

Autumn and winter nocturnal activity of bats in the Erlenbusch forest (Germany).

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Abstract

An exceptional effort to observe the hunting and social activity of bats was undertaken in a deciduous forest in western Germany. From 20th September 2020 to 20th March 2021, 17 ultrasound recorders provided 1,176,748 files containing 203,557 acoustic contacts belonging to 19 species during 37,458 hours of surveillance. The activity indices by decade show a drastic decline between September and mid-November, followed by reduced but uninterrupted hunting activity until March, even at temperatures of -6°C. The effects of rain, fog, temperature thresholds and structural parameters of the forest habitat on hunting, transit and social activities are presented and discussed.



Introduction

European bats are known to enter hibernation in autumn, only to resume regular hunting activity in early spring, depending on weather conditions (FURMANKIEWICZ & GORNIK, 2002; HOPE & JONES, 2012; THOMAS, 1995; WERMUNDSEN & SIIVONEN, 2010).

In the Mediterranean context, winter thermal conditions and the presence of a species (*Tadarida teniotis*) with reduced lethargy capacity generate occasional hunting activity in winter (BARROS *et al.*, 2021). The climatic conditions that prevail further north are thought to force bats into a more continuous lethargy (RODRIGUES *et al.*, 2003). However, even in the northern half of Europe, it has been observed that hibernation is more or less frequently interrupted for grooming, drinking, and even flying outside the roost (AVERY, 1983; SIMON & KUGELSCHAFTER, 1999; CEL'UCH & KANUCH, 2005; WINKLER & RÁKOS, 2023). Little is known about the determinism of this flight activity outside the roost; motivations may be linked to a need to change roost under various constraints: temperature variations, disturbances, occasional social activity, weak physiological state, influence of moonlight or atmospheric pressure, need to drink or feed (BLOMBERG *et al.*, 2021; CICHOCKI *et al.*, 2015; GIESE, 2024; HOPE *et al.*, 2014; RANSOME, 2002).

The flight activity of bats in European temperate forests has been increasingly well studied since the advent of acoustic detection tools (AHLÉN & BAAGØE, 1999; BARATAUD & GIOSA, 2021; GRANJEAN, 2011; JUNG *et al.*, 2012). These studies are most often carried out during the spring and summer periods, when hunting activity is at its peak. Autumn flight activity (combining hunting to accumulate the reserves needed for hibernation, and movements

to prepare for mating) and winter flight activity are less well studied, and mostly concern habitats along watercourses or forest edges (ZAHN & KRINER, 2016).

Since 2017, the Erlenbusch forest in central-western Germany has been the focus of intense acoustic monitoring (CRETU *et al.*, 2022), with the originality of carrying out numerous permanent nocturnal count points, including during autumn and winter. This study uses automatic recordings made at 23 listening points in the forest, between September 2020 and March 2021, to assess the phenology and determinism (social, hunting, transit) of flight activity in autumn and winter, for each of the 18 species contacted and identified with a high level of confidence.

Method and material

Description of the study site

The Erlenbusch (also known as Buschbeller forest), is located in the Atlantic zone of western Germany, near the town of Frechen to the west of Cologne (Figure 1). The average altitude is 116 metres (99 to 133 m), with little relief. Average monthly temperatures range from 6°C in January to 25°C in July. Average annual rainfall is just under 600mm, with a peak in July and August, which account for 25.6% of total annual rainfall.

This 80-hectare forest is isolated from other forest areas: In the north it is bounded by the A4 motorway, in the south by an open-cast mine with a few artificial waterbodies in its exploited and recultivated part. In the west, intensive agricultural areas border the forest area; in the east, in addition to smaller agricultural areas, urbanised commercial and residential areas.

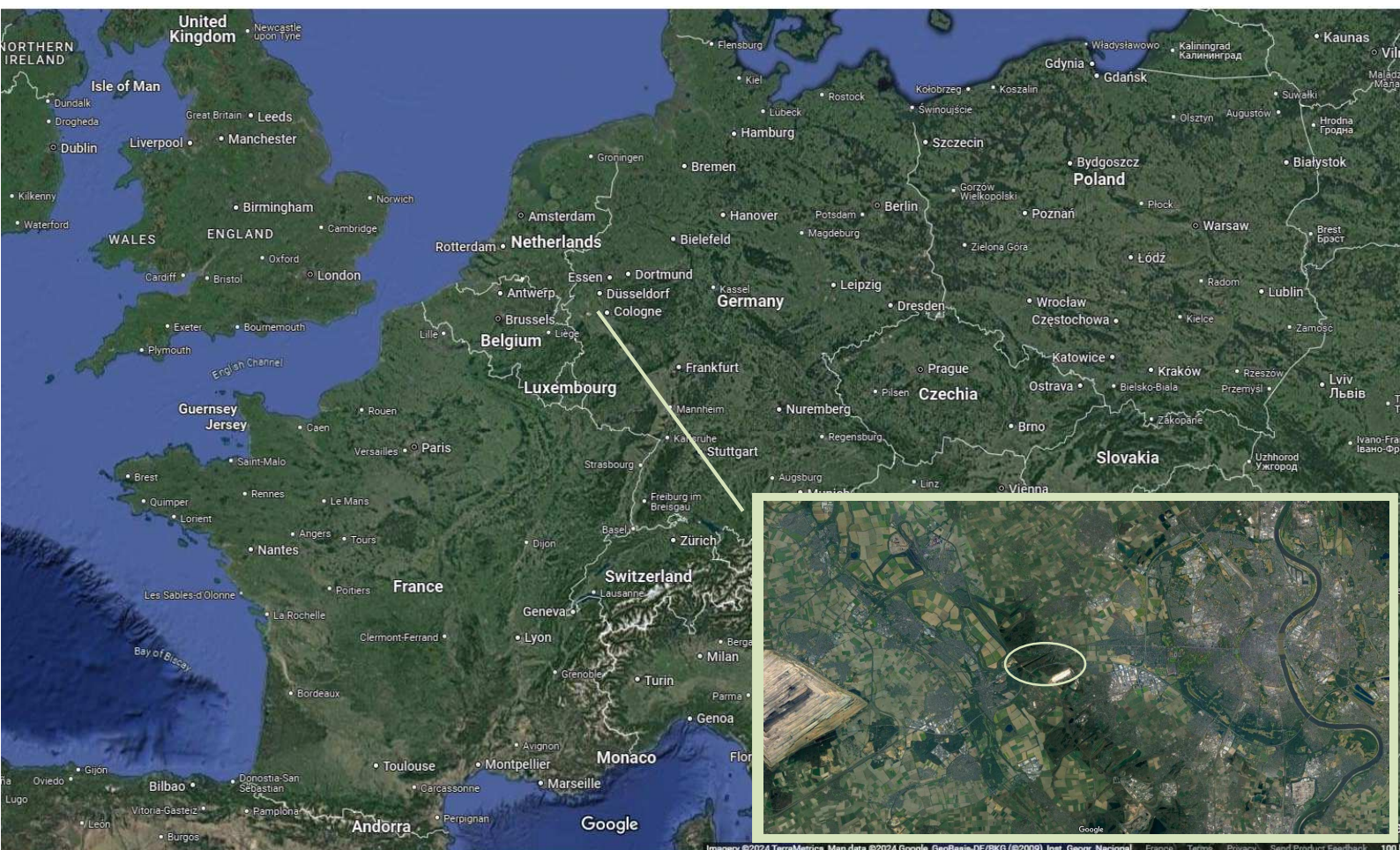


Figure 1. Satellite image (Google maps) of Europe, showing the Erlenbusch forest to the west of Cologne (Germany). The box shows the landscape context around the forest (in the centre of the ellipse), with intensive agricultural areas, and the city of Cologne to the east through which the Rhine flows; the light-coloured strip to the south of the forest is a sand quarry, which is steadily expanding at the expense of the forest area.

The Erlenbusch forest is threatened to the south by the open-cast quarry that is gradually reducing its surface area. On a larger scale, the surrounding landscape is made up of large plots of intensive agriculture and urbanised areas. The entire forest is designated as a 'biotope network area of exceptional importance' (**Landesamt für Natur, Umwelt und Verbraucherschutz**, 2017).

The forest consists mainly of beech *Fagus sylvatica*, accompanied in places by oak *Quercus* spp., hornbeam *Carpinus betulus*, birch *Betula pendula*, ash *Fraxinus excelsior*, willow *Salix* spp., spruces *Picea abies*, chestnut trees *Aesculus hippocastanum*, lime trees *Tilia* sp., alders

Alnus sp., maples *Acer* sp.

Several forest ponds are spread over the area, in which f.e. a special ecotyp (pond breeding ; indicator for old beech forests) of *Salamandra salamandra terrestris* and a lot of insects with aquatical cycle reproduce. The forest floor is occasionally (up to several months) flooded during rainy spells. The abundance of insects is partly due to this and contribute to the bat species diversity.

Acoustic survey sites and count points

Number and location:

23 recording sites were covered during all or part of the period; 6 of these sites contained only one count point (volume of perception of a microphone around a precise geo-referenced point). The other sites contained between 2 and 4 count points, as various constraints linked to human activities in the forest meant that some detectors had to be moved, usually by a few metres, and sometimes more in the case of 5 of them (Figure 2). The identifier for each site corresponds to that of the recorder, with a different letter if the recorder covered several stations (Table 1). Most of the forest south of the motorway was covered.

Dates and number of nights:

Recordings were made from 20th September 2020 to 20th March 2021, for a total of 182 nights. Subject to various meteorological and technical contingencies (weather,

batteries, maintenance), the 17 recorders provided usable data over a total of 2627 nights (37458 hours), with a variation of 127 to 174 nights per recorder (Table 2).

Types of recorders and microphones:

The detectors used in automatic mode are Batlogger type (Elekon AG, Lucerne, Switzerland) equipped with waterproof FG black electret condenser microphones (with integrated temperature sensor), sensitive from 10 to 150 kHz with a sampling frequency of 312.5 kHz; 17 devices (10 Batlogger A; 1 Batlogger A+; 4 Batlogger C; 2 Batlogger M) were used continuously during the period under consideration. These detectors, whose sensitivity is currently considered to be among the best (DISCA, 2023), can be triggered in response to weak signals, with feedback of 1 second and automatic stopping of the recording after the last perceptible signals; this greatly reduces the risk of failing to collect a sequence of bats. The microphones are placed at the end of a cable, on a branch at a maximum height of 2.5 m, and oriented horizontally.



Figure 2. Positioning of the 23 recording sites in the Erlenbusch forest; the site names correspond to the Batlogger identifiers. For sites split into two distant count points (1053, 1121, 1225, 1577, 4027), see Table 1 for recording periods.

Table 1.

List of recording points, with their characteristic of dates, descriptions and locations (see **Table 3** for the legend of the habitat codes).

Nb of listening point	Batlogger id.	Start recording period	End recording period	Microphone directed towards	Habitat typology	X (WGS 84)	Y (WGS 84)
1	BLA 1118	24/09/2020	18/03/2021	Clearance	OF_ed-h_4	67697	509250
2	BLA 1119-a	24/09/2020	31/10/2020	Underwood, hilltop	OF_und_1	677787	5092547
2	BLA 1119-b	01/11/2020	12/12/2020	Underwood, hilltop	OF_und_1	677758	5092501
2	BLA 1119-c	13/12/2020	18/03/2021	Underwood, hilltop	OF_und_1	677737	5092535
3	BLA 1121-a	24/09/2020	21/10/2020	(Forest) path	OF_ed-h_0	678333	5092703
3	BLA 1121-b	22/10/2020	27/10/2020	Underwood, hilltop	OF_und_1	677758	5092501
4	BLA 1121-c	29/10/2020	20/03/2021	Underwood	OF_und_3	675929	5092423
5	BLA 1122	24/09/2020	18/03/2021	Clearance	OF_ed-h_2	67654	509232
6	BLA 1124	24/09/2020	18/03/2021	Forest path	OF_und_3	67772	509268
7	BLA 1125	24/09/2020	18/03/2021	Forest path	OF_und_3	677301	5092705
8	BLA 1126	24/09/2020	25/07/2021	Underwood, hilltop	OF_und_3	67756	509261
9	BLA 1133-a	24/09/2020	07/10/2020	Forest edge - field	OF_ed-h_0	67666	509215
9	BLA 1133-b	08/10/2020	07/11/2021	Forest path	OF_und_2	676645	5092174
9	BLA 1133-c	08/11/2020	17/03/2021	Forest path	OF_und_2	676607	5092166
10	BLA 1135-a	24/09/2020	15/03/2021	Clearance	OF_ed-h_4	676807	5092339
10	BLA 1135-b	16/03/2021	20/03/2021	Forest path	YF_ed-h_2	676478	5092463
11	BLA 1136	24/09/2020	18/03/2021	Clearance	OF_ed-h_2	6767228	50924106
12	BLA+ 1577-a	24/09/2020	12/12/2020	Forest edge - pit	OF_ed-h_1	67691	509217
13	BLA+ 1577-b	13/12/2020	10/07/2021	Underwood	OF_und_2	67710	509255
14	BLC 1048-a	08/10/2020	12/12/2020	Underwood	OF_und_2	67738638	509238
14	BLC 1048-b	13/12/2020	18/03/2021	Clearance	YF_ed-h_2	6772975	509240389
15	BLC 1053-a	08/10/2020	10/10/2020	Underwood	OF_und_2	676506	509264278
16	BLC 1053-b	11/10/2020	17/10/2020	Paved forest path/closed canopy	OF_ed-h_0	676905	509260528
15	BLC 1053-a	18/10/2020	20/03/2021	Underwood	OF_und_2	676506	509264278
17	BLC 1309-a	08/10/2020	20/11/2021	Forest path	OF_und_2	67632361	509245528
17	BLC 1309-a'	21/11/2020	10/02/2020	Forest path	OF_und_2	676305	5092478
17	BLC 1309-a'	21/02/2021	20/03/2021	Forest path	OF_und_2	676305	5092478
18	BLC 1225-a	08/10/2020	30/10/2020	Forest path, semi-permanent puddle	OF_und-w_2	677079	5092285
18	BLC 1225-a'	31/10/2020	14/11/2020	Path/Clearance	OF_und_2	6771150	50922790
18	BLC 1225-a	15/11/2020	12/12/2020	Forest path, semi-permanent puddle	OF_und-w_2	677079	5092285
19	BLC 1225-b	13/12/2020	15/03/2021	Clearance	OF_ed-h-w_4	676956	5092408
20	BLC 1225-c	16/03/2021	20/03/2021	Underwood	OF_und_2	6762290	50923750
21	BLM 4026-a	01/10/2020	11/12/2020	Underwood, hilltop	OF_und_3	6775543	5092472
21	BLM 4026-b	12/12/2020	17/03/2021	Underwood, hilltop	OF_und_3	677515	5092495
22	BLM 4027-a	01/10/2020	05/12/2020	Forest edge, valley, semi-permanent water	OF_ed-g-w_4	677782	50924600
23	BLM 4027-b	06/12/2020	26/07/2021	Underwood, "valley"	OF_und_3	6773734	50925874

Description and typology of habitats:
Several photographs were taken of each count point (**Appendix 2**), and a description of the main habitat variables (**Table 3**) that generally influence bat hunting activity during spring and summer (BARATAUD *et al.*, 2016).

Sound data analysis

Method:

The auditory and computer analysis (BatSound version 4.4 software; Pettersson Elektronik AB) of the sequences was carried out using the criteria of the acoustic ecology method (BARATAUD, 2020). This method uses the classic measurements carried out on the signals (see below). However, the originality and performance

of the method lie in the fact that the measured values are part of a process that also incorporates the flight behaviour of the individual (distance from frontal and lateral obstacles, degree of curiosity, more or less active search for prey and/or obstacles, etc.) This behaviour is judged on the basis of a combination of two parameters: the structure of the signals (bandwidth, duration, curvature, timbre, energy distribution, end frequency) and their rhythm (duration and regularity of intervals), taking into account any variations in these during a sequence, and the quality of signal reproduction.

Processing sound sequences:

The sequences collected (n = 1,176,748) were analysed manually. Each sequence

Table 2.

Information on listening pressure (in no. of nights and hours) and on the number of files collected by the 17 Batlogger recorders (named according to their numbers) in the Erlenbusch forest from 20th September 2020 to 20th March 2021.

	1118	1119	1121	1122	1124	1125	1126	1133	1135	1136	1157	1048	1053	1309	1225	4026	4027	Total
N. recorded files	22044	10435	55441	44494	70247	119672	43844	66188	38608	46784	106994	61767	44226	153090	66879	130256	95779	1176748
N. files with bat contacts	11133	4462	21743	9355	11522	29716	7032	2579	7236	3958	3944	1292	1246	4858	1297	4074	1643	127090
%	50,5%	42,8%	39,2%	21,0%	16,4%	24,8%	16,0%	3,9%	18,7%	8,5%	3,7%	2,1%	2,8%	3,2%	1,9%	3,1%	1,7%	10,8%
N. nights	154	157	129	174	155	167	165	162	169	127	162	154	152	144	138	162	156	2627
N. hours	2173,5	2212,5	1820	2472,5	2230	2377	2347	2301,5	2396	1780,5	2308,5	2219	2187	2089,5	1994,5	2319,5	2229,5	37458

Table 3.

Forest habitat variables (including the codes used in **Table 1**) described at each recording count point.

Variable	Code	Description	Definition
Age	VOF	Old forest	trunk diameter 0,6 to 0,8 m
	YF	Young forest	trunk diameter 0,3 to 0,5 m
Ecotone	und	underwood	no ecotone
	ed-h	edge hole	hole canopy 200 to 500 m ²
	ed-g	edge glade	edge on clearing > 500 m ²
	w	water	river (> 2 m wide) or pond, distance < 20 m
Shrub layer (< 4 m high)	0	0 to 10%	ground projection coverage
	1	10 to 25%	ground projection coverage
	2	25 to 50%	ground projection coverage
	3	50 to 75%	ground projection coverage
	4	75 to 100%	ground projection coverage

was displayed on the BatSound software, and a visual examination was carried out to determine the presence of chiropteran signals among the various background noises (wind, rain, orthopteran stridulations, bird songs, small mammal calls, the sound of movement in leaf litter, etc.). If chiropteran signals are present and visual analysis is not sufficient to determine the species (*Pipistrellus pipistrellus*, for example, which accounts for 80-90% of contacts, is instantly identifiable with a little experience), the sequence is listened to and, if necessary, measurements are taken on signals selected non-randomly on the basis of their characteristics (quality, structure and rhythm); the sampling unit in this identification method is not the individual producing a sequence, but each of the different acoustic behaviours adopted by an individual in the same sequence. The 'wave' files are scrolled through very quickly using the 'N' (forwards) or 'B' (backwards) keys on the keyboard, allowing, depending on the content of the sequences, an output of 500 (heterogeneous series of several species, each requiring listening and/or measurements) to 5,000 (long homogeneous series of background noise

or *P. pipistrellus*) files per hour, including data entry into the database.

