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Bat Community Composition and Activity of Migratory Bats in Southwest Norway – Spatiotemporal Patterns and Influence of Weather

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Abstract

1. Several temperate bat species undertake seasonal long-distance migrations (>1000 km). Such long-distance movements require significant energy expenditures, putting the bats at risk of exhaustion - especially if they encounter harsh weather along the way. Additionally, they are increasingly facing human-made obstacles that can pose a direct threat, such as wind turbines. The knowledge of bat migration routes in Norway is poor. Southwestern Norway has been suggested as a potential migratory pathway for bats crossing the North Sea. To understand how wind energy development in this area could impact migrating bats, there is a need to gain more knowledge about bat migration patterns and potential migratory pathways. In this study, I aim to explore migration patterns and how environmental factors influence the activity of long-distance migratory bats in the Norwegian southwest.

2. The main goal of this study is to get a better understanding of autumn migration patterns of bats along the coast in southwest Norway and how environmental variables influence their activity. More specifically, this study aims to (1) quantify the overall activity of migratory and sedentary bats across the study sites; (2) for the migratory species (a) understand when the autumn migration period occurs, (b) identify potential activity peaks across sites, and (c) compare the activity patterns of the migratory species; (3) quantify any seasonal patterns in commuting, social and feeding behavior of migratory bats; and (4) explain how precipitation, temperature, wind speed and wind direction influence the activity of migratory bats within the migration period.

3. Coastal areas of southwestern Norway were monitored for bat activity by deploying nine automated ultrasonic detectors between June and October in 2024. A subset of bat recordings targeted at migratory species was manually identified and categorized by behavior. Environmental data of air temperature, precipitation, wind speed, and wind direction for each study site were gathered from senorge.no.

4. I found that both migratory and sedentary bat species were active along the coast of Rogaland. The activity of the migratory species *N. noctula* was relatively low but continuous throughout the season, while *P. nathusii* activity peaked during the typical migration period. Feeding and social behaviors of *P. nathusii* were generally observed in early autumn, whereas *N. noctula* foraged by the coast during summer. *P. nathusii* activity within the migration period was low on rainy nights, but increased on nights with low wind speed and high temperatures. In the migration period, *P. nathusii* was most active at northern wind directions with wind speeds around 2.5 m/s, suggesting bats were migrating southward along the coast.

5. *Implications for management and conservation*. In light of the existing and planned wind energy facilities offshore and along the Norwegian North Sea coastline, the findings of this study have important applications for the renewable energy sector. To fulfil their responsibilities under the EUROBATS Agreement, Norway should carefully plan the placement of wind turbines and implement mitigation measures in high-activity periods to avoid future bat-wind conflicts.

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1. Introduction

Seasonal or annual movements are performed by many animal species across the globe as a response to changes in biotic and environmental conditions, commonly known as migration (Shaw, 2016). Migration is mainly used to seek or avoid certain conditions, such as seeking favorable foraging and breeding areas or avoiding detrimental environmental changes (Chapman et al., 2014; Shaw, 2016). The phenomenon of migratory behavior is observable across all classes of vertebrates, including birds, fish, amphibians, reptiles, and mammals (Chapman et al., 2014; Fleming et al., 2003; Shaw, 2016). While migration is a more widespread phenomenon among birds and fish, several mammal groups are known to perform seasonal or annual movements, including whales, ungulates, and bats (Chapman et al., 2014; Fleming, 2019; Shaw, 2016). Migratory animals may be more vulnerable to changes relative to more sedentary species, such as climate change (e.g. mismatch in migration timing and food resource availability), habitat destruction (e.g. loss of habitat in stopover sites) and an increase in anthropogenic obstacles along migrations routes such as roads, dams and wind turbines (Ahola et al., 2004; Fleming, 2019; Wilcove & Wikelski, 2008). Although bird migrations have been studied in more detail, less is known about the migratory behavior of bats, as the study efforts on bat migration have been limited in comparison (Fleming et al., 2003).

Several bat species in temperate regions undergo seasonal movements between summer and winter habitats, as most bats living in higher latitudes hibernate during winter (Fleming, 2019). Among temperate bat species, these seasonal movements are primarily driven by food resource availability and hibernation (Fleming et al., 2003). While most bat species in temperate and boreal regions move shorter distances between breeding areas and hibernacula, some species may travel thousands of kilometers to reach hibernation areas in a milder climate (Fleming et al., 2003). Fleming (2019) suggested that the seasonal movements of temperate bats could be broadly categorized in three main groups: (1) sedentary bats travelling less than 50 km between breeding and hibernation sites, (2) regionally migrating bats which travel between 100-500 km from summer to winter habitats, and (3) long-distance migrators who may perform seasonal movements of over 1000 km. It is generally assumed that the need to migrate over longer distances increases at higher latitudes; however, this phenomenon varies among species, as some species are adapted to colder temperatures and use winter roosts with more stable temperatures (Fleming et al., 2003; Lučan & Bartonička, 2024). Although long-distance migration in bats is not as common as in birds, several European bat species can migrate vast distances to reach suitable breeding and hibernation areas (Fleming, 2019; Hutterer et al., 2005, as cited in Krauel & McCracken, 2013).

