pipistrellus*. Even if the increase in temperature is correlated with early emergences and a more important presence of insect prey, this could lead to a divergence between prey and predator timing of emergence (Andrews *et al*., 2024). As torpor is favourable for bats by decreasing water loss and metabolic cost in winter, it plays a role in reproduction by allowing delayed pregnancy (Sherwin *et al*., 2013). An increase of temperature leads to an early insect prey emergence and is correlated with a decrease of their density throughout the following month. This decrease has a negative impact on bat food intake. For most species, the hibernation period uses their body reserves (Racey and Swift, 1981). Correlated with this lack of insect prey during arousals, it thus leads to a higher mortality rate, amplified by potential return of cold temperature events in spring (Jones *et al*., 2009). This may also bring about a delay in gestation and a higher mortality rate for newborns due to lactation difficulties (Swift *et* *al*., 1985; Ransome and McOwat, 1994; Andrews *et al*., 2016). This may be more harmful for cold weather adapted species (Rebelo *et al*., 2010). Mediterranean and temperate species may be less affected, depending on the pace of climatic evolution, due to their ability to tolerate warmer temperatures (Rebelo *et al*., 2010). Habitat loss and disturbance due to anthropic activities can also reduce bat populations. (Frick *et al*., 2020). It is then important to take habitat measures, such as retaining mixed forest habitat, associated gites as natural caves, and standing deadwoods to increase bat resilience to climate change. Landscape connectivity to support bat access to habitats within reach of more suitable climatic conditions is also important (Bouvet *et al*., 2016; Law *et al*., 2016; Le Roux *et al*., 2017). As a more tolerant species with the capacity to adapt to anthropic sites, and in terms of the 2007–2020 average integrated air temperature trend recorded in this study, *P. pipistrellus* seems to be one of the species with the greatest tolerance to climate change (Mimet *et al*., 2020; McGowan *et al*., 2021), leading to stable or increased populations and distribution range throughout north France.

The significance of our findings must be qualified due to the limited study period (one season) and the restricted study area (a single site). Other studies comparing similar habitats, including those conducted over more winters, would be interesting to validate these observations, especially if they agree with those carried out in other biogeographical regions (Boyles *et al*., 2006; Turbill, 2008). Furthermore, our work paved the way for future studies on the effect of climate change on *Pipistrellus* species in France.

SUPPLEMENTARY INFORMATION

Contents. Supplementary Tables: Table S1. Species emission characteristics and associated detectability coefficient (Barataud, 2020); Table S2. Chiropterological activity level by quantile (Bas *et al*., 2020); Table S3. National activity referential (Bas *et al*., 2020); Table S4. Monthly variations in maximum/minimum temperatures and precipitation for January, February, and March based on detailed recorded climatic data from the 1991–2020 period, followed by observed variations for 2023 (shown in parentheses). Data for precipitation were not available for the 1991–2001 period. Bold text indicates the minimum and maximum variations for each variable in 2023. Supplementary Information is available exclusively on BioOne.

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AUTHOR CONTRIBUTION STATEMENT

FL: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing and critical revision of the article; MJ: critical revision and final approval of the article; VS: collection and/or assembly of data, data analysis and interpretation; PC: critical revision and final approval of the article.

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