Signal measurements:

The criteria taken into account are: the total duration of the signal (in milliseconds) ; the start frequency (SF) in kHz and the end frequency (EF) of the fundamental ; the width of the frequency band (BW) ; the frequency of maximum energy (FME) of the first harmonic (H1), and of the second harmonic (H2) only for *Plecotus* signals. The FME is defined as the frequency with the highest energy concentration based on spectral density analysis. For frequency modulated (FM) signals, the duration, BW and EF are measured on a spectrogram (512-point FFT window, Hanning type). Power spectrum measurement is also made with 512-point FFT window, except for SF measurement of quasi constant frequency (QCF) signals, which is made with a 256-point FFT window (BARATAUD, 2020). As atmospheric attenuation acts mainly on high frequencies, the most intense signals are selected in order to obtain more accurate measurements of bandwidth and duration. For the complete sequence, variations in rhythm (regularity and recurrence) are assessed audibly, then specified if necessary by computer measurement of the duration of the intervals (including the signal, in milliseconds).

Quantifying and qualifying activity :

The method of measuring activity is known as « precise »: a contact corresponds to the occurrence of signals from an individual of a species of chiroptera, in five-second intervals (BARATAUD, 2020). With 3601 levels/hour, this method is powerful to express variations in activity; its high sensitivity to detection bias has been corrected here in terms of data collection (standardisation of equipment and installation method) and data processing (analysis of files



Photo of station I121c taken on 17th January 2021. The Batlogger microphone is visible in the top centre.

by a single observer, use of weighting coefficients for the disparity in emission intensity between species). The intensity of sonar emissions varies from one species to another, which makes it impossible to compare their respective raw activity indices (number of contacts/hour). To compensate for this disparity, we used a detectability coefficient (BARATAUD, 2020), correlated with the perception distance of each species in a forest environment (Table 4). These coefficients are applied to the raw contacts to allow comparison between species or groups of species. The flight context is taken into account when assigning the coefficient (for example, as the intensity of the signals from *Plecotus* varies according to their behaviour and the openness of the environment, the coefficient of detectability therefore varies from 1.25 to 5). The activity indices are

therefore always expressed in terms of the number of adjusted contacts per hour, unless otherwise stated « raw contact ».

The type of activity is assessed using criteria that combine variations in the rhythm (recurrence and regularity) of a sound sequence and variations in the structure (duration and bandwidth, curvatures, energy distribution, etc.) of the signals. Hunting activity can of course be deduced from the presence of a characteristic phase of prey pursuit (so called « buzz »). But this event generally occurs only fleetingly and at intervals during the nocturnal periods when a bat is constantly searching for prey. The acoustic ecology method, built on the basis of auditory and visual monitoring of marked individuals over long periods, has been able to highlight rhythmic criteria characterising more or less active searching for prey or obstacles, with the possibility of separating the two lenses in many cases; for species with an FM structure (*Myotis*, *Plecotus*) in particular, successions of acoustic types make it easy to distinguish an obstacle approach from a prey approach.

In addition, the duration of an individual sequence (correlated with the species' sonar intensity) is a reliable indicator of flight time within the listening volume (adjusted by the intensity coefficient, taking into account the speed of flight), which can then be judged to be greater than that of a single linear passage (which is the case during transit), and even testifies to back-and-forth prospecting routes (BARATAUD, 2020).

Thus, hunting activity during the winter period (December to March), when prey is less numerous and, consequently, capture phases are rarer, has in many cases been distinguished from that of transit. Transit activity is characterised by a single, rapid crossing of the listening volume, with sonar

Table 4. List of bat species with their detection distance (in metres) in a forest context, with the resulting detectability coefficient which is used to obtain the adjusted contacts (BARATAUD, 2020).

Sonar intensity	Species	Detection distance (m)	Detectability index
weak	<i>Plecotus</i> spp. (duration < 4 ms)	5	5,00
	<i>Myotis emarginatus</i>	8	3,13
	<i>Myotis nattereri</i>	8	3,13
	<i>Myotis alcathoe</i>	10	2,50
	<i>Myotis mystacinus</i>	10	2,50
	<i>Myotis brandtii</i>	10	2,50
	<i>Myotis daubentonii</i>	10	2,50
	<i>Myotis bechsteinii</i>	10	2,50
	<i>Myotis oxygnathus</i>	15	1,67
	<i>Myotis myotis</i>	15	1,67
medium	<i>Pipistrellus pygmaeus</i>	25	1,00
	<i>Pipistrellus pipistrellus</i>	25	1,00
	<i>Pipistrellus nathusii</i>	25	1,00
	<i>Plecotus</i> spp. (duration > 4 ms)	20	1,25
loud	<i>Eptesicus serotinus</i>	30	0,83
very loud	<i>Nyctalus leisleri</i>	80	0,31
	<i>Nyctalus noctula</i>	100	0,25
	<i>Nyctalus lasiopterus</i>	150	0,17

signals indicating a passive search for obstacles: slow and often irregular rhythm; narrower bandwidth and longer duration, characteristic FM curvatures. Social activity is inferred from the presence of signals known to be part of vocal repertoires for intra-specific communication (PFALZER, 2017; RUSS, 2021; MIDDLETON *et al.*, 2022; VINET & BAS, 2023; DISCA, in prep.).

The probable presence of a roost near the listening point is deduced from the emission of types of social calls which, in some species, are produced mainly or exclusively near the roost.

Exploitation of raw data

Data entry:

The database includes 34 fields; most of the variables are filled in by automatic formulae, linked to: the title of each file (containing information on the count point identifier - which provides a cascade of information on the characteristics of the habitat - as well as the date and time); the species (--> coefficient of detectability); the size of the file (--> no. of contacts: 3 Mb = 1 contact of 5 sec). Listening pressure is calculated using the date, which indicates the length of the night, varying from 12 to 15.5 hours during the survey period. Thus, once the name and size of the files for a complete night have been entered into the database (lists obtained using the free software Free Commander), the information entered for the analysis of each sequence is reduced to the species (simplified code) and the level of confidence of the identification. Temperature data (in degrees Celsius) are collected thanks to the microphones with integrated temperature sensors, and appear in the metadata files associated with the sound files (wave).

Descriptive statistics:

The spatial sampling unit is the recording

count point; for all calculations of the distribution of values by quartiles, the temporal sampling unit is the complete night (from sunset time to sunrise time).

Results

Species diversity

Reliable criteria for identification to species level with a high level of confidence were found in 94.7% of cases; identification was qualified as probable (low risk of confusion with another species) for 3.8% of contacts; the remaining 1.5% corresponded to the acoustic complexes *M. myotis-blythii*, *Eptesicus-Nyctalus* spp. and *Plecotus* spp. (in absence of reliable specific criteria), or to poor sequence quality (*Myotis* sp.).

At least eighteen species frequented the Erlenbusch forest during this period (Table 5). A 19th species, *Eptesicus serotinus*, is uncertain: of the many sequences attributed to the *Eptesicus-Nyctalus* group, only 4 (at sites 1119b, 1136 and 1577a) are attributable to this species, but with a low level of confidence (weakly discriminating criteria, risk of confusion with *N. leisleri*). As *N. leisleri* is very active in the forest, it is highly probable that a large majority of the contacts attributed to the *Eptesicus-Nyctalus* complex come from this species.

Several species that were definitely identified at Erlenbusch are currently considered rare or absent from this part of Germany (*Myotis alcaethoe*, *M. emarginatus*, *Nyctalus lasiopterus*).

Two other species are far from their known distribution: *M. blythii* was identified on the basis of a reliable criterion in its sympatric zone with *M. myotis* (signal duration > 9 ms for the «absence of a terminal mid-frequency peak» type);

Plecotus macrobullaris was identified on the basis of reliable frequency criteria in its sympatric zone with *P. auritus* and *P. austriacus* (SF x EF; FME H1 x FME H2).

Table 5.

List of 19 chiropteran species (white lines; in decreasing order of activity level) inventoried in the Erlenbusch forest, with their types and levels of activity, and their ecological and legal status. The yellow lines correspond to non-specific identifications (acoustic complexes), and the orange lines correspond to the sum of contacts attributed to the *Myotis myotis* and/or *blythii* group and to the *Plecotus* genus.

Species	Hunting	Transit	Social	Roost probable in vicinity	No. contact (raw)	No. contact (adjusted)	Activity index (No. c/h)	Habitats Directive 92/43/EEC	Forestry specialist	Forestry partially
<i>Pipistrellus pipistrellus</i>	X	X	X		175279	172986,51	4,6181			X
<i>Myotis daubentonii</i>	X	X	X		3857	9640,03	0,2574			X
<i>Myotis myotis/blythii</i>					2842	4968,35	0,1326			
<i>Plecotus</i> spp.					1756	4340,58	0,1159			
<i>Pipistrellus nathusii</i>	X	X	X		4314	4313,83	0,1152			X
<i>Myotis myotis</i> or <i>blythii</i>					1315	2357,45	0,0629			
<i>Plecotus</i> sp.					1206	2258,33	0,0603			
<i>Myotis mystacinus</i>	X	X			902	2255	0,0602		X	
<i>Myotis nattereri</i>	X	X			727	2184,1	0,0583		X	
<i>Myotis myotis</i>	X	X			1270	2162,8	0,0577	X		
<i>Nyctalus leisleri</i>	X	X	X	X	4489	1335,28	0,0356			X
<i>Plecotus auritus</i>	X	X	X	X	287	1225	0,0327		X	
<i>Plecotus austriacus</i>	X	X	X	X	228	802,25	0,0214			X
<i>Myotis blythii</i>	X	X			257	448,1	0,0120	X		X
<i>Eptesicus/Nyctalus</i> sp.					474	397,7	0,0106			
<i>Myotis bechsteinii</i>	X	X			112	276,8	0,0074	X	X	
<i>Myotis alcathoe</i>	X	X			97	242,5	0,0065		X	
<i>Myotis emarginatus</i>	X				77	226,7	0,0061	X	X	
<i>Myotis</i> sp.					72	180	0,0048			
<i>Pipistrellus pygmaeus</i>	X	X	X		154	154	0,0041			X
<i>Plecotus macrobullaris</i>	X	X			35	55	0,0015			X
<i>Myotis brandtii</i>	X				15	37,5	0,0010		X	
<i>Nyctalus noctula</i>	X	X	X		45	11,95	0,0003			X
<i>Eptesicus serotinus</i> (poss)		X			4	3,32	0,0001			X
<i>Nyctalus lasiopterus</i>		X			2	2,5	0,0001			X
Total	17	17	8	3	195218	203556,65	5,43	4	7	11

Activity by species and count point

Once the activity has been weighted according to the differences in emission intensity of each species, it is possible to compare their activity indices.

Figure 3 shows the species or taxa ranked in descending order of activity. *P. pipistrellus* is the dominant species, with 172 987 contacts (85%); the 2nd most active species, with 9 640 contacts (0.05%), is *M. daubentonii*, which is unexpected in a non riparian forest environment; *M. myotis-blythii* (4968.3 contacts), the genus *Plecotus* (4340.6 contacts) and *P. nathusii* (4313.8 contacts) are still at high levels, as are 2 other species of *Myotis*: *M. mystacinus* (2255 contacts) and *M. nattereri* (2184.1 contacts).

The sequences identified as *N. leisleri* are from individuals in flight above the canopy (a context that optimises identification of this species). The sequences captioned *Eptesicus-Nyctalus* spp. are all emitted in a context of flight in undergrowth (truncated flat-ended FM signals, or FM signals), which generates a high degree of overlap between the large species with a QFC component. *N. leisleri* is probably the main author, as these FM structure sonar sequences often appear in a context of social activity of this species on the same count point at the same time; the song produced by a male of *N. leisleri* with the intention of forming a harem, is likely to

generate in the undergrowth a circulation of conspecifics whose sonar signals cannot be distinguished from other acoustically close species in this type of context, such as *E. serotinus* and *N. noctula*.

All the species were contacted while hunting, except *N. lasiopterus* and *E. serotinus*, for which the number of contacts (2 and 4 raw contacts respectively) and their quality (short duration sequences) are too low to characterise hunting activity with confidence.

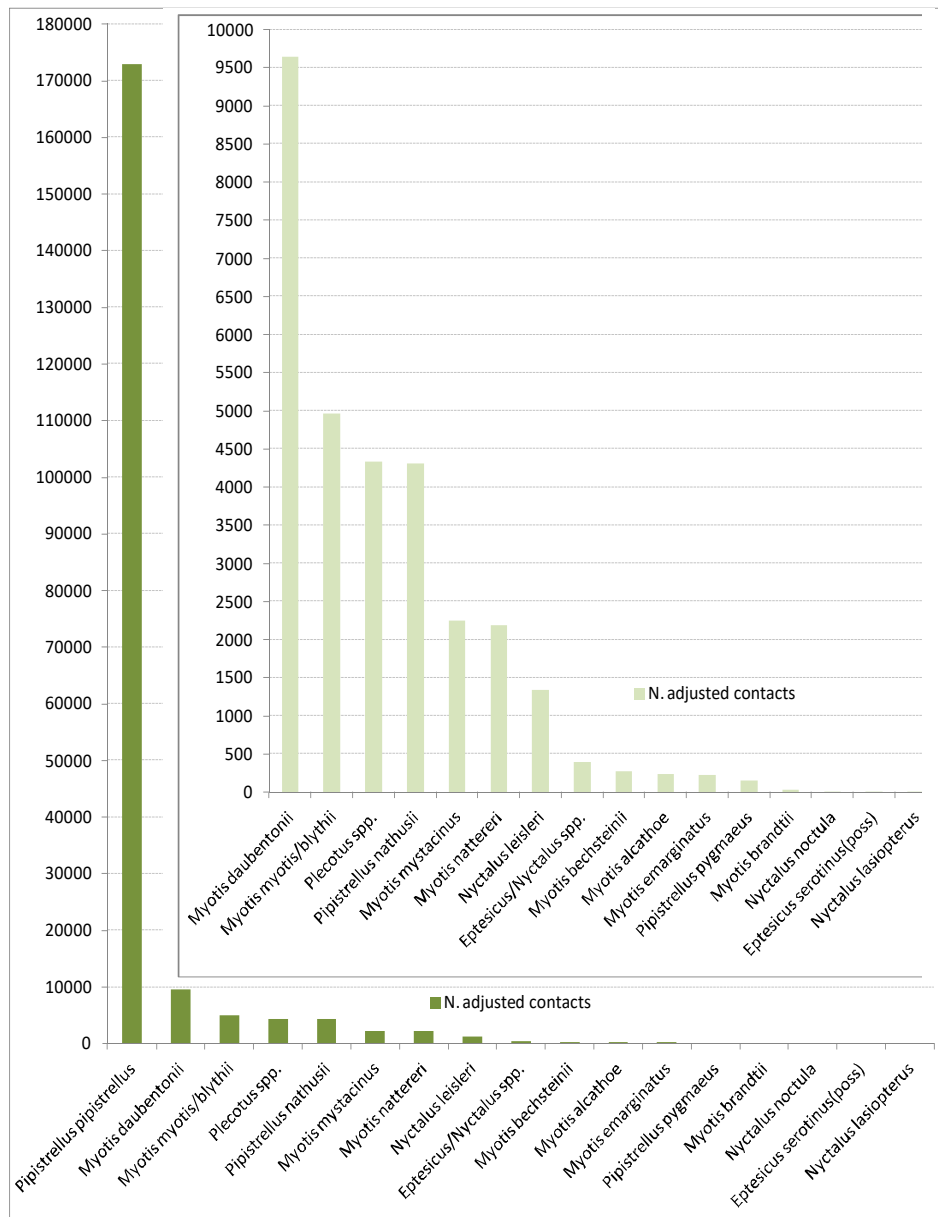


Figure 3.

Acoustic activity levels for each of the species identified in the Erlenbusch forest, ranked in descending order of the number of weighted contacts. The superimposed graph shows the species again, but without *P. pipistrellus*, as its very high activity level masks the details of the other distributions.

Several species provided social communication signals in addition to sonar signals (Table 5). For *P. pipistrellus* (24 count points; 26818 social trills), *P. pygmaeus* (count point 1121a; 69 social trills) and *P. nathusii* (count point 1122; 24 social trills), the social calls collected correspond to interactions on the hunting grounds or territorial marking during the mating season. The low number of social contacts recorded for *N. noctula* (count points 1121a and 1577a; 0.75 contacts) and *M. daubentonii* (count points 1119a and 1122; 7.5 contacts) does not allow any interpretation. For *N. leisleri* and the genus *Plecotus*, which do not generally emit social calls on their hunting grounds, the number and type of signals collected indicate the very likely presence of at least one breeding site in the immediate vicinity of each count point. A total of 28 count points were involved: 1048a, 1118, 1119b, 1121a, 1122, 1126, 1133a+b, 1135a, 1225a, 1577a, 4026a, 4027a for *N. leisleri* (13 count points; 522 social contacts indicating breeding sites); 1048a+b, 1053a+b, 1118, 1119a+b+c, 1121a+c, 1122, 1124, 1125, 1126, 1133b, 1135a+b, 1136, 1225b, 1309, 1577b, 4026a+b, 4027a+b for *P. auritus* and *P. austriacus* (25 count points; 1590 social contacts).

The figures in Appendix 1 show the distribution of each species and the density of use of each site throughout the survey area.

M. alcaethoe is found mainly in the southern half of the forest, while *M. mystacinus* is often more active in the center. The rare sites frequented by *M. brandtii* are in areas of mixed deciduous and coniferous woodland. *M. daubentonii* is present everywhere, with areas of very high activity in the centre and east; the same goes for *M. nattereri* and *M. myotis-blythii*, but with a higher abundance

respectively in the east (mixed woodland) and south-west (dominant deciduous trees). *M. blythii* could be distinguished from the *M. myotis-blythii* complex at 13 count points, 2 of which (1122 and 1577a) accounted for 68.5% and 11.1% of total contacts respectively. *M. emarginatus* provided few contacts, but they were well dispersed spatially: the whole forest seems to be used, without it being possible to identify sites that are more frequented than others.

P. auritus, identified at 17 count points, was particularly active at count points 1577a, 1118, 1122 and 4026a. *P. austriacus*, identified at 17 count points, was most active at 1122 (47.3% of contacts) and 1118 (17% of contacts). *P. macrobullaris* was identified at a certain level at 3 count points (1225b, 1577a, 4026b), and at a probable level at 2 other count points (1118, 4026a); count point 4026b recorded 30 contacts out of a total of 55 contacts. Of the 4,340.6 contacts attributed to the genus *Plecotus*, 52% could not be attributed to a particular species, due to frequency values overlapping 2 or even 3 taxa, or due solely to the presence of social calls, which are currently considered to be non-discriminatory.

P. pipistrellus, *P. nathusii* and *N. leisleri* were active everywhere, with several sites of high abundance. *P. pygmaeus* provided most of the contacts (97.4%) at site 1121a to the east of the forest, over a limited period from 24th September to 19th October. The few contacts of *N. noctula* were well distributed both spatially and temporally (absent only during the months of January and March, which are the months with the lowest overall activity). *N. lasiopterus* was identified at 2 count points (1121a on 27/09/2020; 1121c on 05/11/2020), with a single crude contact on each occasion: this species was only in transit occasionally during the study period.