Some of the bat species that undertake the longest seasonal movements in Europe are the insectivorous species *Pipistrellus nathusii*, *Nyctalus noctula,* and *Vespertilio murinus* (Hutterer et al., 2005, as cited in Krauel & McCracken, 2013). While *N. noctula* and *V. murinus* can migrate over 1500 km between their seasonal habitats (Hutterer et al., 2005, as cited in Krauel & McCracken, 2013), *P. nathusii* holds the record of the longest bat migration of over 2200 km (Alcalde et al., 2021). In broad terms, these species migrate seasonally from hibernacula in southwestern and central Europe to breeding areas in north-northeastern Europe (Lindecke et al., 2020; Russ, 2023). All three species are known to occur in Norway during summer or autumn, but information about their migratory patterns is mainly anecdotal or lacking. *N. noctula* has been confirmed to cross the Baltic Sea, but migration patterns of Norwegian populations are unknown (Rydell et al., 2014). Several migration routes of *P. nathusii* have been identified along coastlines and across the sea (**Figure 1.1**) (Russ, 2023). However, not all populations, nor even individuals within these populations, of these species opt to migrate. Some populations are more sedentary, traveling shorter distances between breeding areas and hibernacula (Fleming, 2019; Fleming et al., 2003).

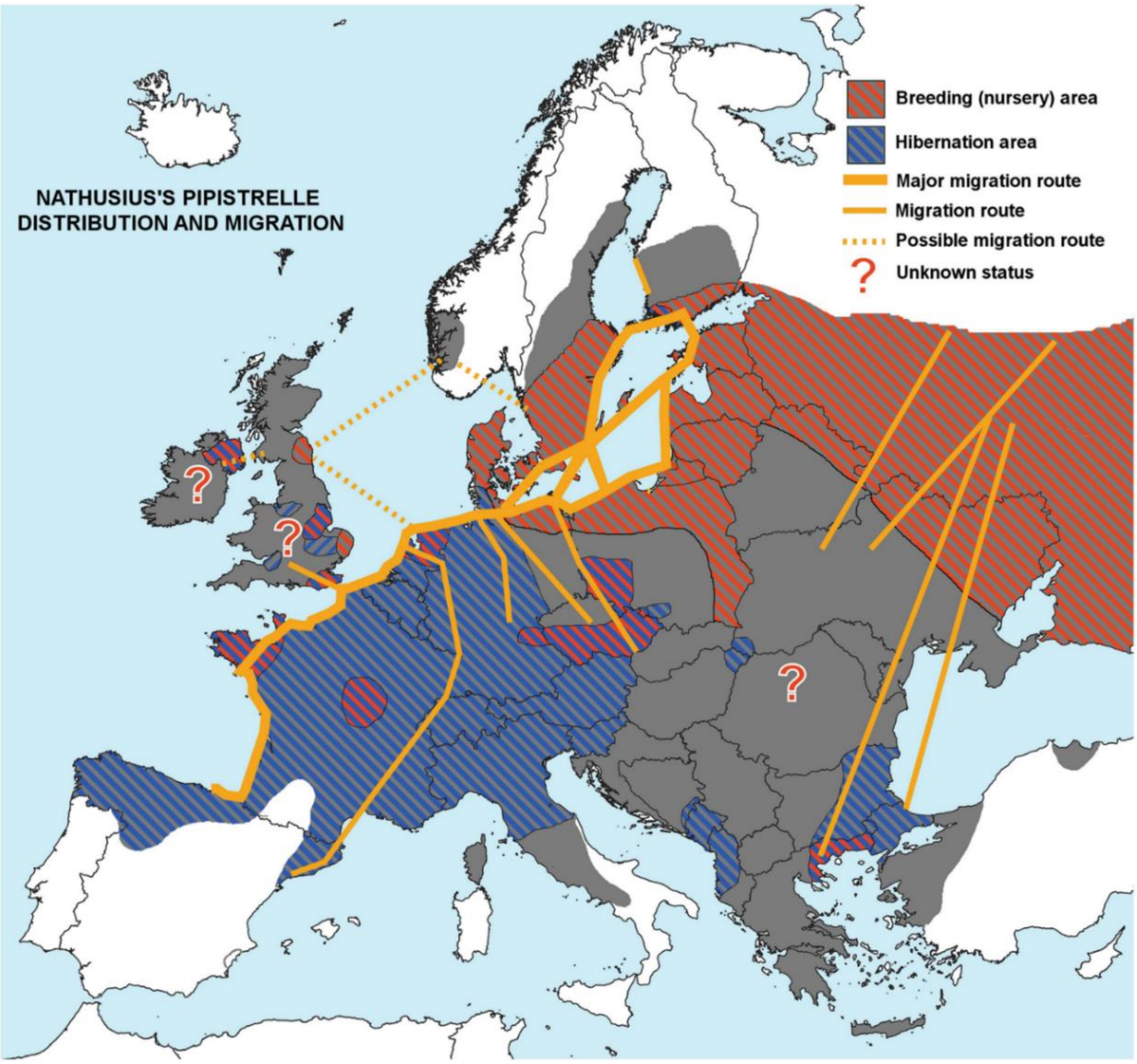

Figure 1.1. *Map of the distribution range (grey) and spatial migration patterns of Nathusis's pipistrelle, Pipistrellus nathusii. Including current knowledge of migratory routes, breeding, and hibernation areas. From Russ (2023), modified by Russ (2023) from original: Kurvits et al. (2011).*

Long-distance migration is energetically costly and risky, and therefore, bats migrate under optimal environmental conditions to conserve energy and maximize success (Fleming et al., 2003; Russ, 2023). In Great Britain, the number of individuals of *P. nathusii* found grounded increases in April and September, which is assumed to be exhausted migrants (Russ et al., 2001). As migration occurs during a period when bats must accumulate fat reserves in preparation for hibernation, foraging and roosting opportunities along migration routes (e.g., stopover sites) are vital for migratory bats (Fleming, 2019). While many migratory birds use stopover sites to forage during the day and migrate by night, bats, which are nocturnal, need to both forage and migrate during the dark hours (McGuire & Guglielmo, 2009). Although instances of migrant bats flying during daylight hours have been documented (Lučan & Bartonička, 2024), such behavior is relatively uncommon, with bats predominantly migrating and foraging at night (McGuire & Guglielmo, 2009). So, instead of engaging in extensive feeding sessions like birds, bats seem to forage more continuously during migratory flights (Hurme et al., 2025; Šuba et al., 2012).