Autumn and winter phenology of hunting and social activities

Depending on the species, acoustic contacts for all activities combined decline drastically, or even stop altogether, from the 3rd decade of November (Figure 4). They then pick up again much later in the 3rd decade of February, before becoming very low again until 20th March.

Figures 5 and 5a to 5f show the monthly variations in adjusted activity for 7 taxa. *P. pipistrellus* has been placed against the total activity to indicate the extent to which the latter is influenced by this species alone (Figure 5). *M. daubentonii* (Figure 5a) and *M. myotis-blythii* (Figure 5b) are inactive from December to February. *M. nattereri* (Figure 5e) continues hunting until around

10th December and then stops completely until 20th March. *P. nathusii* remains active throughout the period, with a more marked decline in January and March (Figure 5d); the situation is the same for *N. leisleri* and the *Eptesicus-Nyctalus* group (Figure 5f). The genus *Plecotus* (Figure 5c) shows a decline in December and January.

On average over the entire study period, *P. pipistrellus* provided 40 times more contacts than *P. nathusii*, but this overall ratio masks a marked monthly disparity (Figure 5g). The most marked difference is in September, when *P. pipistrellus* (24576.6 contacts) is 223 times more active than *P. nathusii* (110 contacts); then a sharp decrease is observed in October, which continues until January, when their activities become almost identical (137 and 114 contacts respectively).

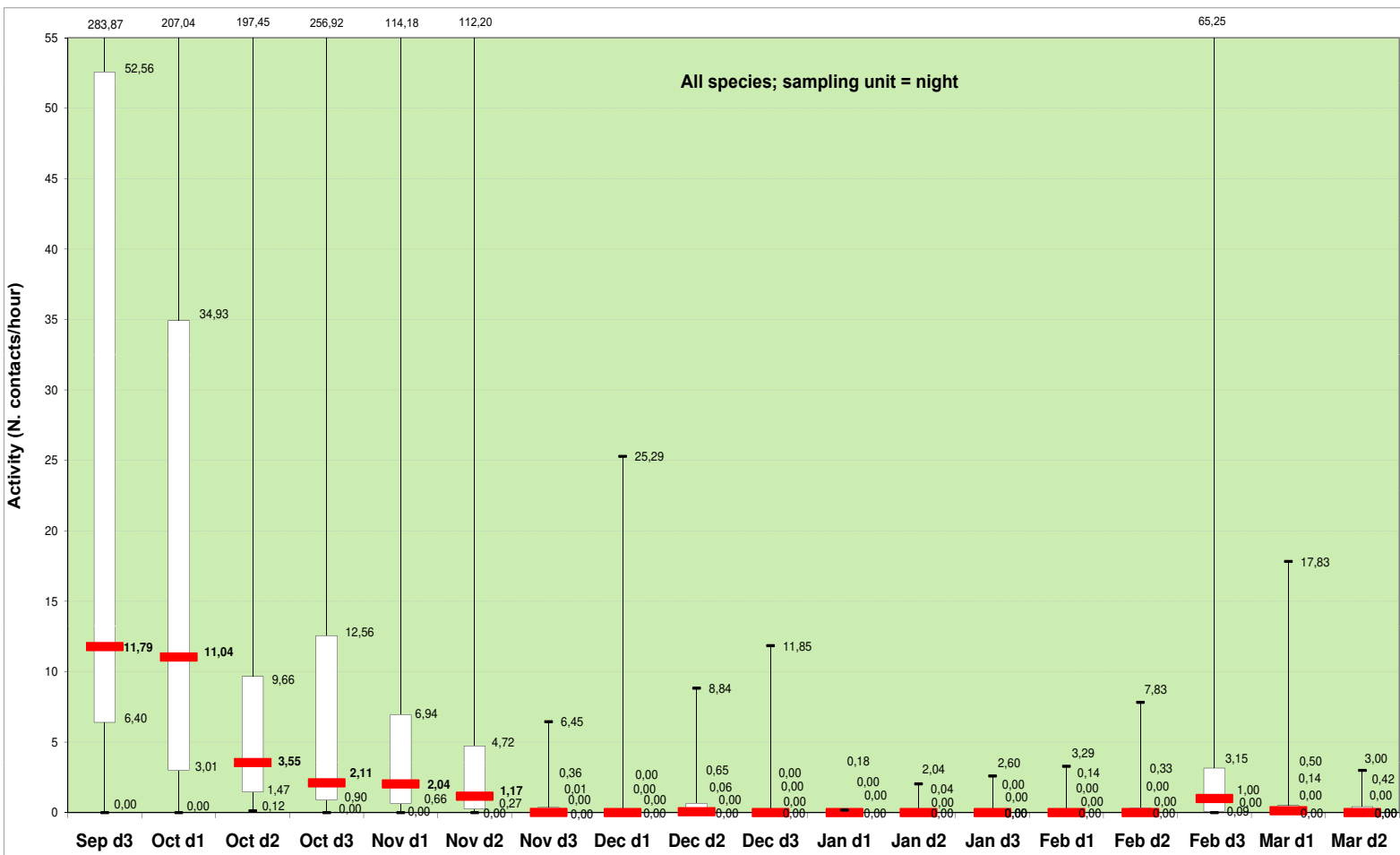


Figure 4. Medians of activity indices (no. of adjusted contacts/hour) with variations (1st and 3rd quartiles, extremes), all species combined, throughout the autumn-winter period divided into decades.

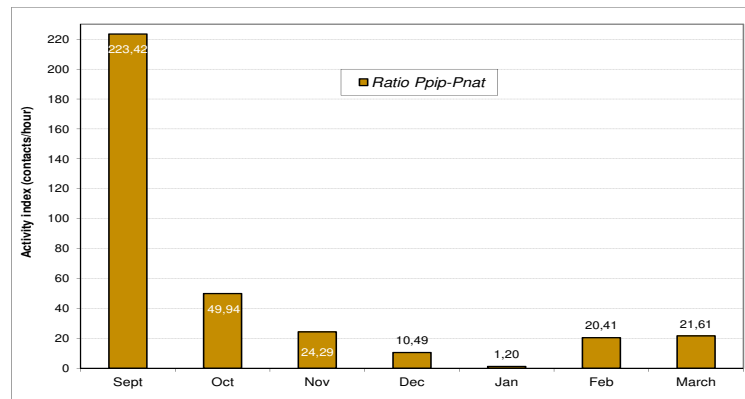
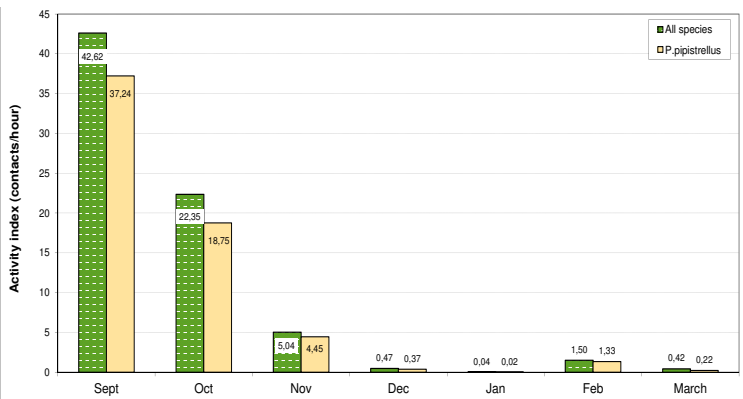


Figure 5. Monthly activity (adjusted contacts/hour) for all types and all species combined, compared with that of *P. pipistrellus* in order to judge the influence of this species.

Figure 5g. Activity ratio between *P. pipistrellus* and *P. nathusii* between September and March. The value associated with each plot of the histogram indicates a multiplication factor: in September *P. pipistrellus* is 223.43 times more active than *P. nathusii*, etc.

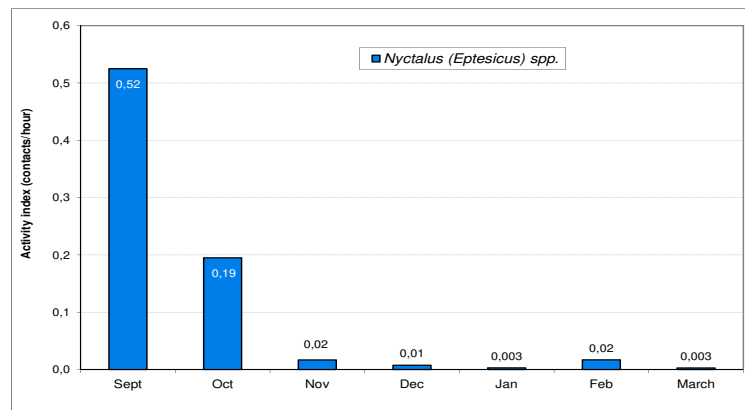
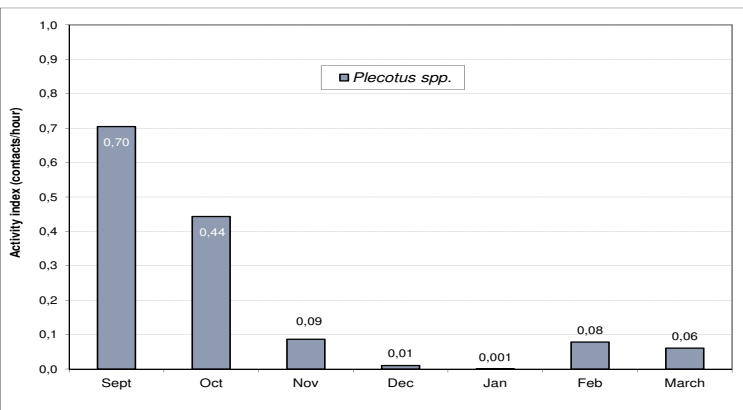
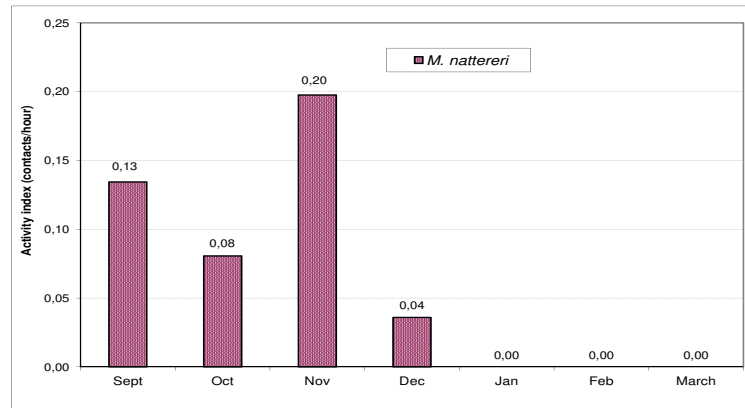
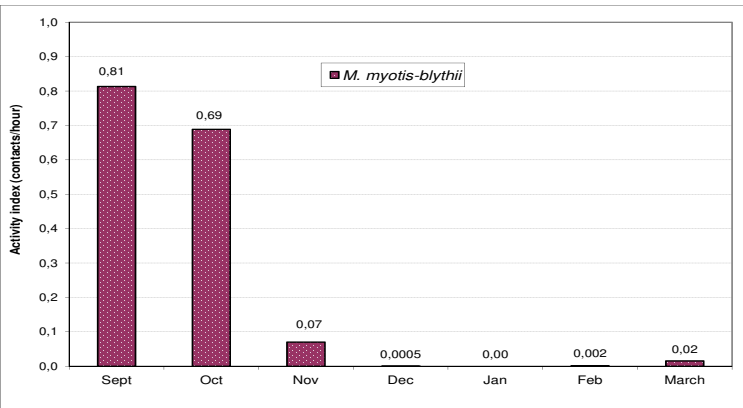
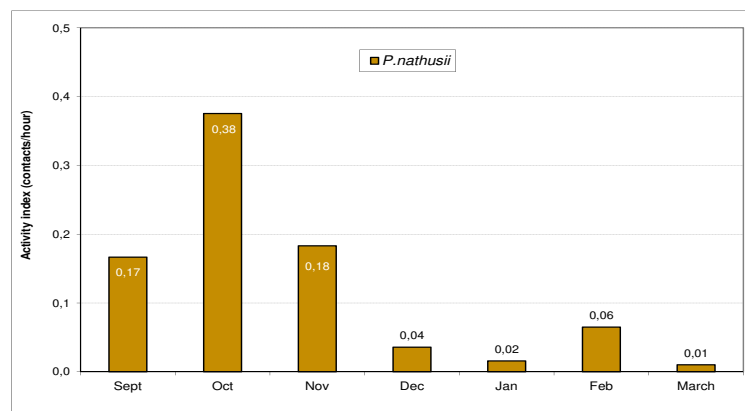
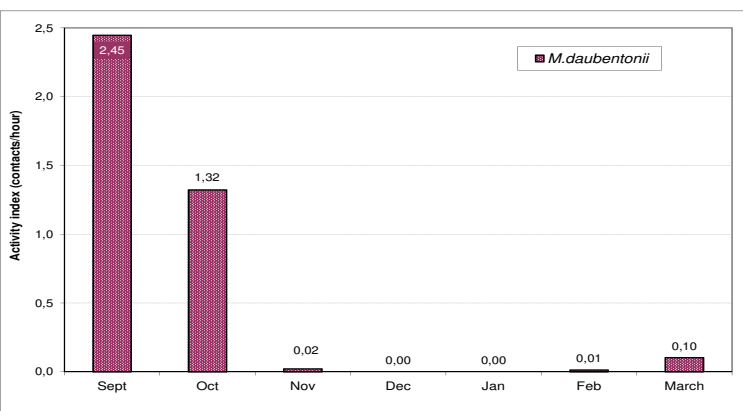


Figure 5a to 5f. Monthly activity (adjusted contacts/hour) for all types of the six most frequently contacted taxa after *P. pipistrellus*.

It is interesting to be able to separate the two main types of activity during this period: hunting vs social.

For each species, depending on its hunting behaviour (pursuit or gleaning), it is possible to distinguish hunting activity using the criteria of rhythm (active search with approach or capture phases) and duration (greater than a simple linear passage indicating transit) of a sequence of sonar signals. Hunting is of course intensive during the autumn, in line with the need to accumulate fat reserves for the winter lethargy. From December onwards, as temperatures fall, it might seem logical that most flight movements would be motivated by transits between roosts. On the contrary, **Figure 6** shows that hunting activity predominates (70 to 94%) between December and March. In December, the only species hunting were *P. pipistrellus* (2451 contacts), *P. nathusii* (227 contacts), *M. nattereri* (211.2 contacts), *N. leisleri* (39.47 contacts), the genus *Plecotus* (35 contacts) and *N. noctula* (1.25 contacts).

In January, hunting activity is considerably reduced, with only 3 species: *P. pipistrellus* (124 contacts), *P. nathusii* (98 contacts) and *N. leisleri* (14.81 contacts).

P. nathusii's hunting activity declines proportionately much less in winter than that of *P. pipistrellus*. This phenomenon was confirmed during the first 2 decades of February, with even a reversal during the first decade, the only time when *P. nathusii* (168 contacts) was more active (1.2 times) than *P. pipistrellus* (137 contacts); during the 3rd decade *P. pipistrellus* (7,301 contacts) became more active in hunting than *P. nathusii* (126 contacts).

For the other species during the first and second decades of February, only the genus *Plecotus* (36.25 and 16.25 contacts respectively) and *N. leisleri* (8.09 and 8.5 contacts respectively) were hunting; the 3rd decade shows an increase in activity for these two taxa (*Plecotus*: 106.25 contacts; *N. leisleri*: 70.21 contacts), with the return of *M. daubentonii* (37.5 contacts), *M. myotis-blythii* (8.5 contacts) and *N. noctula* (2.25 contacts).

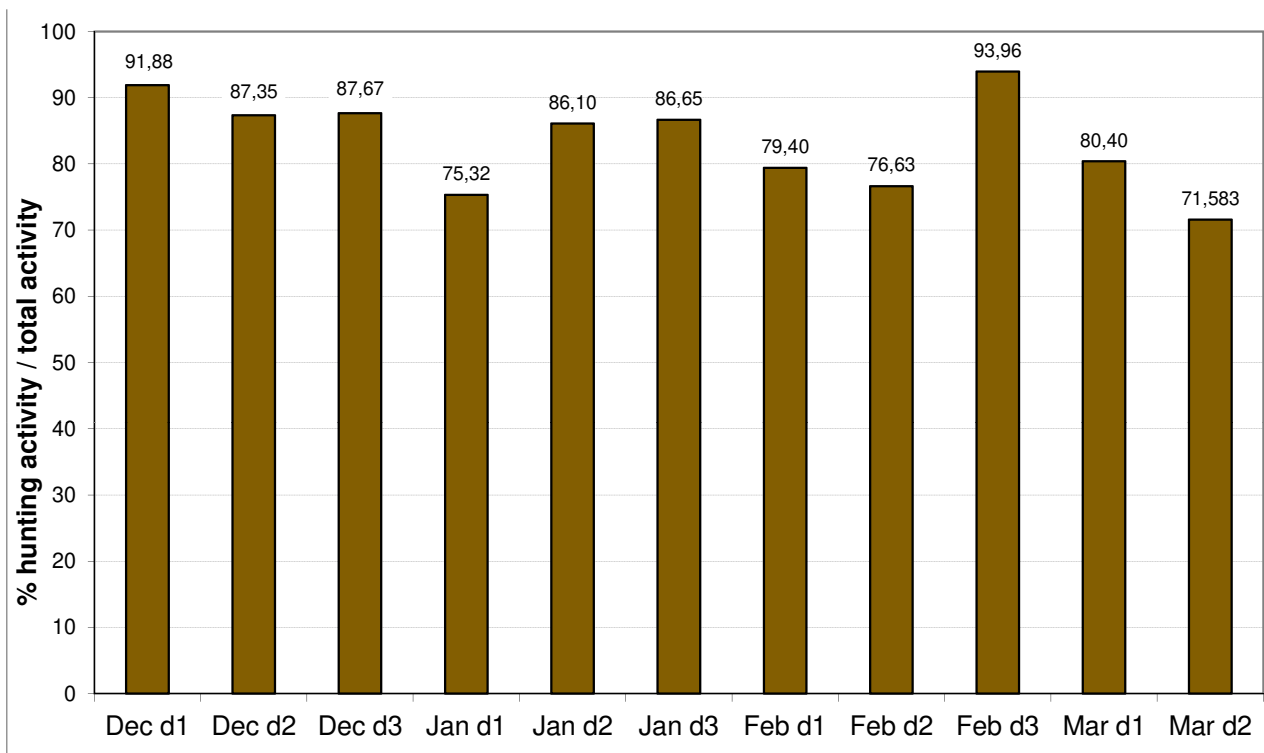


Figure 6.

Proportion of hunting activity out of total activity, by decade between 1st December and 20th March.

Social activity (territorial interactions, mating songs, probable proximity of a roosting site, etc.) is predominant in September and October (Figure 7) for all the species in which it is expressed. It mainly concerned the genus *Plecotus* and *P. pipistrellus*, taxa that became exclusive in November; a renewed activity was observed in *P. pipistrellus* in December only at 4 sites (1119, 1126, 4026, 4027, all concentrated in the south-east of the forest, see Figure 1, Appendix 1). Social calls were again weakly resumed in February-March, only for the genus *Plecotus* and *P. pipistrellus*.

Activity depending on weather conditions

The night fog (deduced from the sound sequences from the regular but infrequent sounds of water droplets falling from the branches) immediately neutralises the flight activity of the bats, sometimes for entire nights.

Rain (detectable in the sound files from the nature of the background noise) occurred frequently (5939 h ; 15.8% of the total time) during the period, on all or part of a night. When it is triggered while bats are hunting, they maintain their activity for several minutes (up to more than 30 minutes in some cases); then the activity ceases, often when the rain intensifies and is accompanied by wind (also deducible from the background noise). Activity may resume after the rain, sometimes fairly quickly, if the temperature is above 9-10°C; if it is below this, activity ceases until dawn (when however a few contacts may appear again when the temperature is between 5 and 10°C).

Separating the respective influences of rain and temperature is not easy. When rain occurs at temperatures above 10°C and no activity is detected, it is possible to conclude that it is probably precipitation that is at work. However, 91.9% of the rainy hours occurred at temperatures between

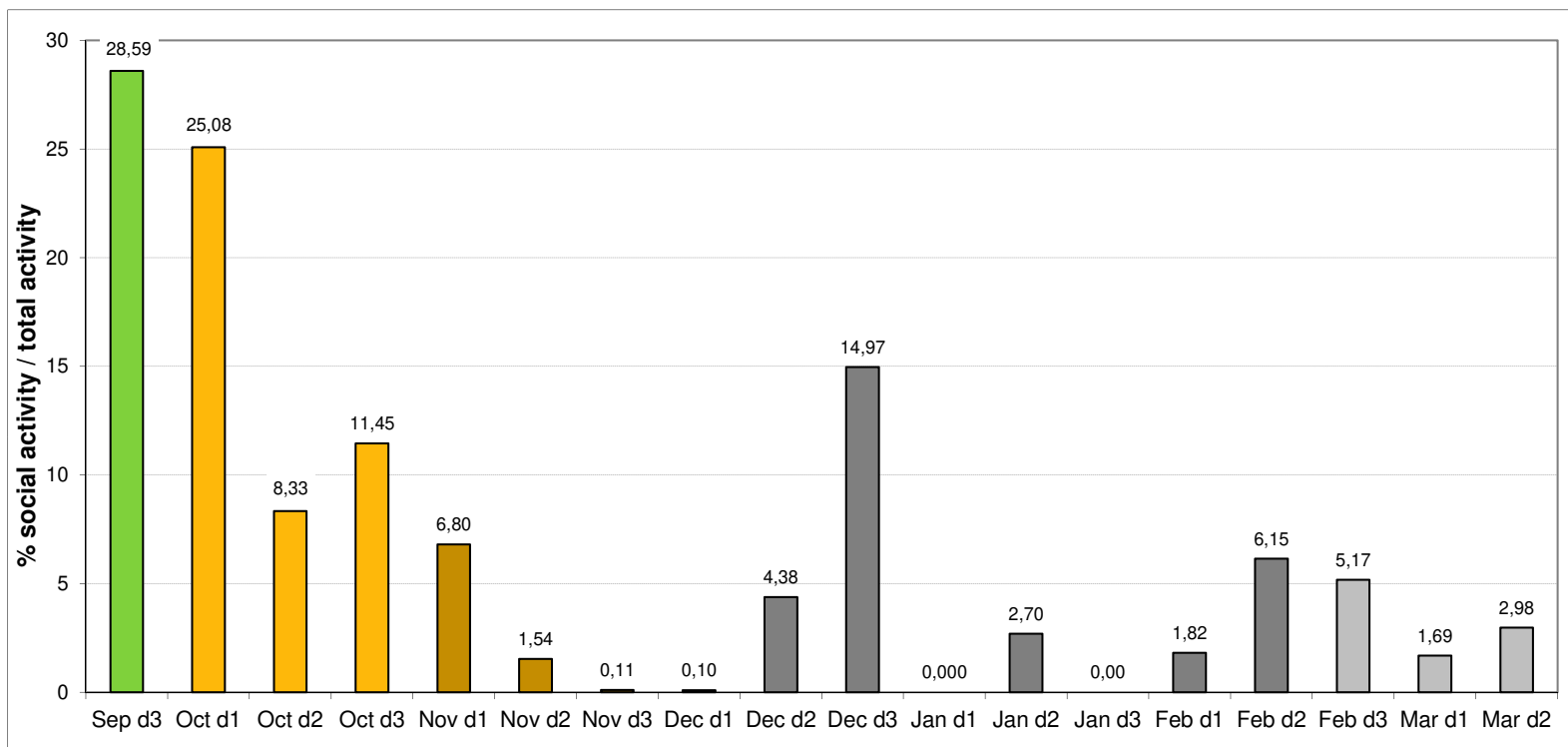


Figure 7. Proportion of social emissions in total acoustic activity, by decade between 20th September and 20th March.

0 and 10°C (including 68% between 0 and 5°C), which are also likely to reduce activity. **Figure 8** shows the median temperatures and their variations throughout the study period, which are interesting to compare with the phenology of activity for all species combined (**Figure 4**): there is a correlation between the fall in values in the 3rd decade of November, the slight rise in the 2nd decade of December and the more marked rise in the 3rd decade of February, followed by a further fall in early March. This suggests that temperature has a strong influence, which is borne out by the trend shown in **Figure 9**: 88% of contacts were recorded at temperatures of 10°C or above. This figure also shows a slight increase in the flight activity of bats between -6 and -8°C; this only concerns 3 taxa: *P. nathusii* (76.5% of the 34 contacts recorded at this temperature range), *N. leisleri* (Ept-Nyc. sp.) and *P. pipistrellus*; 82.3% of these contacts correspond to hunting activity by the two Pipistrelle species.

The sensitivity of the various taxa to low temperatures is outlined in **Table 6**, which shows *P. nathusii* as the most active species at sub-zero temperatures. The hours without bat contacts represent less than 10% of the total time above 13°C, 44% between 7 and 9°C, then vary between 72 and 87% below 6°C.

Activity according to forest habitat type

The activity rate for all species combined was calculated for each descriptive variable of the forest habitat and compared with the listening pressure during the months of September, October and November, the period before most individuals enter hibernation (**Table 7**). It was not possible to make use of the young forest age class: it only concerns 2 count points (1048b and 1135b) which total only 13 weeks. The values presented therefore only concern mature stands with trunk diameters greater than 0.60 m.

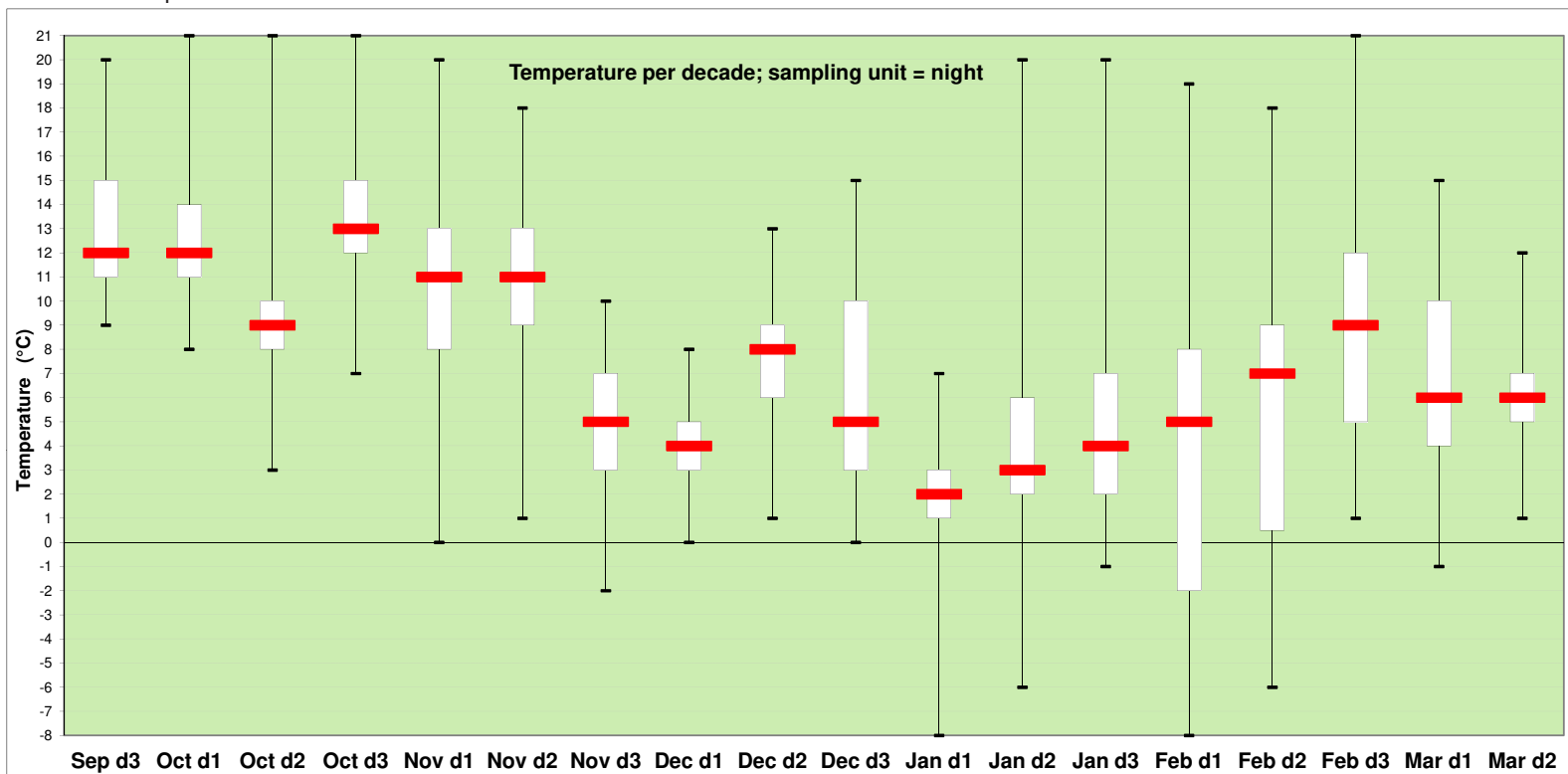


Figure 8. Medians of temperatures (in degrees Celsius) with variations (1st and 3rd quartiles, extremes), recorded during each contact at all listening count points, throughout the autumn-winter period, divided into decades.

The variables with a high level of activity in relation to the listening duration devoted to them are the edge of a gap (20.8 contacts/hour) and shrub cover of 0 to 10% (59.47 c/h) and 50 to 75% (18.73 c/h). The edge over clearing (2.45 c/h) and shrub cover of 10 to 25% (6.04 c/h) and 25 to 50% (8.54 c/h) appear to be less used. The other variables were used in proportion to the listening time devoted to them.

For *N. leisleri*, the edge of the clearing seems more attractive than the undergrowth (0.075 c/h compared with 0.007 c/h). For *M. bechsteinii* and *M. nattereri* it is the undergrowth (0.01 and 0.09 c/h respectively) that is the most frequented, with the edges being little used (around 10 times less) or not used at all. The edge of a gap is the ecotone that receives the most activity for all the other species.

M. myotis-blythii is more active when shrub cover is between 25 and 50% (0.26 c/h compared with indices of less than 0.08 c/h for the other levels of cover). *M. bechsteinii* is more active when it is between 0 to 10% and 50 to 75% (respectively 0.013 and 0.016 c/h; lower than 0.004 c/h elsewhere); it's the same for *M. nattereri* (respectively 0.115 and 0.163 c/h; lower than 0.008 c/h elsewhere). For all the other species, the coverage between 0 and 10% was the most used.

The presence of water does not seem to attract bats during this period; only *P. pipistrellus* provided numerous contacts at the water's edge, but the vast majority in October (65.5% of contacts of this species at the water's edge; n = 2146), particularly in the first decade (46.6%), then until the end of November (22.3% of contacts during this month).

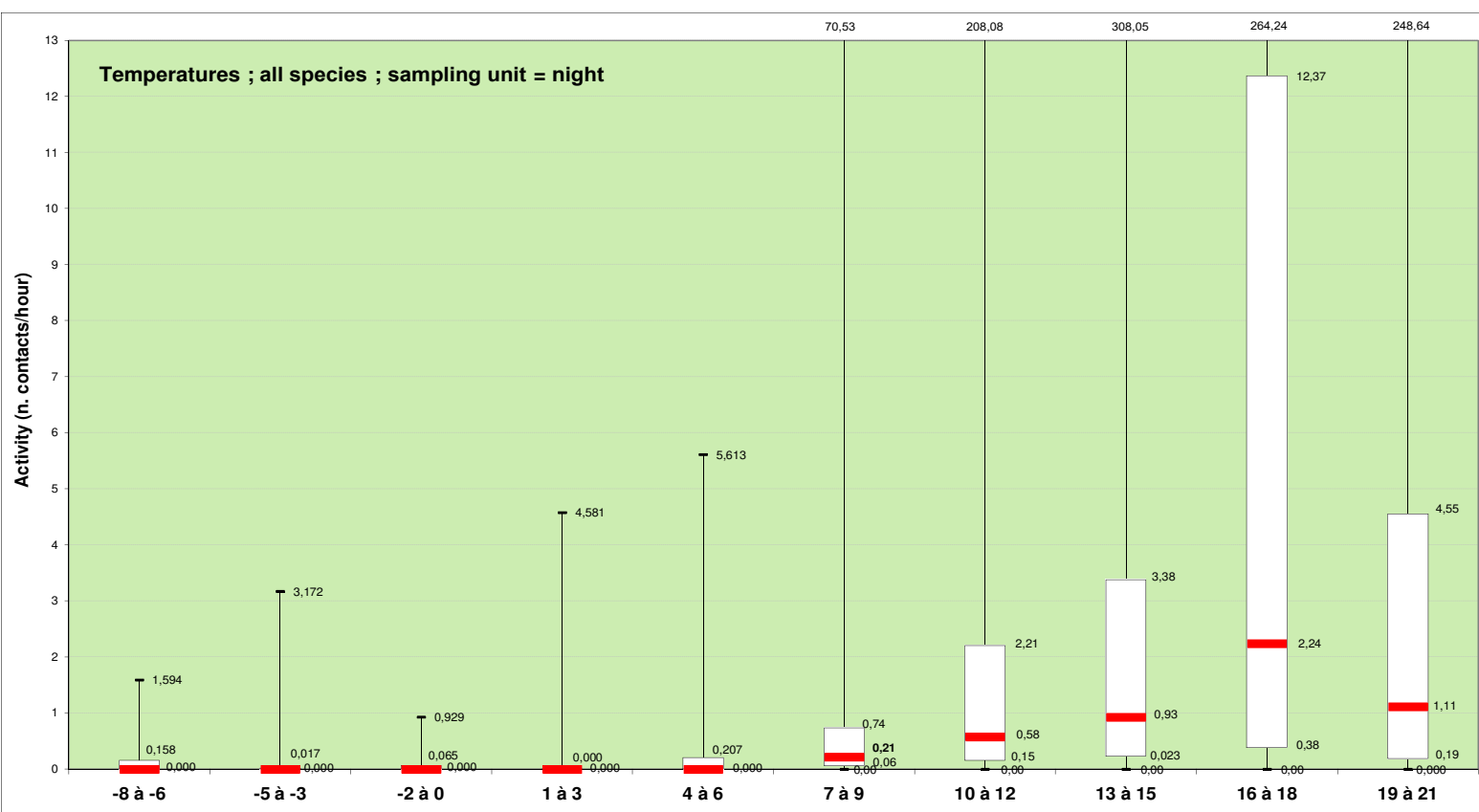


Figure 9. Medians of activity indices of all types (no. weighted contacts/hour) with variations (1st and 3rd quartiles, extremes), all species combined, in relation to the temperatures (in degrees Celsius) recorded during each contact.

Table 6.

Flight activity (no. adjusted contacts/hour) of bat taxa as a function of outdoor temperature (in degrees Celsius) ranges; values in bold are those that exceed a minimum threshold for each taxa.

Taxa	-8° to -6°	-5° to -3°	-2° to 0°	1° to 3°	4° to 6°	7° to 9°	10° to 12°	13° to 15°	16° to 18°	19° to 21°
<i>P.nathusii</i>	0,16	0,18	0,02	0,01	0,02	0,08	0,11	0,23	0,75	6,00
<i>P.pipistrellus</i>	0,02	0,02	0,02	0,02	0,15	2,58	7,35	11,18	26,39	21,01
<i>Ept-Nyc spp.</i>	0,03	0,01	0,003	0,001	0,004	0,01	0,01	0,03	0,03	0,01
<i>N.leisleri</i>	0	0	0,002	0,002	0,001	0,03	0,06	0,10	0,62	0,13
<i>Plecotus spp.</i>	0	0	0,02	0,005	0,03	0,16	0,25	0,21	2,27	0,09
<i>M.nattereri</i>	0	0	0	0,04	0,04	0,06	0,12	0,08	0,05	0,004
<i>M.daubentonii</i>	0	0	0	0,01	0,03	0,19	0,75	0,53	0,34	0,12
<i>M.alcathoe</i>	0	0	0	0,001	0	0,001	0,02	0,03	0,001	0
<i>M.bechsteinii</i>	0	0	0	0,001	0,001	0,002	0,01	0,02	0,04	0,004
<i>M.emarginatus</i>	0	0	0	0,002	0,001	0,01	0,02	0,003	0,002	0
<i>M.mystacinus</i>	0	0	0	0,003	0,0003	0,05	0,15	0,17	0,08	0,03
<i>M.myotis-blythii</i>	0	0	0	0,0004	0,0050	0,07	0,25	0,48	0,38	0,11
<i>N.noctula</i>	0	0	0	0,0001	0,0002	0,00004	0,001	0,001	0,0004	0,0004
<i>P.pygmaeus</i>	0	0	0	0	0	0,003	0,01	0,01	0,01	0,002
<i>M.brandtii</i>	0	0	0	0	0	0	0,004	0	0,001	0,01
No. hours without contacts	119,00	516,00	1530,00	5936,50	5637,00	2899,50	1147,50	388,00	97,50	59,00
Total hours	161,50	645,00	1991,50	6824,50	7814,50	6602,50	7011,00	4129,50	1695,50	582,00

Table 7.

Listening pressure and percentage of activity for all species, in relation to the habitat variables recorded at each listening count point.