It is widely recognized that environmental conditions, including wind, precipitation, and temperature, heavily influence the activity patterns of insectivorous bats. In temperate regions, where the activity of bats has been more well-studied, bat activity is generally expected to taper off when wind speeds are above 5 m/s and temperatures fall below 10 °C (McKay et al., 2024; Rydell, 1989). Bats are also usually less active during nights with heavy rainfall (Pettit & O'Keefe, 2017), as the energetic flight costs may increase when bats are wet (Voigt et al., 2011). However, temperature and wind conditions seem to be some of the most important environmental factors influencing the activity of migratory bats (Hurme et al., 2025; Lagerveld et al., 2021, 2023, 2024). To minimize energetic costs, migrating *P. nathusii* and *N. noctula* bats use the benefit of tailwinds and mainly migrate at nights with high temperatures (Hurme et al., 2025; Lagerveld et al., 2021, 2023, 2024).

In recent decades, there has been growing concern about the additional challenges that wind turbines pose to migratory bat populations (Arnett et al., 2016; EUROBATS, 2023; Kunz et al., 2007; Voigt et al., 2024). Migratory bats and other aerial- hawking bat species face a high risk of collisions with turbine blades (Rydell et al., 2010), and many bat carcasses discovered at wind facilities belong to migratory bat species during the migration period (Arnett et al., 2008, 2016; Kunz et al., 2007; Voigt et al., 2024). Deadly collisions with wind turbines have been suspected to contribute to population declines in *N. noctula* and the North American migratory species *Lasiurus cinereus* (Frick et al., 2017; Petermann, 2022). At the same time, the global demand for more sustainable energy is rising, particularly in Europe (Henrique et al., 2025). Therefore, a deeper insight into the spatiotemporal patterns and environmental influence of bat migration is crucial to avoid bat mortalities caused by wind turbines. Although European research efforts have improved the understanding of migratory bats, knowledge of bat migration patterns in Norway and the Norwegian North Sea remains largely unknown.

Southwest Norway represents a potentially significant area for migrating bats (**Figure 1.1**) (Eldegard et al., 2021d; Kurvits et al., 2011; Lund Hoel & Reinkind, 2019), but the existing knowledge about bats in this region is very limited. This region also has the highest number of wind turbines per land area in Norway, and there are ambitious plans for the development of wind energy offshore (NOU, 2023; NVE, 2023, 2024). It has been suggested that bats, particularly *P. nathusii*, migrate along the coastline to cross the North Sea, ultimately reaching Great Britain and the British Isles (Eldegard et al., 2021d). During winter, there are no confirmed observations of either *P. nathusii* or *N. noctula* in Norway, but whether individuals of these species overwinter in Norway is unknown (Eldegard et al., 2021c, 2021d). However, migratory bats have occasionally been seen on remote islands and oil installations in the North Sea (Petersen et al., 2014), which indicates that bats depart from the Norwegian coast. As both onshore and offshore wind energy are expected to expand rapidly in southwest Norway (NOU, 2023; NVE, 2023), gaining further insight into the activity of both migratory and sedentary bats in these areas is crucial to avoid future bat-wind conflicts.

To the best of my knowledge, no prior studies in Norway have been published that investigate the temporal, spatial, and behavioral patterns of migratory bats, while also exploring the influence of environmental variables on the activity of migrant bats. Therefore, this study aims to answer the following questions:

1. *How does the overall activity of migratory and sedentary bat taxa vary across the study sites?*
2. *For the migratory species P. nathusii and N. noctula:*
    a. *When does the autumn migration period occur?*
    b. *When does activity peak across the study sites?*
    c. *Are there differences in the spatial and temporal activity patterns of P. nathusii and N. noctula?*
3. *How does the commuting, social, territorial, and feeding behavior of migratory bats vary seasonally?*
4. *How do precipitation, temperature, wind speed, and wind direction influence the activity of migratory bats within the migration period?*

In relation to these research questions, and based on existing scientific evidence, I have made the following predictions:

I. As the study sites are located in open areas along the coast, most bat activity will consist of migratory and sedentary aerial-hawking bat species.
II. Activity of migratory species will primarily occur in late August and September, with activity peaking in September. The activity of *N. noctula* will be lower than that of *P. nathusii*.
III. Feeding, social interactions, and territorial behaviors will coincide and intensify during the migratory period.
IV. Elevated temperatures and wind directions originating from the north and east will enhance the activity of migratory bats, while activity will decrease in the presence of high wind speeds and heavy rainfall.

2. Materials and methods

2.1. Study area

This study was part of the Coastal Monitoring project, conducted by Batlab Norway at the Norwegian University of Life Sciences (NMBU). The study area of the Coastal Monitoring project spans from the island of Utsira in the North to Lista in the South, with 50 acoustic monitoring sites within coastal areas and by inland lakes (**Figure 2.1**). In this thesis, I use a selection of nine sites from the Coastal Monitoring project.