Ecotone	N. hours	% h. total	% contacts
underwood	7737	58,2%	46,0%
edge hole	4825,5	36,3%	53,1%
edge glade	725	5,5%	0,9%
Shrub layer	N. hours	% h. total	% contacts
0 to 10 %	592,5	4,5%	18,6%
10 to 25 %	1739	13,1%	5,6%
25 to 50 %	4644,5	35,0%	21,0%
50 to 75 %	3785	28,5%	37,5%
75 to 100 %	2526,5	19,0%	17,3%
Water	N. hours	% h. total	% contacts
no	12197,5	91,8%	98,7%
yes	1090	8,2%	1,3%
Total	13288		189073,89

Discussion

Diversity of species

The fact that *E. serotinus* was only the subject of 4 (raw) contacts, only qualified as « probable », seems to indicate a one-off activity (or even an absence?) of this species at Erlenbusch. A very brief acoustic study (BUND NRW, 2013; p. 29-31) carried out in 2013 in the Erlenbusch forest only mentions *E. serotinus* in the form of short and indistinct contacts, not identified with certainty. However, in geographical areas where this species is present, it is quickly and unambiguously identified acoustically in forest habitat (BARATAUD *et al.*, 2016; BARATAUD & GIOSA, 2021). *E. serotinus* may be rare in this part of Germany according to the data of Global Biodiversity Information Facility (<https://www.gbif.org/fr/species/2432359>).

Nyctalus lasiopterus has a fragmented distribution in Europe (IBÁÑEZ & JUSTE, 2023) and is only seen sporadically in Germany, where its status is unknown (DIETZ & KIEFER, 2016). The only two contacts collected at Erlenbusch do not coincide with a regular presence; the dates (late September and early November) correspond to the migration period and the early hours (7pm and 7.30pm respectively) correspond to a flight shortly after leaving the daytime roost, which was probably in the forest given the surrounding landscape not favourable.

M. alcathoe, morphologically close to *M. mystacinus* and *M. brandtii*, was suspected as a different taxon already in 1996 in the Massif Central of France (JOURDE, 2000; Roué, pers. comm.), described in Greece as a new species a few years later (HELVERSEN *et al.*, 2001), and immediately confirmed in France (RUEDI *et al.*, 2002); it is now considered to be

present in a large part of Europe (NIEMANN *et al.*, 2007; TILLON *et al.*, 2010). Its sonar signals, described from the outset as concentrated at high frequencies (HELVERSEN *et al.*, 2001), are easily identifiable in many circumstances (BARATAUD, 2020). Its presence, discovered at Erlenbusch during acoustic surveys in 2017 and described as the first record for North Rhine-Westphalia (CRETU *et al.*, 2022), is confirmed here by 242.5 adjusted contacts despite its low detectability (low-intensity high-frequency signals).

M. emarginatus is a relatively common species in southern Europe, and is even expanding towards the north-west (Dietz & Pir, 2023). Its reputation for entering hibernation early and waking up late (DIETZ *et al.*, 2009; SPITZENBERGER *et al.*, 2023) corresponds well with the data collected at Erlenbusch, with the latest contacts on 11th November and no definite records until the end of the surveys on 20th March. The low number of contacts is usual for this species with a very faint intensity of sonar signals, but it may also be indicative of a low-density population.

M. blythii was identified in a non-anecdotal manner (448.1 adjusted contacts out of a total of 4968.4 contacts for the *M. myotis-blythii* group, = 9%), at 13 count points, 11 of which with a 'certain' level of confidence according to acoustic criteria that have proved their worth in areas of sympatry with *M. myotis* (BARATAUD, 2020; DISCA, in prep.). These records, well to the north and east of the known distribution, have already been commented on by CRETU *et al.* (2022). Two plausible hypotheses remain:

1. an actual presence of the species (perhaps moving northwards under the effect of current global warming?) in this area of Germany where populations of *M. myotis* are known and doubtless

monitored by chiropterologists; but several examples, reported by observers in central France, show that their search image during counts in *M. myotis* colonies excludes the distinctive morphological criteria of *M. blythii* (light patch on forehead, narrower ears and snout); thus, when a few pioneer or erratic individuals of *M. blythii* are present in a group of *M. myotis*, they go unnoticed;

2. in geographical areas where *M. myotis* is never in contact with *M. blythii*, it is possible that the sonar signal repertoire of *M. myotis* extends and overlaps with that of *M. blythii*: a phenomenon of acoustic niche competition already observed in European Pipistrelles (BARATAUD, 2020). Each of these two hypotheses presents a major knowledge challenge.

It is easy to distinguish between *P. auritus* and *P. austriacus* in many circumstances, in geographical areas where *P. macrobullaris* is absent. On the other hand, the sonar signals of *P. macrobullaris* partially overlap

acoustically with those of the other two species (BARATAUD, 2020); this species can therefore only be identified acoustically in a few specific circumstances (exclusive frequency criteria in certain duration ranges, behaviour in open environments with long-duration hunting signals, initial convex curvature sometimes present). The Erlenbusch forest is outside the published distribution of *P. macrobullaris*, which is still little known as this species has only recently been described (KIEFER & VEITH, 2001). However, during our analyses of sequences of the genus *Plecotus*, we have on several occasions encountered sonar signals whose frequency measurements corresponded to exclusive distributions, with no overlap with *P. auritus* and *P. austriacus* (see example in **Figure 10**). Similar acoustic identifications have already been attributed with certainty to *P. macrobullaris* in the Pyrenees or the Alps, where they have been confirmed locally by captures or discoveries of breeding sites.

Nevertheless, Erlenbusch is more than 400 km north of the areas where this species is present in the Alps and Jura. ALBERDI *et al.* (2014) modelled the potential European distribution of *P. macrobullaris* on the basis of existing data; the geographical sector of the Erlenbusch forest coincides with an area of possible presence, albeit with a low probability (**Figure 11**).

The actual presence of this species on our study site therefore needs to be confirmed by capturing individuals. Another option, as in the case of *M. blythii*, would be that of an overflow of the acoustic niches of *P. auritus* and/or *P. austriacus* in the historical absence of *P. macrobullaris*; however, our numerous acoustic surveys in lowland areas of south-west France, where the probability of historical presence of *P. macrobullaris* is close to zero, have never

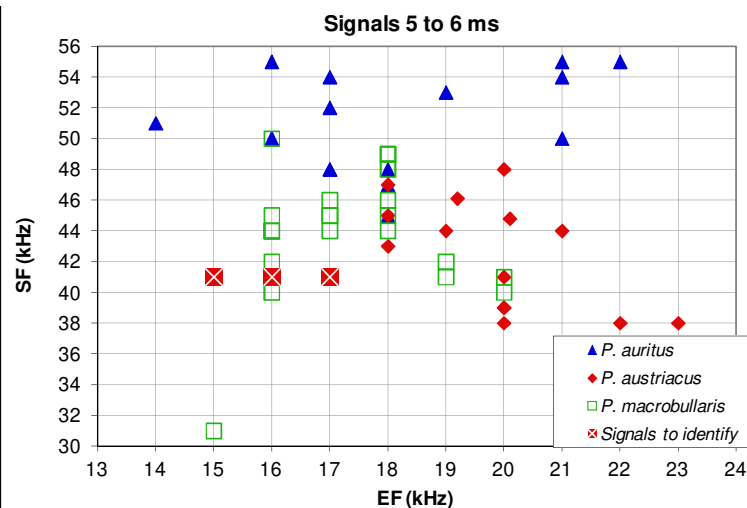


Figure 10. Graph showing the distribution of frequency values (SF = start frequency; EF = end frequency) measured on signals definitely belonging to the 3 species of *Plecotus* (BARATAUD, 2020); the red square symbols with white crosses indicate measurements made on signals from a sequence (count point 1577a, 06/10/2020; 21h18'08") in the Erlenbusch forest: they fall within the exclusive distribution of *P. macrobullaris*.

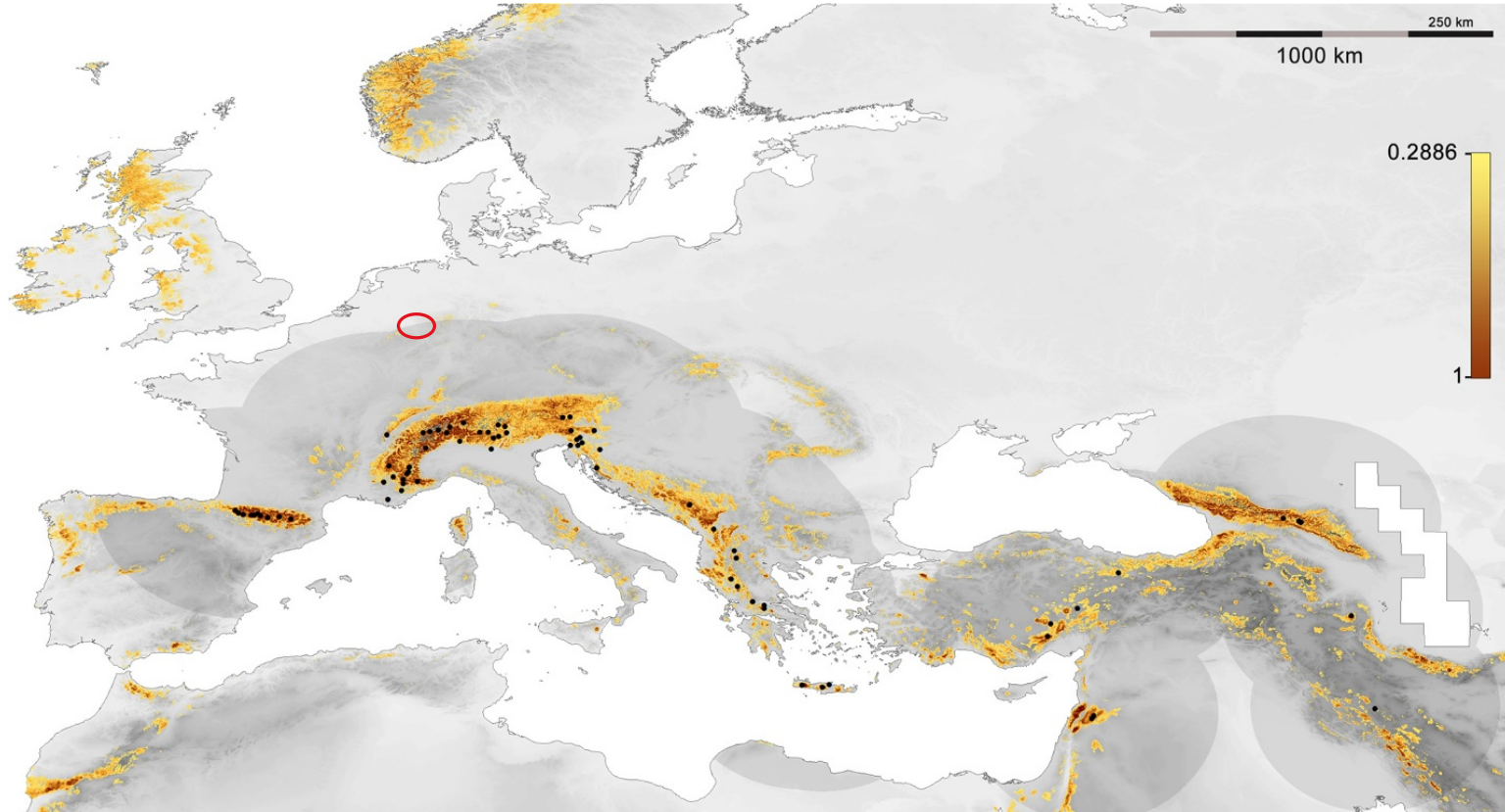


Figure 11.

Map showing the potential distribution of *P. macrobullaris* in Europe (as a function of habitat characteristics), based on modelling results by ALBERDI *et al.* (2014), courtesy of the authors. The black dots designate the locations of proven presence of the species used to build the model, the shaded area was used as a reference to calibrate the model, and the colour gradient designates more (brown) or less (yellow) favourable habitats for potential presence. The red ellipse indicates the location of the Erlenbusch forest, which is situated on the Rhine river plain between two areas of land coloured pale yellow (an area where *P. macrobullaris* may be present, but with a low probability).

revealed such frequency measurements, which does not support this hypothesis of overflow of frequency niches in an allopatric situation.

Activity by count point

The comparative spatial distribution of *M. alcaethoe* and *M. mystacinus* in our study (Figures 6 and 10, Appendix 1) shows little overlap, which could support the hypothesis of ecological niche competition between these two species, which may in some cases be resolved by a difference in stratum: *M. alcaethoe* is more often found in the canopy and *M. mystacinus* closer to the ground (BARATAUD & GIOSA, 2021). They both frequent riparian woodlands along rivers, either at the edge or in the undergrowth (BERGE, 2007; LUČAN *et al.*, 2009); however, a large part of the Erlenbusch forest is wet, and sometimes even flooded in autumn and winter, but these times do not correspond to the main

period of development and emergence of insects in the aquatic larval stage, which reduces the abundance of trophic resources in autumn; this could encourage interspecific territoriality.

The very high activity of *M. daubentonii* in the Erlenbusch forest during the study period is particularly interesting, as it is unusual in the forestry contexts we have studied to date (BARATAUD *et al.*, 2016; BARATAUD & GIOSA, 2021). This species specialises in hunting close to calm aquatic surfaces (lowland rivers, streams, lakes). A region rich in ponds, or an alluvial valley, is likely to harbour large populations (KALKO & BRAUN, 1991). However, the Rhine valley is only 13 km from the Erlenbusch forest, a much shorter distance than has been observed for this species during its movements between summer and breeding or wintering sites (ENCARNAÇÃO & BECKER, 2023). If large populations exist thanks to this context, in autumn when

insect emergence slows down *M. daubentonii* can disperse to favourable forest habitats (rare in this highly urbanised region), to find sufficient food availability before entering hibernation. The Erlenbusch forest could therefore be a refuge area for this part of their life cycle. In addition, there is a long, vast underground aqueduct beneath the forest and its surrounding, the entrances to this are screened to prevent human intrusion: this underground site is a potential hibernation site with a high accommodation capacity.

The increase in social activity of *P. pipistrellus* in December at 4 of the 5 count points it frequents during that month could be linked to the low availability of food resources at that time for a non-gleaning species, as the social trills recorded are known to indicate competition between individuals on hunting grounds in relation to prey density (BARLOW & JONES, 1997; RACEY & SWIFT, 1985).

Most of the species recorded frequent the southern part of the forest (**Appendix 1**), the edge of which is regularly being pushed northwestwards by the quarry extension. This puts local populations at risk of seeing their hunting grounds and roosting sites reduced or even disappear in the long term.

Phenology of autumn and winter activity; influence of external conditions

Several studies reporting hunting activity by European bats during the autumn and winter periods concern the Mediterranean area (AUGUSTO, 2008; BARROS *et al.*, 2017; BARROS *et al.*, 2021; MAS *et al.*, 2022), which does not have the same climatic conditions as western Germany.

In temperate zones, AVERY (1983; 1985; 1986) showed that *P. pipistrellus* hunts

frequently in winter, and *N. noctula* occasionally. BLOMBERG *et al.* (2021) in southern Finland suggest that *P. auritus* may use variations in barometric pressure to trigger awakenings and hunting trips on favourable nights; CICHOCKI *et al.* (2015) in south-west Poland suggest that variations in the magnetic field during different phases of the moon may be detected by *N. noctula*, and that a noticeable rise in temperature, perceptible inside their roosts, is correlated with phases of illumination at 70% of the lunar surface, which facilitates waking up and possibly hunting activity in winter. HOPE *et al.* (2014) in the south of England, showed by means of a diet study that *M. nattereri* regularly hunts a variety of prey in winter, but mainly apterous prey gleaned from a substrate, an aptitude that favours hunting in unfavourable weather conditions; the late hunting dates (06th December) noted in this study for this species agree with the results of SPITZENBERGER *et al.* (2023), which indicate the start of hibernation on 8th December. RANSOME (2002) showed in southern England that *R. ferrumequinum* was able to maintain its body weight until spring thanks to winter hunting, thus optimising its reproductive and survival capacities. REBER (2022) at the foot of the Vaud Jura (Switzerland) recorded sound sequences from 8 species during winter transects; activity ceased below 0°C and became systematic above 7°C. WINKLER & RÁKOS (2023) in north-west Hungary used acoustics to show that 4 species (*N. noctula*, *P. austriacus*, *H. savii*, *P. kuhlii*) had winter activity that was positively correlated with rising temperatures and the absence of rain. ZAHN & KRINER (2016), again using acoustics, regularly recorded sonar signals on hunting grounds between October and March in Bavaria (southern Germany), mainly from *N. noctula*, *P. pipistrellus*, *P. nathusii* and *Vespertilio murinus* (no

Myotis sequences), when temperatures were above 6°C (the temperature below which no activity was recorded was 3°C).

However, recent studies have also shown that bats fly and hunt at sub-zero temperatures in Europe and North America.

FRAEFJORD (2021) conducted winter surveys of *Pipistrellus pygmaeus* in south-western Norway from 21st December 2019 to 4th January 2020, recording flight activity down to -2.2 °C. CELUCH & KANUCH (2005) checked the activity of noctule bats in a hibernation colony in the prefabricated building estate in the city of Zvolen, Slovakia, during season October 2003 – April 2004. They observed that noctules often flew in temperatures between 0 and -5 °C and became inactive on the coldest days, when the average daily temperature dropped below -10 °C. Echolocation calls of bats also included feeding buzzes. ZAHN *et al.* (2003) observed that noctules in the town of Waldkraiburg in SE Bavaria leave the roost on most evenings when the temperature is above freezing. The highest numbers of emerging noctules were observed on the first warm dusk following a period with temperatures below the freezing point. On many evenings, flight activity was recorded over several hours, with the first bats returning 15 to 20 minutes after first appearance. This indicates that the noctule made short flights, possibly to drink. Acoustic surveys and net catches at high alpine altitudes in Austria show that bats also fly at temperatures below zero degrees during the normal activity period: down to -5.8 °C at 2,315 m above sea level (WIDERIN & REITER, 2017), down to -5.0 °C on the Grossglockner (REITER *et al.*, 2016) and down to -2.2 °C at 3,106 m a.s.l. (WIDERIN & REITER, 2018).

Studies over three winters (2012 to 2015) in the Canadian province of Alberta



Erlenbusch flooded in winter.

even revealed winter activity of bats at temperatures as low as -10.4 °C, with the big brown bat (*Eptesicus fuscus*), which is not found in Europe, proving to be the least sensitive species to cold temperatures. At the prevailing temperatures of +0.9 to -15.5 °C at sunset, bat activity was recorded in 34.1% of nights (KLÜG-BAERWALD *et al.*, 2016).

P. nathusii in our study appears to be the species most inclined to hunt in the depths of winter; in fact, it shows the lowest variations throughout the autumn-winter period. The difference in activity between this species and *P. pipistrellus*, as well as its monthly variation (Figure 5g), gives rise to several hypotheses. Almost everywhere in western and central Europe,

P. pipistrellus shows the highest levels of activity in various habitats (BARATAUD *et al.*, 2013, 2019; BAS & BAS, 2011; EDO *et al.*, in press; HINTZE *et al.*, 2016), probably linked to large populations. *P. nathusii*, which is more abundant in northern Europe (KALDA *et al.*, 2014), is a migratory species, with a general pattern showing a breeding area in northern Europe mainly occupied by females, which move south-west from September to join males along migratory paths and on hibernating areas (RUSS, 2023). Thus, the number of *P. nathusii* individuals could increase at Erlenbusch from October onwards (Figure 5d) due to the influx of females and juveniles of the year during the migration period. However, the drop in activity in December does not show the same amplitude between the two species: in *P. pipistrellus* it is a factor of 12 whereas in *P. nathusii* it is only a factor of 4.5; the same applies between December and January with 18.5 and 2 respectively. It would therefore seem that *P. nathusii* hunts more intensively in winter, perhaps because of the higher energy requirements due to migratory flights and/or its tolerance to low temperatures; this implies a minimum profitability of hunting activity during this period.