The study was conducted within coastal areas in Rogaland County between June and October of 2024. Rogaland County is located in South-Western Norway by the North Sea (**Figure 2.1**). The study area spans the outer coastlines of Karmøy and Boknafjorden in the north and the lowlands of Jæren in the south (**Figure 2.1**). Neighboring an open ocean to the west, the climate in the area is wet and mild with strong winds. Most of the study area consists of agricultural land, livestock pastures, and urban and residential areas interspersed with fragments of pine plantations, coastal heathlands, lakes, and forests. While the northern parts are characterized by islands and fjords with steep terrain and exposed bedrock, the southern lowlands are flatter with thick moraine soils, marine sediments, and coastal dunes.

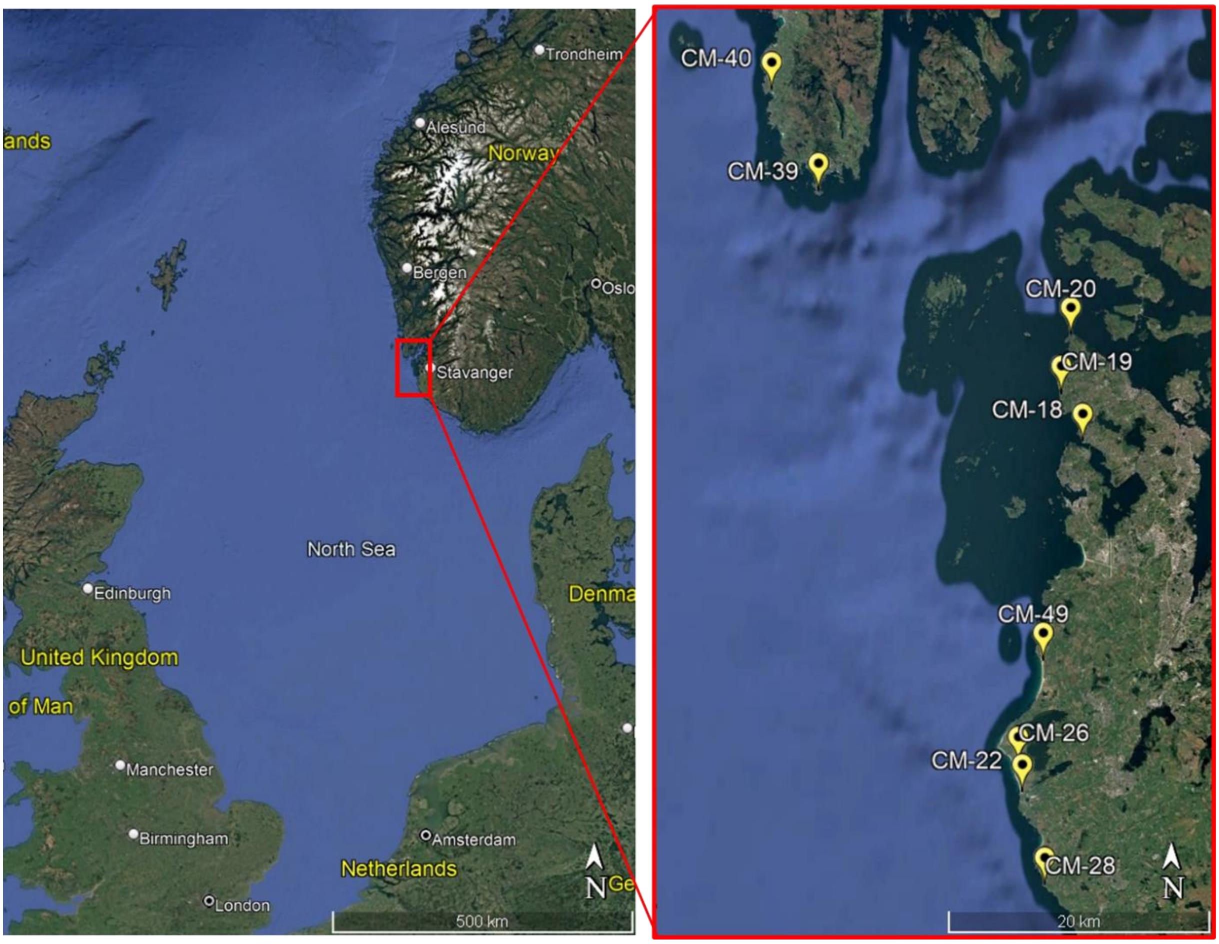

Figure 2.1. Map of the location of the study area in relation to the United Kingdom and the North Sea (to the left), and study site locations (to the right). Maps made in Google Earth Pro.

Rogaland was primarily chosen as the study area because it has been previously identified as a potential bat migration corridor (Eldegard et al., 2021d; Russ, 2023). Additionally, all three bat species capable of long-distance migration (*P. nathusii*, *N. noctula*, and *V. murinus*) have been observed in the region (Artsdatabanken, 2024). The area is also attractive for wind energy development. In addition to several active wind parks in the area, wind energy is expected to expand rapidly both onshore and offshore in adjacent areas in the near future (NVE, 2023, 2024).

2.2. Study species

Out of the eleven bat species confirmed to occur in Norway, three species, *P. nathusii*, *N. noctula*, and *V. murinus*, are known to be capable of long-distance movements between breeding and hibernation habitats (**Table 2.1**) (Artsdatabanken, 2021; Dietz & Kiefer, 2016). Although *V. murinus* is considered a migratory species in parts of Europe and Russia, this species was excluded from this study due to its cryptic echolocation, which can be challenging to differentiate acoustically from *N. noctula* and *Eptesicus nilssonii* (Dietz & Kiefer, 2016; Russ, 2021). Additionally, *V. murinus* is regularly observed in Norway during winter, suggesting that at least parts of the Norwegian population is sedentary (Artsdatabanken, 2024). Therefore, only *P. nathusii* and *N. noctula* were included in this study.

Table 2.1. *Overview of bat species found in Norway. The common names of species are written in English. Movement strategy represents the current knowledge about the species' annual movements. Bat species labelled as migratory are species known to be able to perform long-distance (>1000 km) migration flights, while species labelled as sedentary may perform shorter annual movements between breeding and hibernation sites on a local or regional scale (50-500 km). Status = Conservation status according to the Norwegian Red List of Threatened Species, LC = Least concern, NT = Near threatened, VU = Vulnerable, EN = Endangered, CR = Critically endangered (Artsdatabanken, 2021).*

Scientific name	***Common name***	***Movement strategy***	***Status***
Barbastella barbastellus	Western barbastelle	Sedentary	CR
Eptesicus nilssonii	Northern bat	Sedentary	VU
Myotis brandtii	Brandt’s bat	Sedentary	LC
Myotis daubentonii	Daubenton’s bat	Sedentary	LC
Myotis mystacinus	Whiskered bat	Sedentary	LC
Myotis nattereri	Natterer’s bat	Sedentary	CR
Nyctalus noctula	Common noctule	**Migratory**	EN
Pipistrellus nathusii	Nathusius’s pipistrelle	**Migratory**	NT
Pipistrellus pygmaeus	Soprano pipistrelle	Sedentary	LC
Plecotus auritus	Brown long-eared bat	Sedentary	LC
Vespertilio murinus	Parti-coloured bat	**Migratory**	NT

These species are morphologically adapted for fast flight, with long, narrow wings that are well suited for long-distance travel (Fleming et al., 2003; Popa-Lisseanu & Voigt, 2009). The knowledge of the migratory behavior of these species in Norway is poor. However, most observations of *P. nathusii* have occurred in the autumn (Artsdatabanken, 2025b), while *N. noctula* are observed more during the summer breeding season (Artsdatabanken, 2025a). Partial and differential migration are expressed in both species in other European countries, although regular migratory behavior seems to be more widespread among *P. nathusii* populations across Europe (Lindecke et al., 2020; Russ, 2023).

2.3 Data collection

2.3.1 Acoustic monitoring

Nine study sites were monitored for bat activity between June and October using automated full-spectrum bat detectors (hereafter detectors), with a built-in ultrasonic microphone (Song Meter Mini Bat 2 Li-ion, Wildlife Acoustics). Monitoring sites were located directly at the coast or within 350 meters of the coastline (**Table 2.2**). Sites were selected for proximity to the coastline or other linear landscape features (e.g. rivers, hedgerows) as bats may use such landscape elements as migratory pathways (Ijäs et al., 2017; Jarzembowski, 2003). Detectors were mounted on extendable metal poles or existing objects (e.g. wooden poles, fences, lighthouses) at least 1.8 meters above ground (**Figure 2.2**). Rain and wind against vegetation create ultrasonic sounds, which can trigger the detector to start recording even in the absence of bat echolocation calls. All detectors were placed at least five meters away from clutter to secure the best possible quality of bat recordings and avoid unnecessary noise recordings. Detectors were deployed between mid-June and mid-July and were retrieved in October. Due to the differences in deployment periods, the monitoring period varied between sites (**Table S.1**). Detectors were set to be active from five hours before sunset to one hour after dawn, as bats have been observed flying in daylight in the migration period (**Table S.2**) (Lučan & Bartonička, 2024). For a more detailed overview of detector settings, see **Table S.2**.

Table 2.2. *Overview of the study sites. Site = codenames of each of the study sites, Habitat = broad description of habitat surrounding the detector, Detector h. (m) = the height in meters of which the detector was installed, Coastline dist. = the distance of detector to coastline in meters. The study sites are arranged from the northernmost (CM-40) on the top to the southernmost (CM-28) on the bottom.*

Site	Habitat	Detector h. (m)	Coastline dist. (m)
CM-40	Coastal pasture	3.0	237
CM-39	Island, bedrock	1.8	1
CM-20	Coastline, pasture	2.5	1
CM-19	Coastline, bay	2.2	0
CM-18	Coastline, residential	2.5	0
CM-49	Coastal dunes	2.2	155
CM-26	Coastal dunes	4.0	315
CM-22	Coastal dunes	2.3	139
CM-28	Coastal dunes	2.2	122