The determinism of winter hunting activity in some bat individuals could be linked to a deficient state of health, in particular insufficient fat reserves to spend the winter in lethargy. Juveniles less than one year old could be particularly affected, especially when cool, rainy spring weather causes a delay in births, postponing the normal development cycle (RANSOME, 1990). Winter hunting could therefore reduce the mortality of immatures, playing an important role in population dynamics.

The more or less regular activity of insects in winter concerns several orders: Lepidoptera (HIKISZ & SOSZYNSKA, 2015);

Diptera (ANDERSON *et al.*, 2022; GROSCHUPP *et al.*, 2024; SOSZYNSKA *et al.*, 2015; SOSZYNSKA & WOŹNICA, 2016); Coleoptera (JASKUŁA & SOSZYNSKA, 2011); Dermaptera (SOSZYNSKA & JASKUŁA, 2013); Mecoptera (DVOŘÁK *et al.*, 2022).

Diptera account for more than half of the insects observed in winter in Poland on snow-covered ground; 83 species belonging to 27 families (two-thirds of which are Mycetophilidae and Trichoceridae) show a peak of activity in early December at temperatures between -1 and 5°C (SOSZYNSKA, 2004). Chironomidae such as *Chaetocladius insolitus* and *Brillia bifida* have been observed emerging in Crimea at temperatures of -5°C (BARANOV & FERRINGTON, 2013).

More than a hundred species of spiders, mecopteran insects of the genus *Boreus*, two species of plecopterans, numerous species of diptera including several dozen species of nematocerans and 44 species of brachyceans, are known in Scandinavia to be active when the ground is covered in snow, at temperatures between -4 and -16°C depending on the species, with an antifreeze system enabling them to withstand such sub-zero temperatures (HAVGAR, 2010).

Some species of Lepidoptera, particularly in the Geometridae family, have a reproductive cycle shifted towards autumn, a strategy that enables them to avoid strong predation pressure from bats (SVENSSON *et al.*, 1999); *Operophtera brumata* is the most common species in temperatures as low as -6°C (SOSZYNSKA & BUSZKO, 2011); although tympanous and therefore capable of anti-predation defence (JACOBS & BASTIAN, 2016), it may constitute a possible food resource. This moth is observed at night in Erlenbusch during this period, as are swarms of nematoceran diptera on evenings when the temperature is positive. The winter

hunting activities observed in our study are therefore justified by the existence of a non-anecdotal trophic resource.

Faecal studies by KAŇUCH *et al.* (2005) in two winters (2001 to 2003) in Slovakia and the Czech Republic on *Nyctalus noctula* show that some orders of arachnids and insects are also active at temperatures below zero degrees and are hunted by bats: Araneida, Acarina, Homoptera, Heteroptera, Psocoptera, Neuroptera, Coleoptera, Hymenoptera, Lepidoptera, Diptera and Siphonaptera, with the most important winter food species for *Nyctalus noctula* belonging to the orders Lepidoptera, Diptera and Coleoptera.

MERCKX *et al.* (2021) have shown that the activity phenology of the nocturnal lepidoptera *Chiasmia clathrata* (Geometridae) is lengthened by more than two weeks in autumn by the effects of large urban areas (where temperatures are higher and artificial lighting increases the circadian duration of illumination); even in a rural context in central Europe, artificial lighting can prevent winter diapause in this species (MERCKX *et al.*, 2023). The same observation was made of the *Culex pipiens* mosquito (FYIE, 2023). Unusual winter activity has been detected in western France in several species of parasitoid Hymenoptera of the genus *Aphidius*, in connection with the recent warming of the climate, which is causing a reduction or even an end to winter diapause (VAN BAAREN, 2019). All these studies emphasise the negative impact of these changes on the insect species concerned, as such shifts affect the survival of individuals even in the absence of predation.

The current climate has been causing winter temperatures to rise for several decades; in addition, the high level of urbanisation around the Erlenbusch forest is increasing the temperature locally and



Moths (probably *Operophtera brumata*; Geometridae) in December at Erlenbusch.

generating a halo of light that bathes the entire area at night. These two cumulative artefacts are likely to generate an abnormal abundance of active arthropods in autumn and winter, with a possible positive effect on the hunting activity of bats during the hibernation period. Our results may therefore be influenced by recent disturbances, particularly local ones, which could make it difficult to transpose them to a more natural landscape context. At Erlenbusch, the lack of comparable historical acoustic survey makes it impossible to draw any trends.

Activity according to forest habitat type

The identification of a hunting habitat preference in bats most often uses a time of use in relation to the available surfaces (KUNZ, 1988).

This was not the main objective of this study, but it was interesting to assess the activity indices obtained in autumn for a number of variables that generally influence hunting activity in spring and summer. The listening pressure devoted to each variable describing the forest habitat on our count points varied, but the minimum values totalled between 690 and 725 hours, which is more than sufficient for the interpretation of activity levels, since the latter are not positively correlated with listening time, unlike species diversity (BARATAUD, 2020). However, a listening pressure of several hundred hours tends to smooth out the variations in acoustic activity, giving greater robustness to the sketch of a habitat preference in bats based on this indicator.

The vertical and horizontal structuring of the forest space plays an important role in the specific diversity and level of activity of bats (JUNG *et al.*, 2012; RIEGER & NAGEL, 2007). The few parameters described for the recording count points at Erlenbusch do not allow for a detailed analysis of preferences, but it is interesting to note that the small gaps in the canopy, which generate an edge effect in the heart of a forest and generally facilitate vertical movement in the forest (BARATAUD & GIOSSA, 2021), are also the most used ecotone in our study sector for most species, with the exception of *N. leisleri*, which is more active at the edge of clearings, probably because of its rapid flight pattern and lack of manoeuvrability.

The density of shrub cover is generally

positively correlated with chiropteran activity during the spring-summer period (BARATAUD *et al.*, 2016). However, conditions for hunting in autumn are different, with foliage dying back or becoming absent, losing its attractiveness for many prey species. Bats hunting in pursuit probably find it easier to spot the few prey available in relatively open undergrowth, which corresponds well with our activity results, which are higher (59.5% of total activity) when shrub cover is less than 10%. The two species that appear to be more active in undergrowth, *M. bechsteinii* and *M. nattereri*, are also the only ones to actively frequent shrub cover between 50 and 75%; they are both small gleaning species which could continue to benefit, until leaf fall, from a maximum leaf area. *M. myotis-blythii* is more active when the shrub cover is between 25 and 50%, which corresponds well to the compromise sought by this gleaning species specialising in large ground-dwelling Carabidae beetles, which are more numerous in well-structured vertical forests, but only accessible to this predator on patches of bare ground (ARLETTAZ & PERRIN, 1995).

The presence of water is usually a favourable factor for hunting due to the many insects that thrive there, particularly in spring (MARTEAU *et al.*, 2023). However, this factor does not appear to be attractive at our study site in autumn. During this period, the negative thermal effect in the hollows of depressions containing water, due to a dual effect of evaporation and stagnation of the heavier cold air, accentuates the drop in temperature, which is unfavourable to the activity of insects which, moreover, have completed their annual cycle of emergence or egg-laying for those whose larval development is aquatic.

Conclusion

There is still a great need for further research on bats in the Erlenbusch forest, in particular to verify the actual presence of *M. blythii* and *P. macrobullaris*, and the status of *E. serotinus*; net-capture campaigns and searches for roosting sites would be necessary.

According to the existing literature, the hunting activity of chiropterans at a temperature of -6°C appears to be a record in Europe outside the Alpine context. It indicates the availability of prey in winter in the forest area studied.

It is difficult to establish a comparison between the activity results obtained in the Erlenbusch forest and those of other studies in temperate forests, as the methods for recording acoustic contacts have not been harmonised, and there is little work on autumn and winter activity. If we consider only the activity index (hunting and social) for all species combined during the 3rd decade of September (closest to the peak of the summer hunting season, when indices vary from 20 to 115 c/h depending on the context; BARATAUD, 2020), it seems that 42.6 c/h is an excellent result. The species diversity also appears to be excellent.

This assessment can give rise to two different views.

The first is to consider that the chiropteran fauna at Erlenbusch is representative of what any sub-natural forest area in this geographical zone can support: a normal situation.

The second is the possibility that, given the landscape surrounding Erlenbusch, this area serves as an ultimate refuge, where, depending on the season, populations of bats whose natural habitats have

been reduced by deforestation and land artificialization, come to concentrate.

Erlenbusch itself is not safe from extinction: the sand quarry is gradually destroying the forest and thus one of the last hot-spots of regional biodiversity.

Annex: free download files

Bat species contacted at Erlenbusch forest, 25 time-expanded (x10) sound files (.wav) with comments (.pdf): http://www.plume-de-naturalistes.fr/wp-content/uploads/2024/12/BARATAUD-et-al_2025_Bat-activity-Erlenbusch-forest_sound-files.zip

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Distribution and intensity of nocturnal activity of bat species in autumn and winter in the Erlenbusch forest

(listed in descending order of overall level of activity)

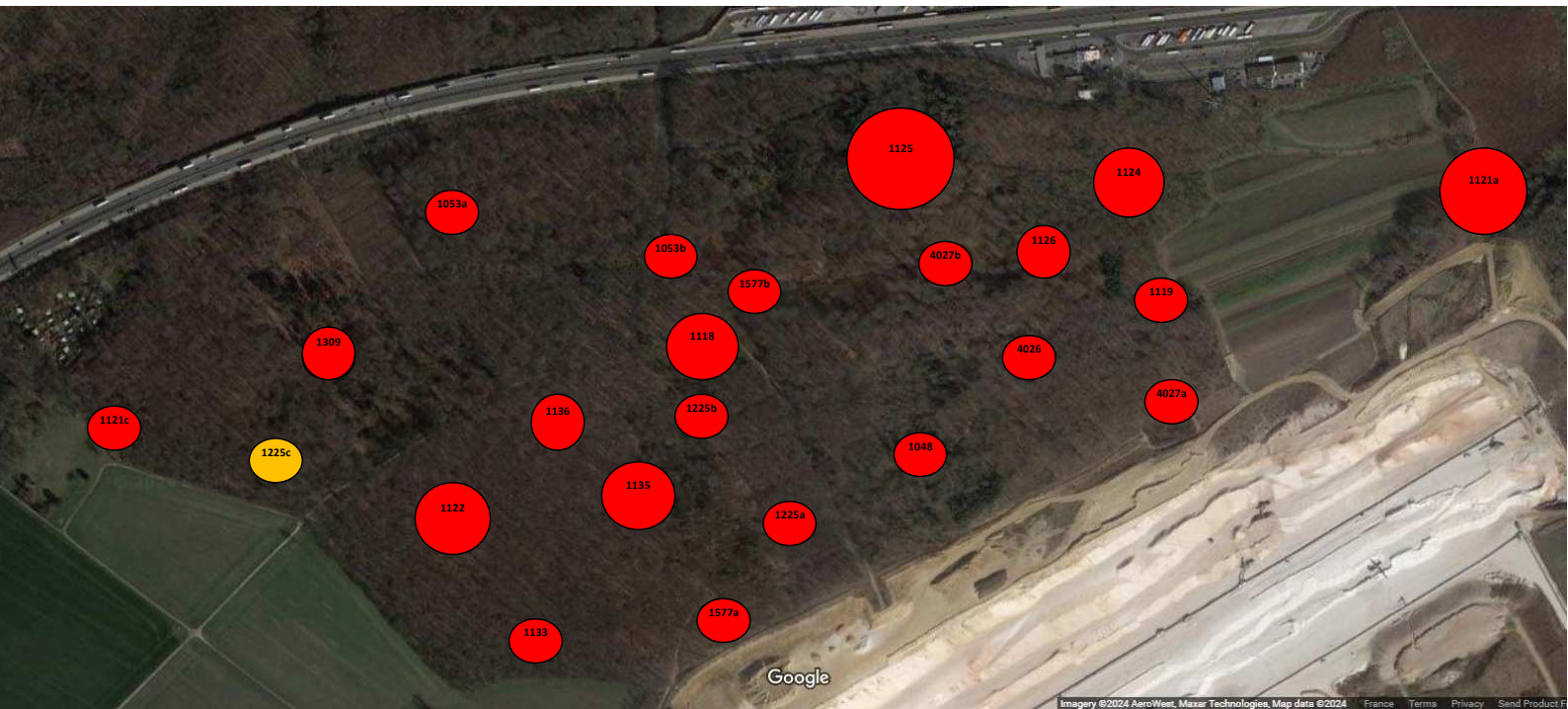


Figure 1 (appendix 1).

Distribution and intensity of the nocturnal activity of *Pipistrellus pipistrellus*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity; only 4 nights of listening were carried out on 1225c in March).

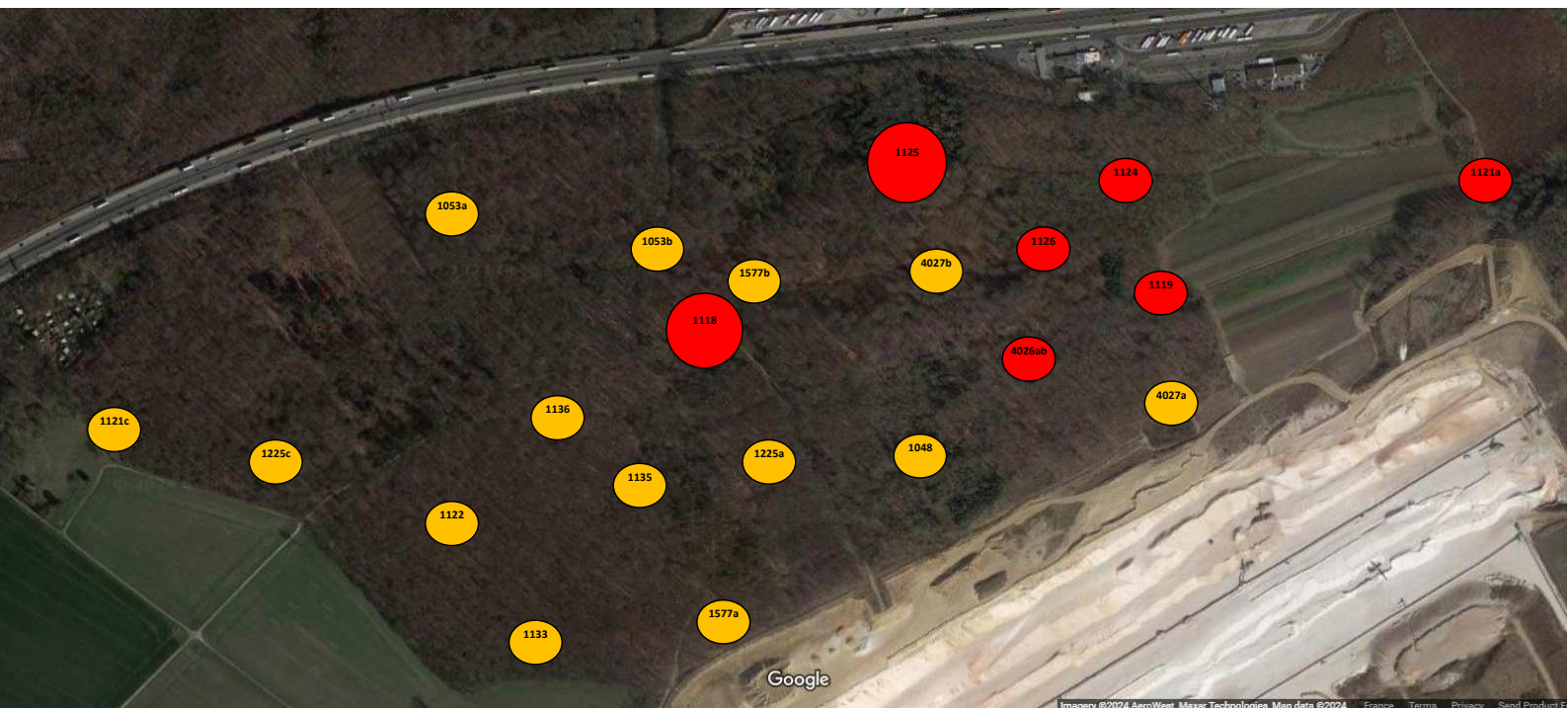


Figure 2 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis daubentonii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

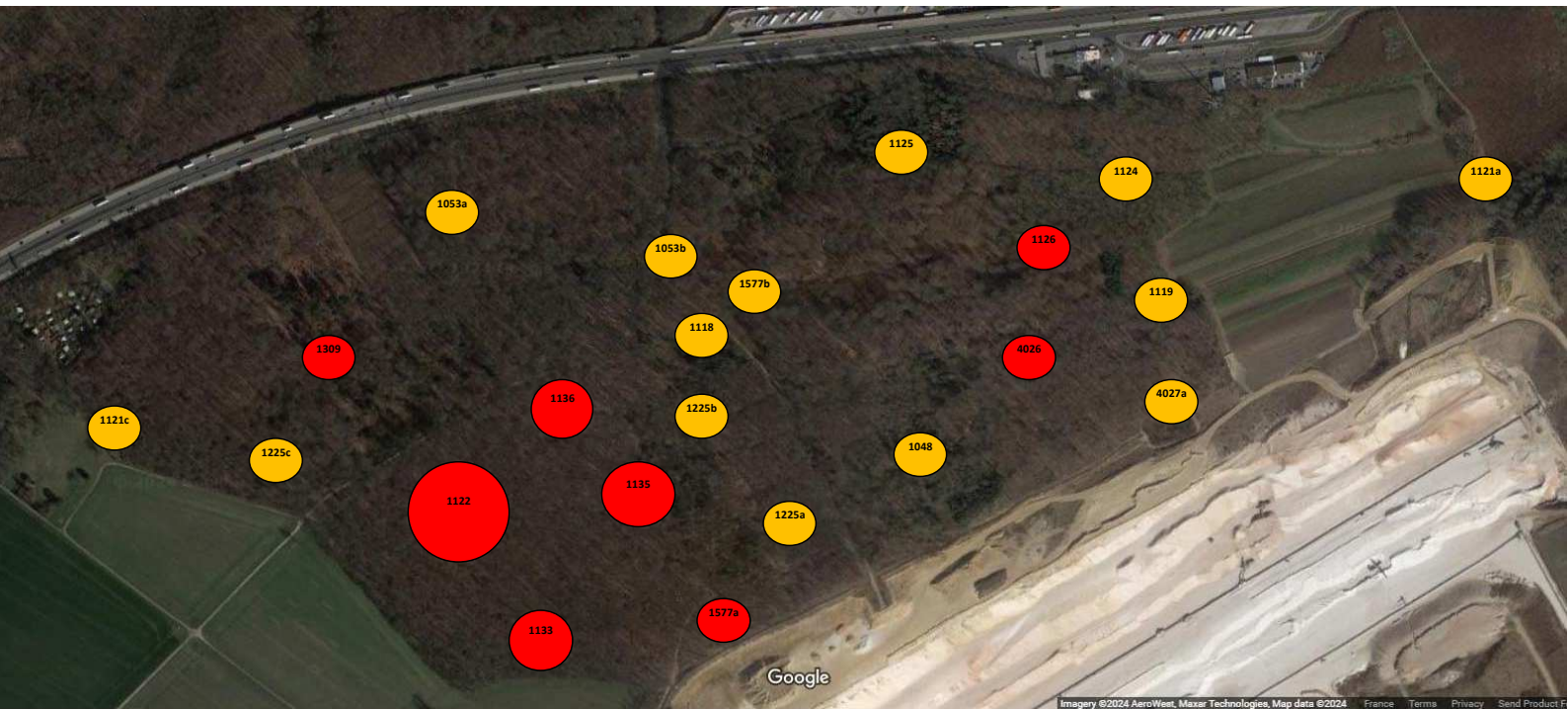


Figure 3 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis myotis-blythii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