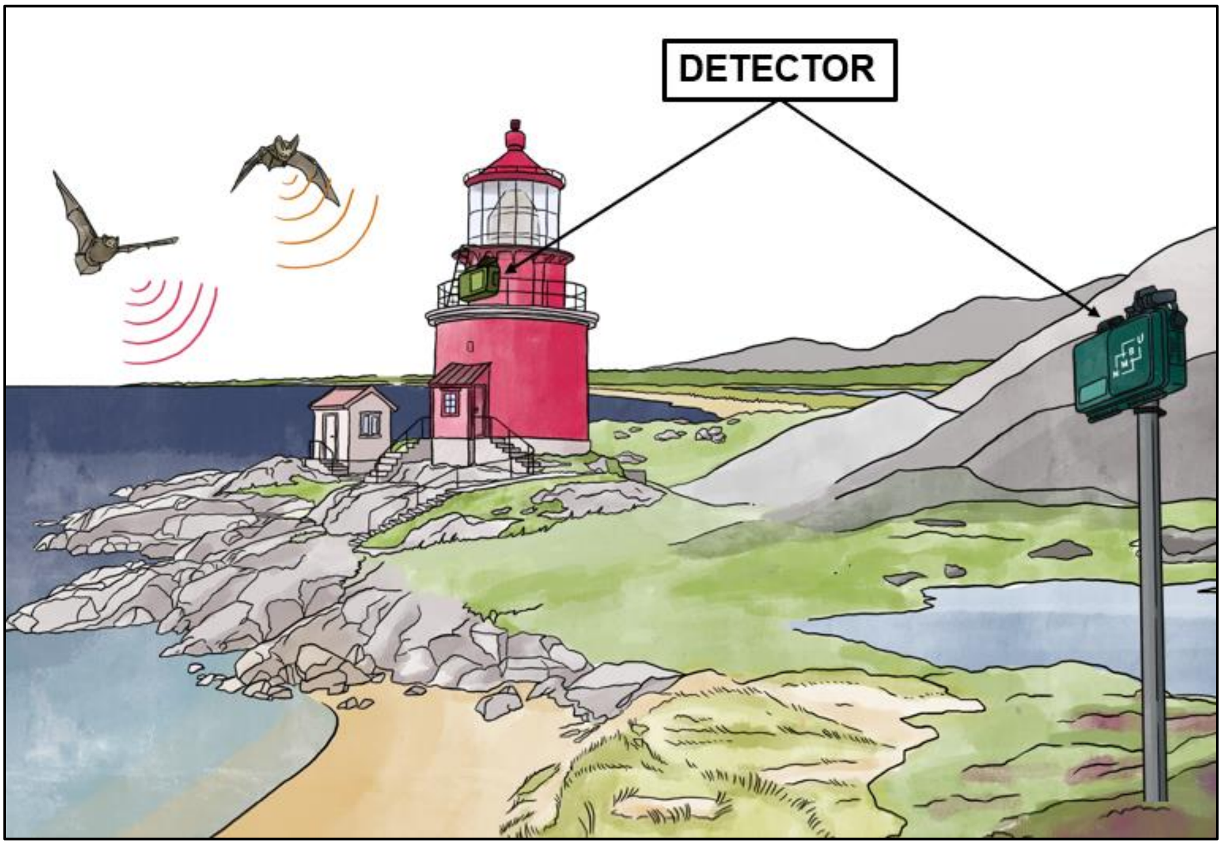

Figure 2.2. *Illustrative overview of bat detector setup at coastal study sites. Detectors were deployed on existing objects (lighthouses, fences, poles) when suitable, or mounted on extendable metal poles secured in the ground. Illustration by Olina Søyland Bru.*

2.3.2 Environmental data

Environmental data on air temperature, precipitation, wind speed, and wind direction were obtained for each study site by downloading modeled weather data from https://senorge.no/. Site CM-39, located on a small island, was situated outside the modeled grid; therefore, data from the nearest location on the mainland were used. Environmental variables had records at three-hour intervals (UTC), with each measurement representing conditions over the preceding three hours. Air temperature (°C) reflected the mean temperature during the three-hour period, while precipitation (mm) represented the total rainfall accumulated over the same interval. Wind speed (m/s) and wind direction (degrees) were recorded as averages measured at a height of 10 meters above ground. As bat activity data were aggregated by night for statistical analysis, the three-hour interval encompassing the period from 23:00 to 02:00 was chosen as a representative proxy for nightly weather conditions.

2.4 Manual acoustic analysis

Analysis of acoustic data collected from bat detectors was done in Kaleidoscope Analysis Software (version 5.6.8, Wildlife Acoustics, USA). Recordings were processed as 5-second full-spectrum .wav files with a minimum of two consecutive bat-call pulses (Fenton et al., 1973), which defines one single bat pass in this study. Signal detection parameters were set to detect frequencies between 8-150 kHz and pulse lengths between 2-500 milliseconds. Recordings were first run through an automatic species classifier (Bats of Europe Classifier, version 5.4.0.), with a selection of bat species known to occur in Norway, see **Table 2.1** (Artsdatabanken, 2021). Manual verification of species identification was then performed on all files automatically classified as *P. nathusii*, *N. noctula*, *Pipistrellus pygmaeus*, *Plecotus auritus,* and *Barbastella barbastellus* to target and maximize the number of bat passes of migratory species. Recordings automatically identified as non-target species (*P. pygmaeus*, *P. auritus*, and *B. barbastellus*) were included in the manual acoustic analysis, as recordings of these species can be misidentified by the classifier. In addition, recordings identified by the classifier as “noise” or “no ID” were manually controlled from all sites. Manual verification of recordings was done in accordance with the guidelines of Marckmann & Pfeiffer (2020) and Russ (2021).

During the manual verification, each bat pass was identified to species, genus or echolocation group (e.g., Nyctaloid). FM-QCF echolocation pulses of *N. noctula*, *V. murinus*, as well as lower frequency echolocation pulses of *E. nilssonii*, is challenging to differentiate when the recording lacks diagnostic features (Marckmann & Pfeiffer, 2020). Such bat passes were therefore grouped together as “Nyctaloid”. When echolocation pulses of *Pipistrellus* species were above or below the diagnostic frequences of *P. nathusii* or *P. pygmaeus*, these were labelled with genus. Bat passes of *Myotis* species were only identified to genus. Recordings were also labelled by behavior. Bat passes containing only echolocation pulses were categorized as “commuting”, while bat passes with at least one feeding buzz (including commuting and approach phase) were categorized as “feeding”. Territorial call sequences characteristic of *Pipistrellus* species were put in the “territorial” category, while other social calls were categorized as “social”.

2.5. Data analysis

All exploratory and statistical analysis was done in R Studio, version 2024.12.1.563 (Posit team, 2025). To investigate the relationships between bat activity and explanatory variables, I fitted generalized linear mixed models (GLMMs), or generalized additive models (GAMs) when the exploratory analyses revealed clear non-linear relationships. The response variable, bat activity, was either quantified as the number of bat passes aggregated per night or as presence (observed)/absence (not observed). I fitted models with negative binomial distribution of errors and log-link when the number of bat passes was used as the response variable, while I fitted models with binomial distribution and a logit link function when the response variable was presence/absence data. I used the DHARMa package (Hartig, 2024) to assess model fit and the validity of model assumptions for all models by inspecting simulated residuals for uniformity and overdispersion.

2.5.1. Activity of migratory and resident bats across the study sites

To quantify the activity of migratory and resident bat taxa among sites, the number of bat passes of each taxon were aggregated for each site. To test for differences in community composition across sites and seasons, the study period was split into three seasons: Early summer (June 27-July 26), Late summer (July 27-August 31), and Early autumn (September 1-October 18). Bat passes of each taxon were then aggregated for each site and season. Differences in bat community composition across sites and seasons were tested with a permutational multivariate analysis of variance (perMANOVA) test.

To test for a correlation in migratory bat activity along a latitudinal gradient, the total number of bat passes of migratory species (*P. nathusii*, *N. noctula*, and *V. murinus*) were aggregated for each site, and sites were ranked from the southernmost site to the northernmost site before analysis. To analyze the predicted relationship between bat and latitude across the ranked sites, I conducted a Spearman's correlation test.

In further analysis of migratory bat activity and composition among sites and seasons, migratory bat taxa with very few observations were excluded. To test for differences in migratory bat abundance among sites, the number of bat passes on *N. noctula* and *P. nathusii* aggregated for each site was analyzed using a Wilcoxon matched-pairs signed-rank test. Differences in migratory bat community composition across sites and seasons were tested with a permutational multivariate analysis of variance (perMANOVA) test.

2.5.2. Seasonal patterns and activity peaks of migratory bats

To identify potential activity peaks of migratory bat species, the maximum number of bat passes per night were calculated for each site. Peak activity nights were tested against non-peak nights to test if peak nights had significantly higher bat activity using a Wilcoxon rank sum test.

To analyze the spatiotemporal patterns of migratory bat activity, I fitted a negative binomial generalized additive model (GAM) with a log-link function. Model parameters were estimated using the restricted maximum likelihood (REML) method. The response variable was the number of bat passes aggregated per night. Explanatory variables were night of the year (date transformed to a numeric variable) and latitude extracted from site coordinates. A smooth term was used for each explanatory variable, and their interaction was modeled using a tensor product smooth. To account for temporal autocorrelation, a Gaussian process smoother was applied to night of the year. A random effect smooth for site was included to account for repeated measures and spatial autocorrelation.

2.5.3. Seasonal patterns in behavior

Due to few observations of feeding and social behavior, migratory bat behavioral activity was investigated with exploratory analysis (data visualization) and compared to activity peak periods of the migratory bat species.

2.5.4. Influence of weather conditions on bat activity and migration

N. noctula observations were excluded from the analysis of weather influence due to few observations and heavily zero-inflated data. The influence of weather conditions on *N. noctula* activity was therefore only investigated with exploratory analysis (visualization of the data).

To investigate the activity of bat activity within the migration period in relation to weather conditions, a subset of nights with peak activity was used for analysis. Exploratory analysis showed that bat activity occurred almost exclusively on nights with no or low precipitation. Precipitation was therefore excluded as an explanatory variable, and only nights with <5 mm precipitation were included in the models. Before analysis, the explanatory variables were checked for multicollinearity using Pearson correlation for numerical variables (temperature and wind speed). Wind direction was transformed from numeric (°) to categorical variables (north = 0-45°, east = 45-135°, south = 135-225°, west = 225-315°, north = 315-360°), and tested for multicollinearity against mean values of temperature and wind speed across wind direction categories using a Kruskal-Wallis test.

To investigate the influence of temperature and wind speed on *P. nathusii* activity, bat presence, and the explanatory variables were fitted in a binomial generalized mixed model (GLMM) with a log-link. The explanatory variables were temperature and wind speed. Site and night nested within site were included as random effects to account for variation among sites and night-to-night variation within sites.

The influence of wind direction and temperature on *P. nathusii* activity was analyzed in two separate generalized mixed models (GLMMs): one with bat presence as the response variable and another with the number of bat passes aggregated per night as the response variable. Explanatory variables were wind direction and temperature in both models. When bat presence was used as the response variable, I fitted the model with binomial distribution and a logit-link function, and with negative binomial distribution of errors and a log-link function when the response variable was the number of bat passes. Site and night nested within site were included as random effects in both models to account for variation among sites and night-to-night variation within sites.

Northern wind directions significantly influenced the number of bat passes, and further analysis was conducted on a subset with only northern wind directions to investigate the influence of wind speed and temperature on migratory bat activity. The number of bat passes was fitted in a generalized additive model (GAM) with a log-link function using the restricted maximum likelihood (REML) method. Explanatory variables were smooth terms of wind speed and temperature. Random effects for site and/or night were not included, as model diagnostics indicated issues with residual patterns and overdispersion when these terms were added.