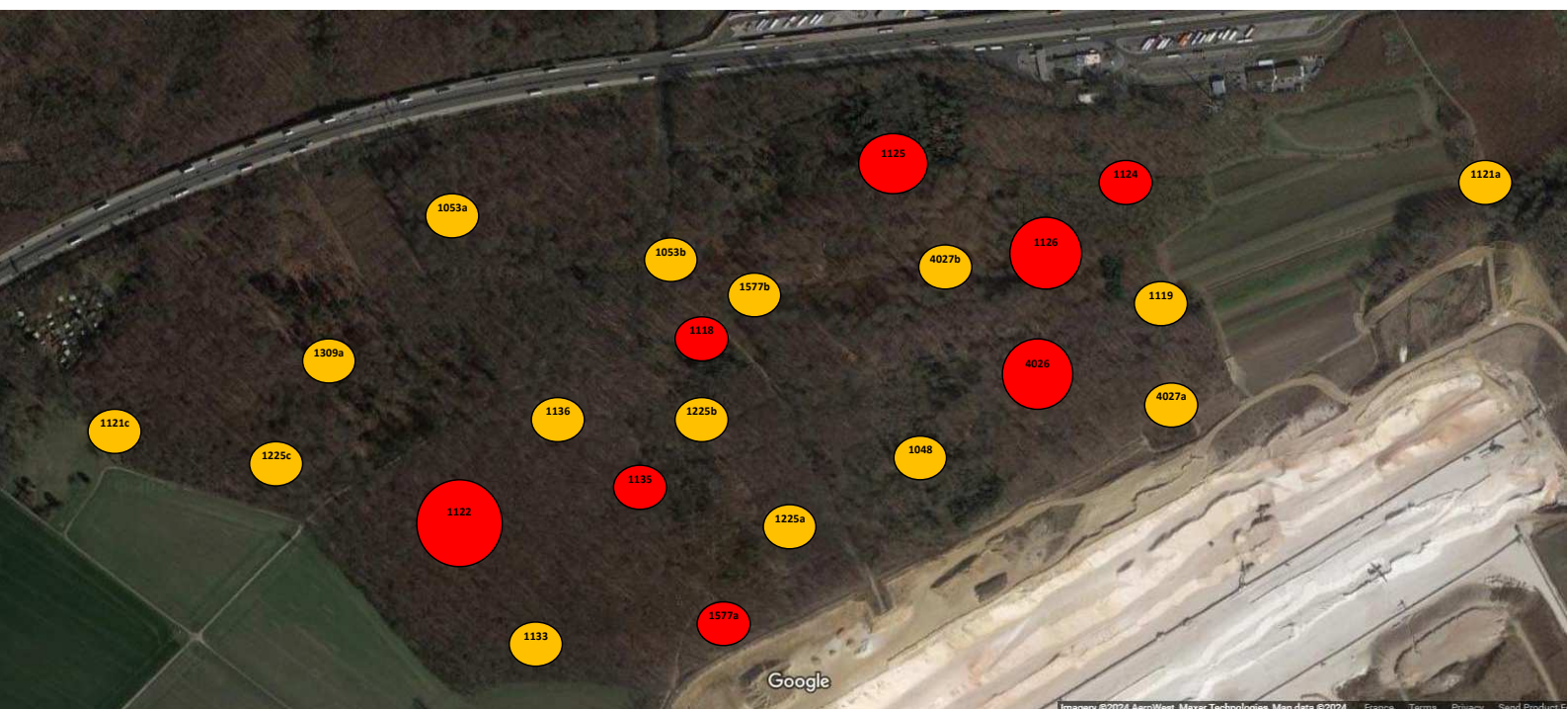


Figure 4 (appendix 1).

Distribution and intensity of the nocturnal activity of genus *Plecotus*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

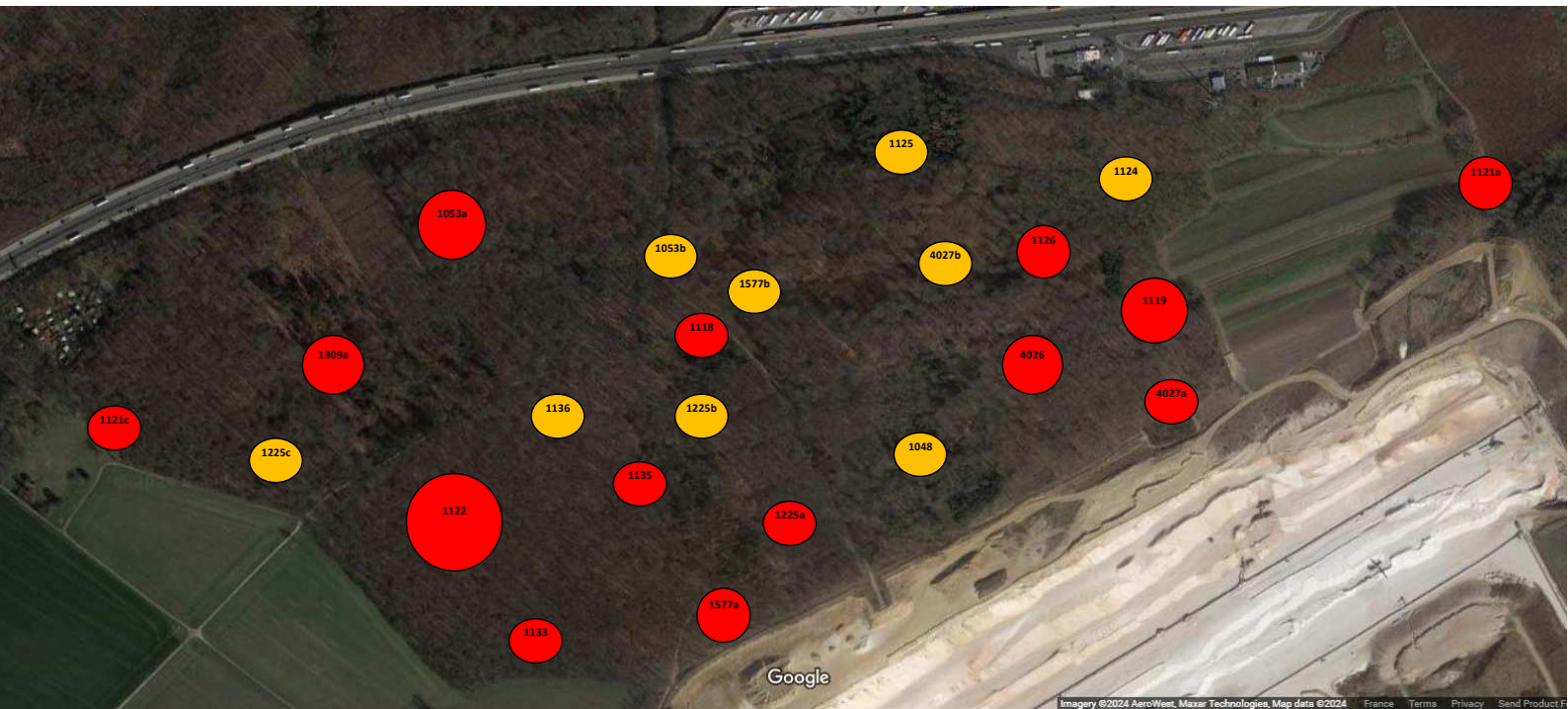


Figure 5 (appendix 1).

Distribution and intensity of the nocturnal activity of *Pipistrellus nathusii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

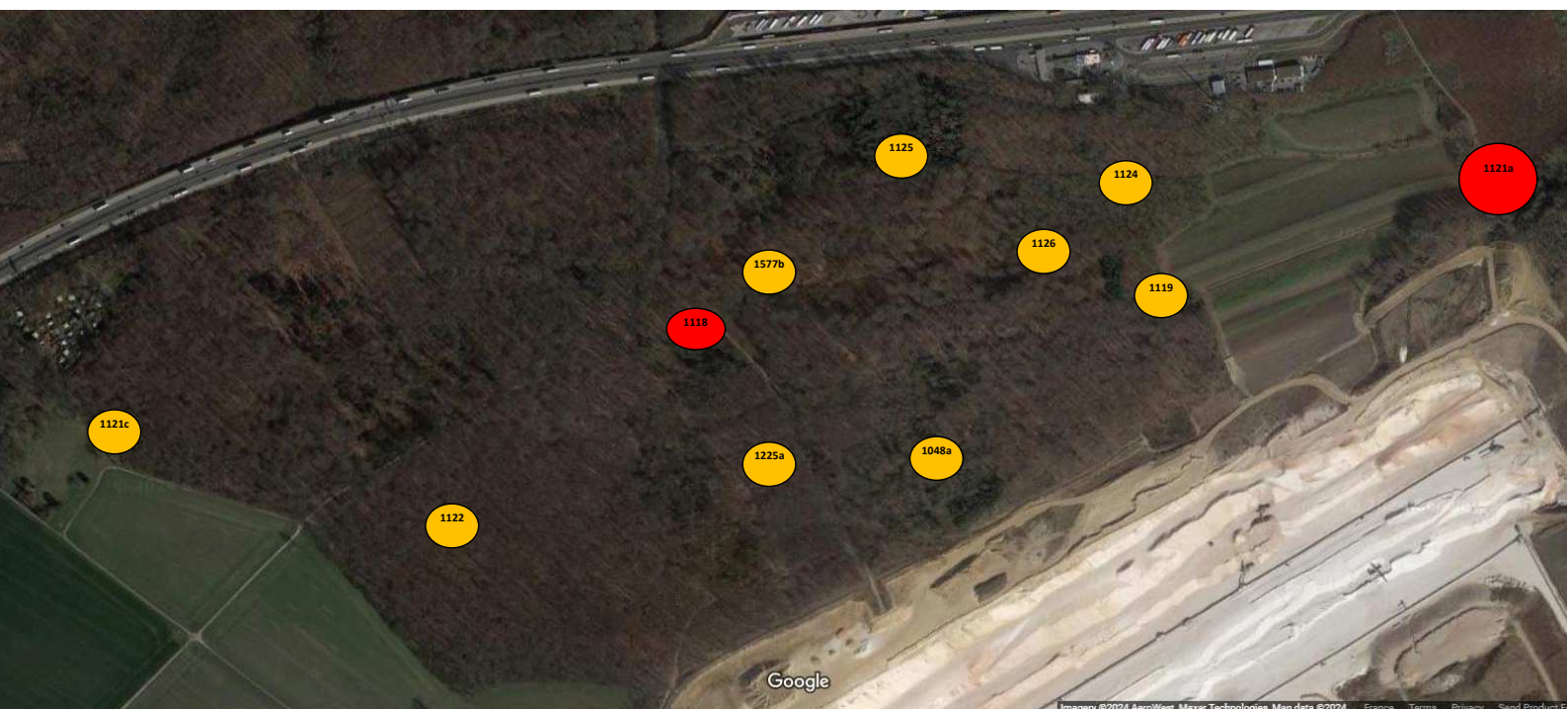


Figure 6 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis mystacinus*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

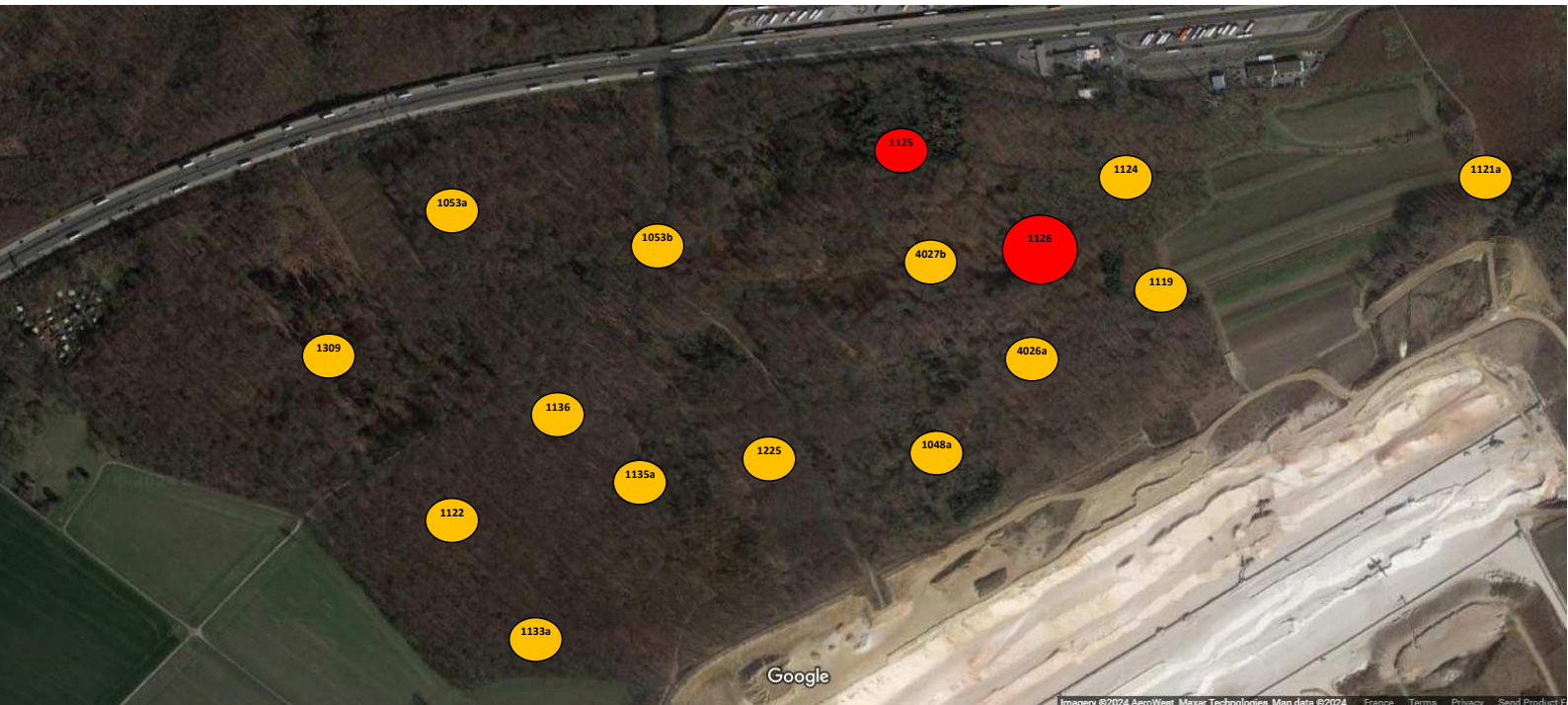


Figure 7 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis nattereri*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

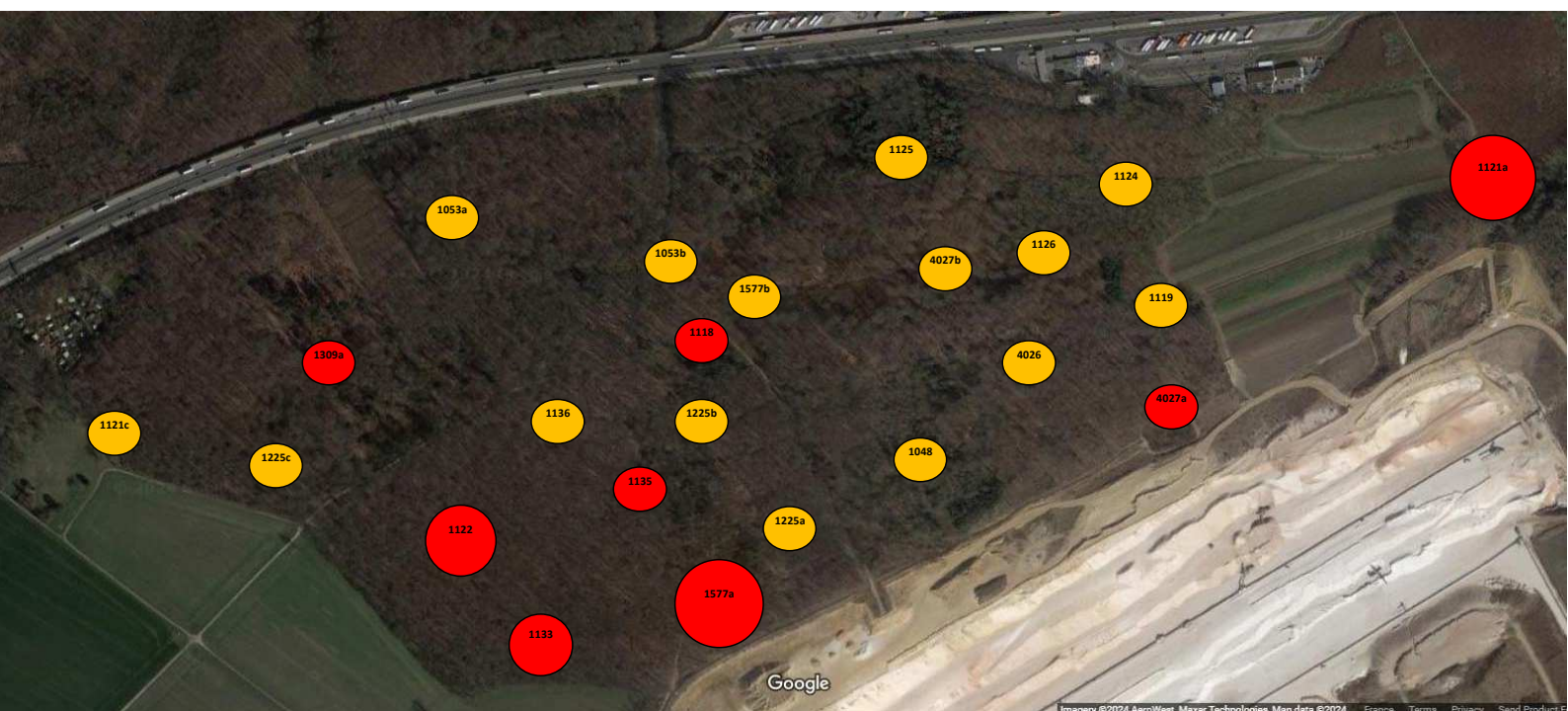


Figure 8 (appendix 1).

Distribution and intensity of the nocturnal activity of *Nyctalus leisleri* (+ *Eptesicus-Nyctalus spp.*), from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

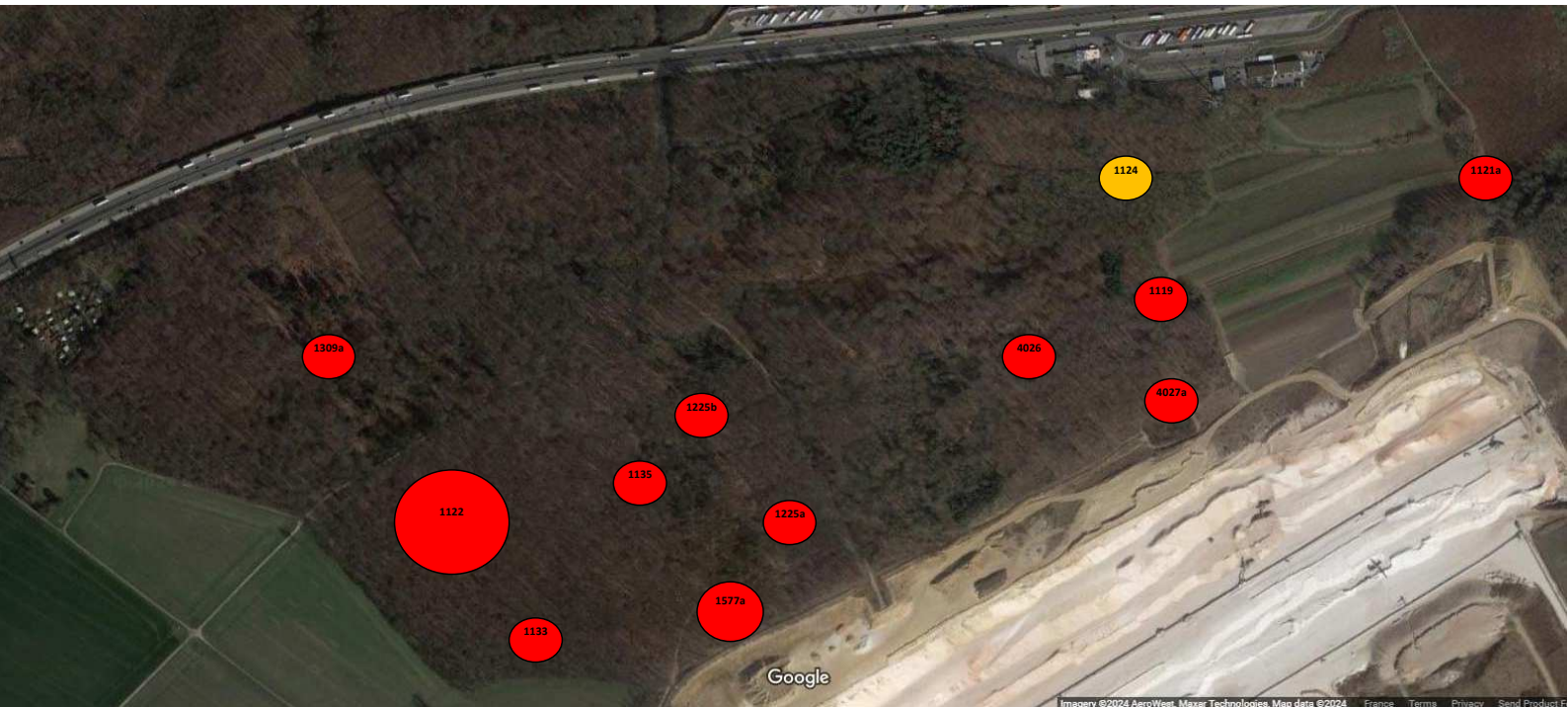


Figure 9 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis blythii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).



Figure 10 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis alcathoe*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

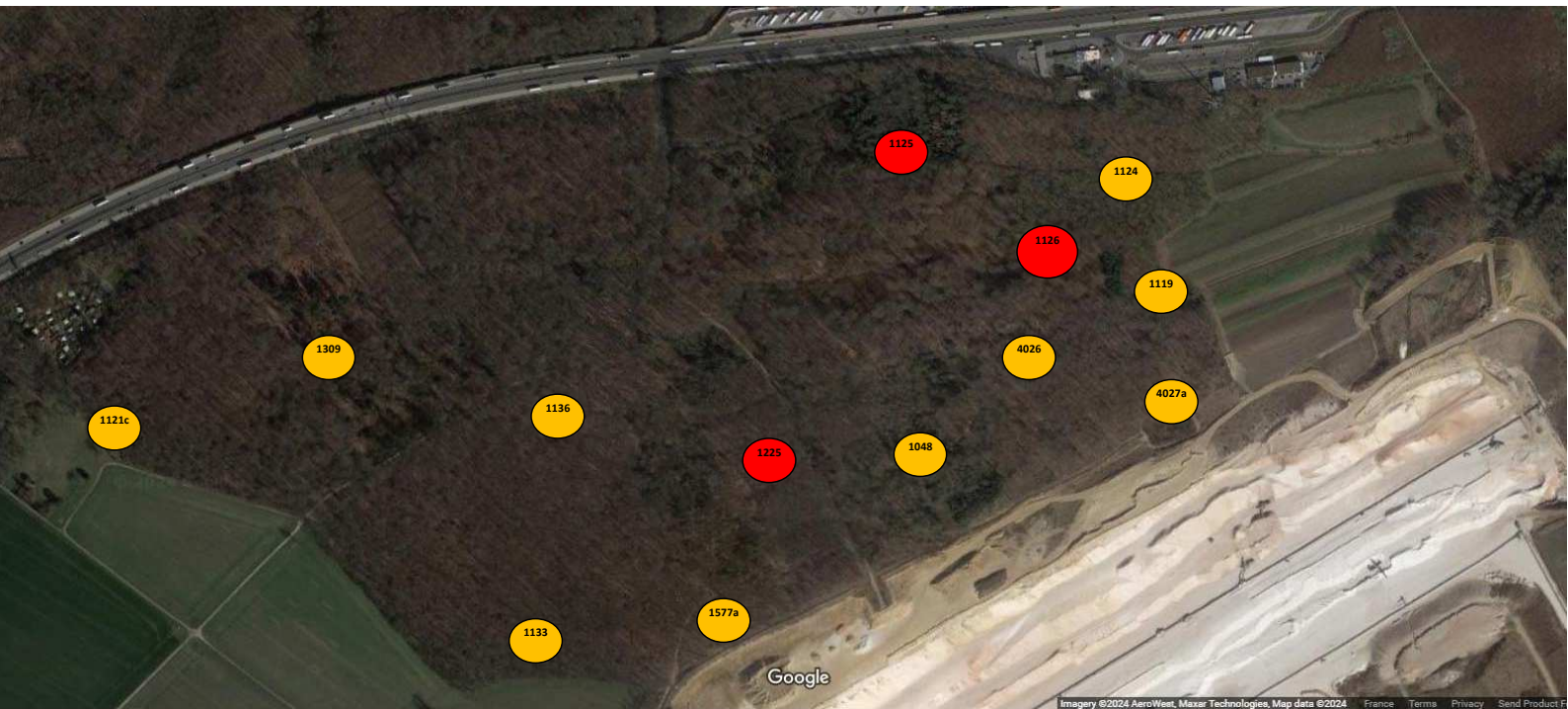


Figure 11 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis bechsteinii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

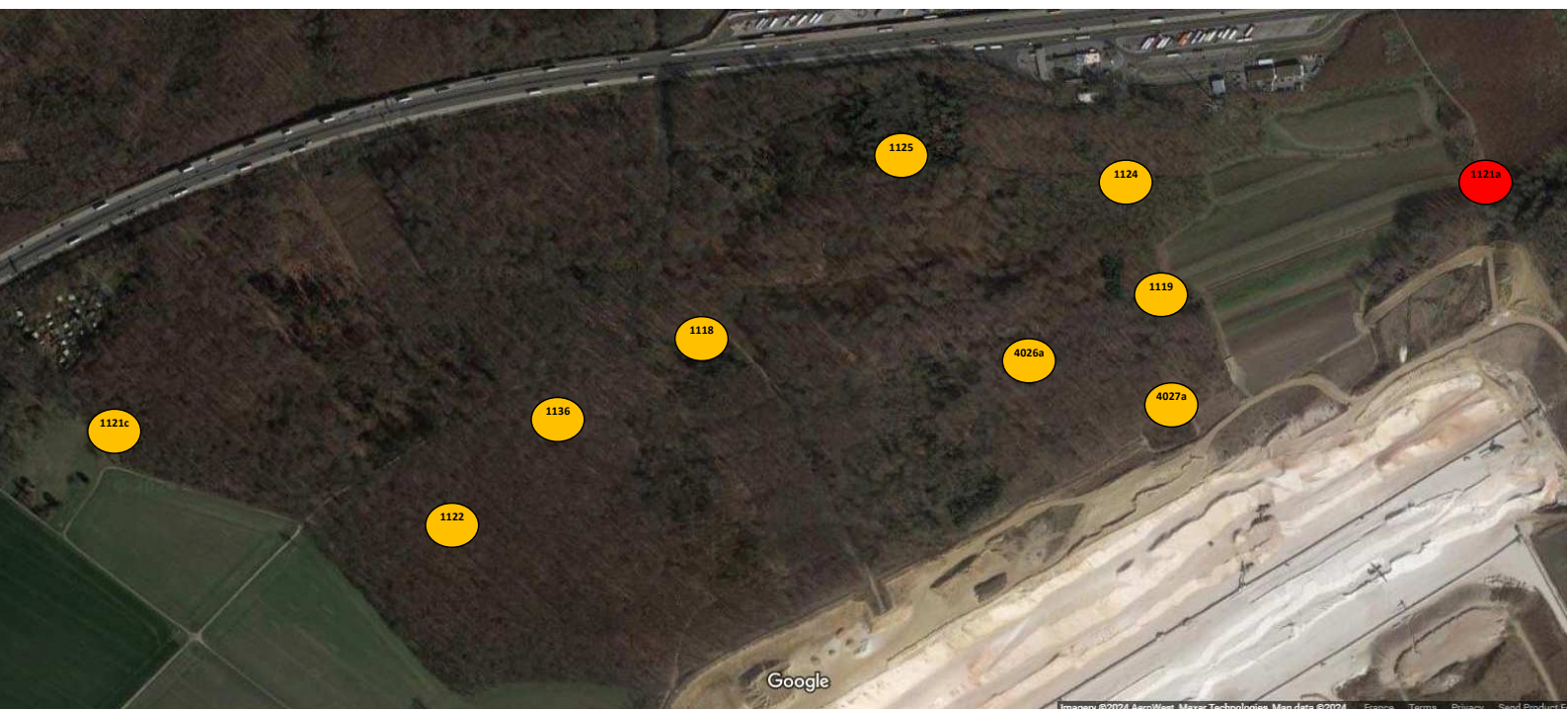


Figure 12 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis emarginatus*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).



Figure 13 (appendix 1).

Distribution and intensity of the nocturnal activity of *Pipistrellus pygmaeus*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

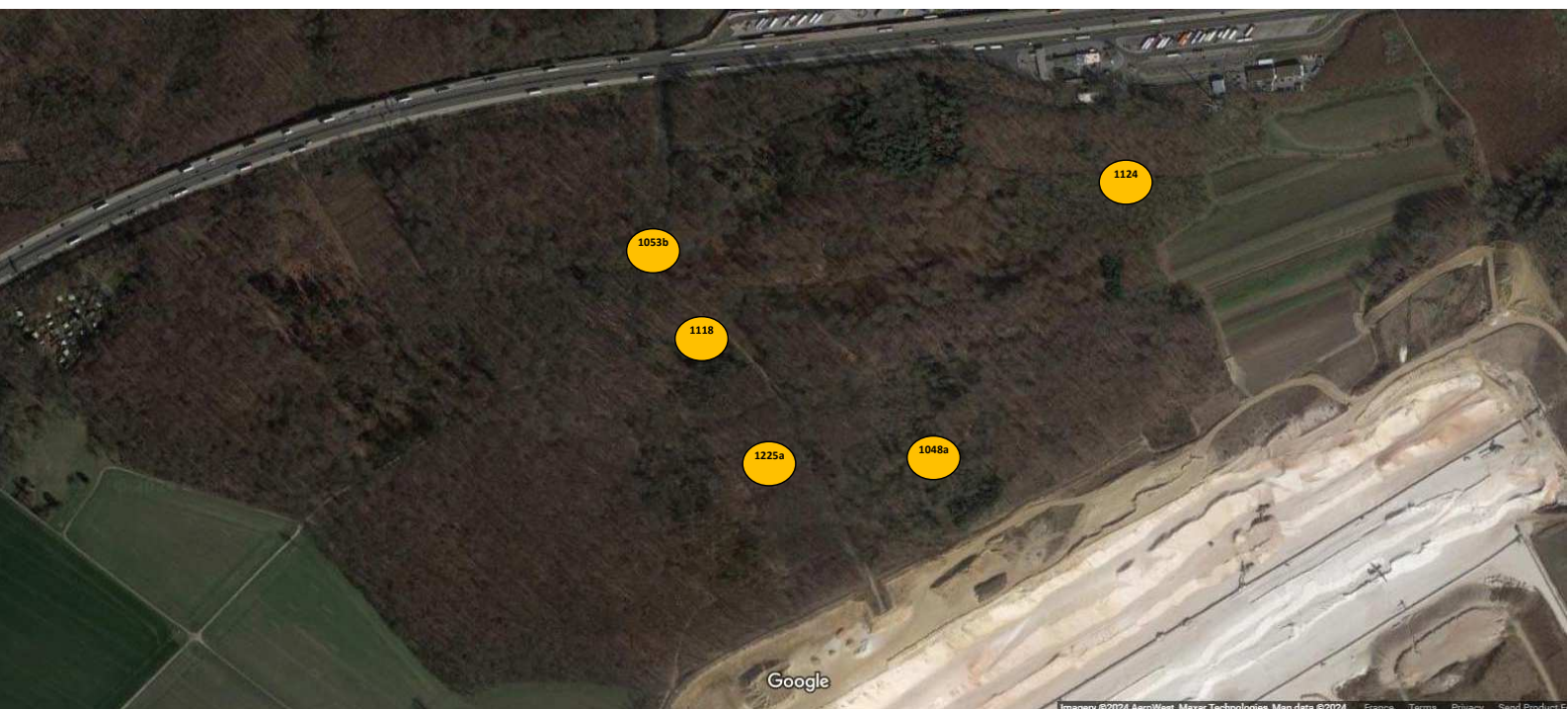


Figure 14 (appendix 1).

Distribution and intensity of the nocturnal activity of *Myotis brandtii*, from 20th September 2020 to 20th March 2021, in the Erlenbusch forest; (the colour red and a larger diameter indicate greater activity).

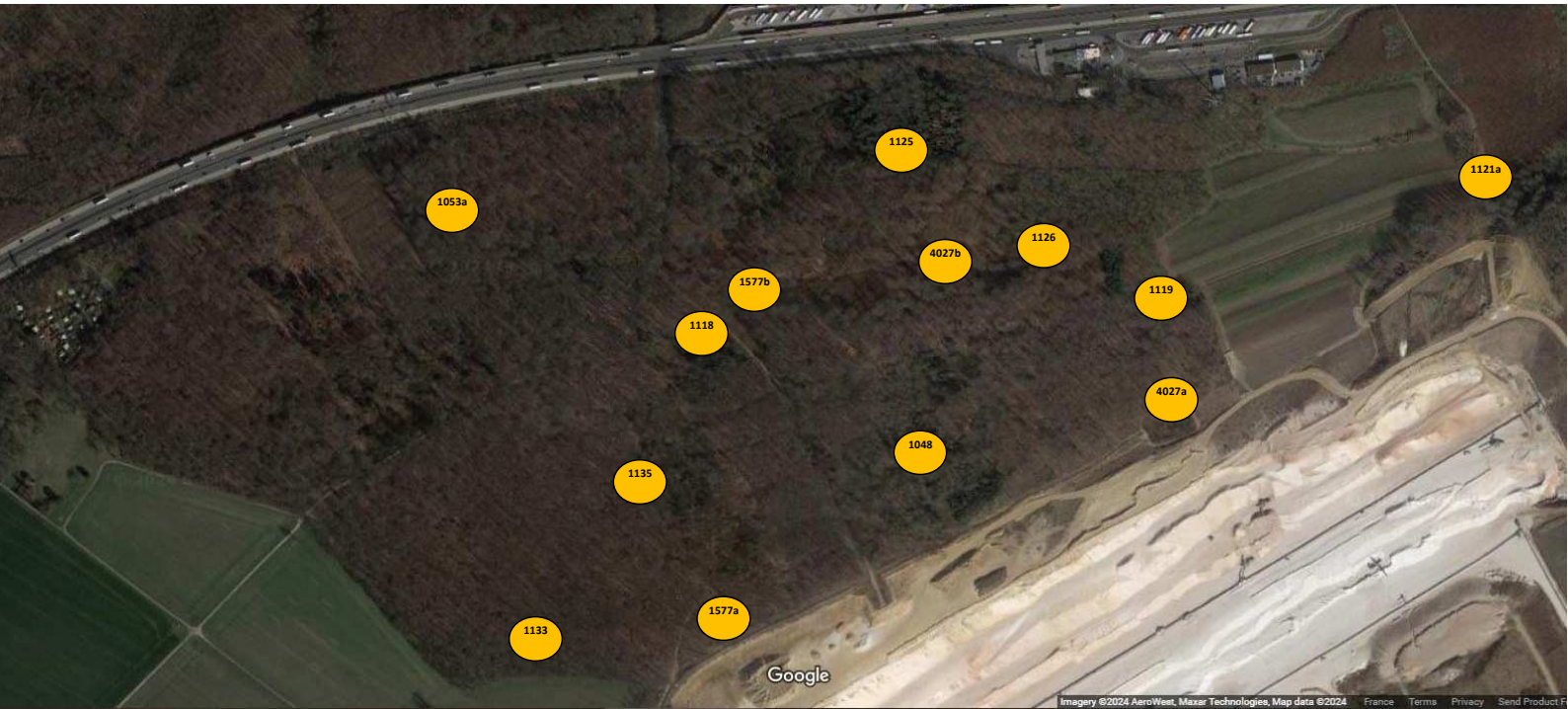


Figure 15 (appendix 1).

Distribution and intensity of the nocturnal activity of *Nyctalus noctula*, from 20th September 2020 to 20th March 2021, in the Erlämbusch forest; (the colour red and a larger diameter indicate greater activity).



Myotis daubentonii

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Photographs of recording points of bat activity inventoried in the Erlenbusch forest from 20th September 2020 to 20th March 2021



