3. Results

3.1. Overview of results

A total number of 22,377 (5 sec) recordings from nine study sites were manually analyzed during acoustic analysis, including recordings of bat passes and unidentified noise recordings (**Table 3.1**). The highest number of recordings was collected on site CM-22 (n=6,479), CM-28 (n=5,915), and CM-26 (n=3,367). Western wind directions were the average wind direction across study sites. There was low variation in air temperature and precipitation across the study sites, while wind speed varied slightly (**Table 3.3**, **Figure S.1**).

Table 3.1. *Summary of sampled results across study sites. Sites are arranged from the northernmost site (CM-40) to the southernmost site (CM-28). N obs. = total number of 5-second recordings of bat passes and unidentified noise from manual acoustic analysis. Mean T (°C) = average nightly air temperature in degrees Celsius. Mean PP (mm) = average nightly precipitation in millimeters. Mean WS (m/s) = average nightly wind speed in meters per second. Mean WD (°) = average nightly wind direction in degrees (north = 0-45°, east = 45-135°, south = 135-225°, west = 225-315°, north = 315-360°). All environmental variables (Mean T (°C), Mean PP (mm), Mean WS (m/s), and Mean WD (°)) were measured over three hours (23:00-02:00) and were used as a proxy for nightly weather conditions.*

Site	***N obs.***	***Mean T (°C)***	***Mean PP (mm)***	***Mean WS (m/s)***	***Mean WD (°)***
CM-40	1,233	13.8	0.4	5.1	176.8
CM-39	308	13.1	0.4	4.8	198.1
CM-20	1,016	13.5	0.5	4.6	208.4
CM-19	1,281	13.6	0.5	4.6	207.7
CM-18	495	13.7	0.5	4.1	202.1
CM-49	2,283	13.1	0.4	4.8	174.2
CM-22	6,479	13.0	0.6	5.1	184.4
CM-26	3,367	13.5	0.5	4.9	180.1
CM-28	5,915	13.4	0.5	5.9	180.2
Sum	**22,377**				

3.2. Activity of migratory and resident bats across the study sites

There was considerable variation in bat activity among sites, with the most active site recording 21 times more bat passes than the least active site (**Figure 3.1**). *P. pygmaeus*, *E. nilssonii*, and *P. nathusii* were the three most common species across the study area, respectively. Community composition - as inferred from the proportion of activity by different bat taxa - also varied substantially across sites and between seasons (**Table 3.2**, **Figure 3.2**). The PERMANOVA results revealed that site explained 43.6% of the variance in bat community composition (p = 0.001), while 22.8% of the variance could be explained by seasonality (p = 0.001) (**Table 3.2**).

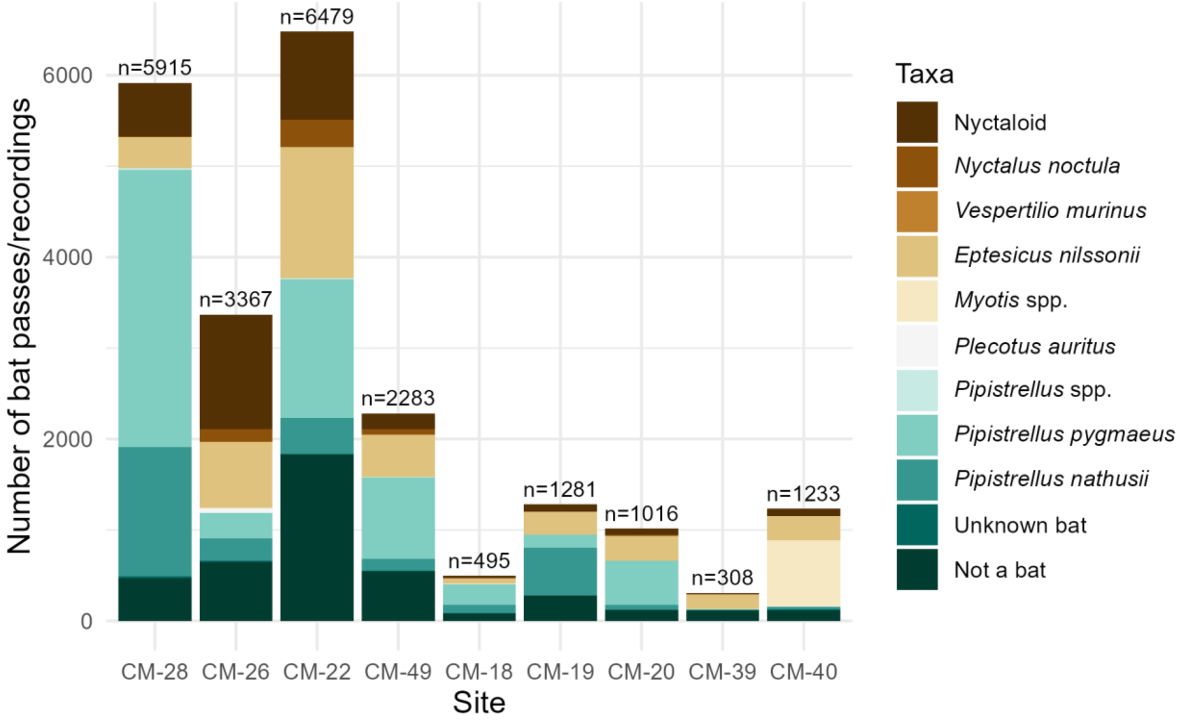

Figure 3.1. *Total activity (number of bat passes) of different bat taxa throughout the study period at the nine study sites. Bat passes of Vespertilio murinus were recorded on site CM-28 (n=1 (territorial)) and site CM-26 (n=2 (territorial)). The study sites are arranged from the southernmost (CM-28) on the left to the northernmost (CM-40) on the right. 'Not a bat' are recordings of noise.*

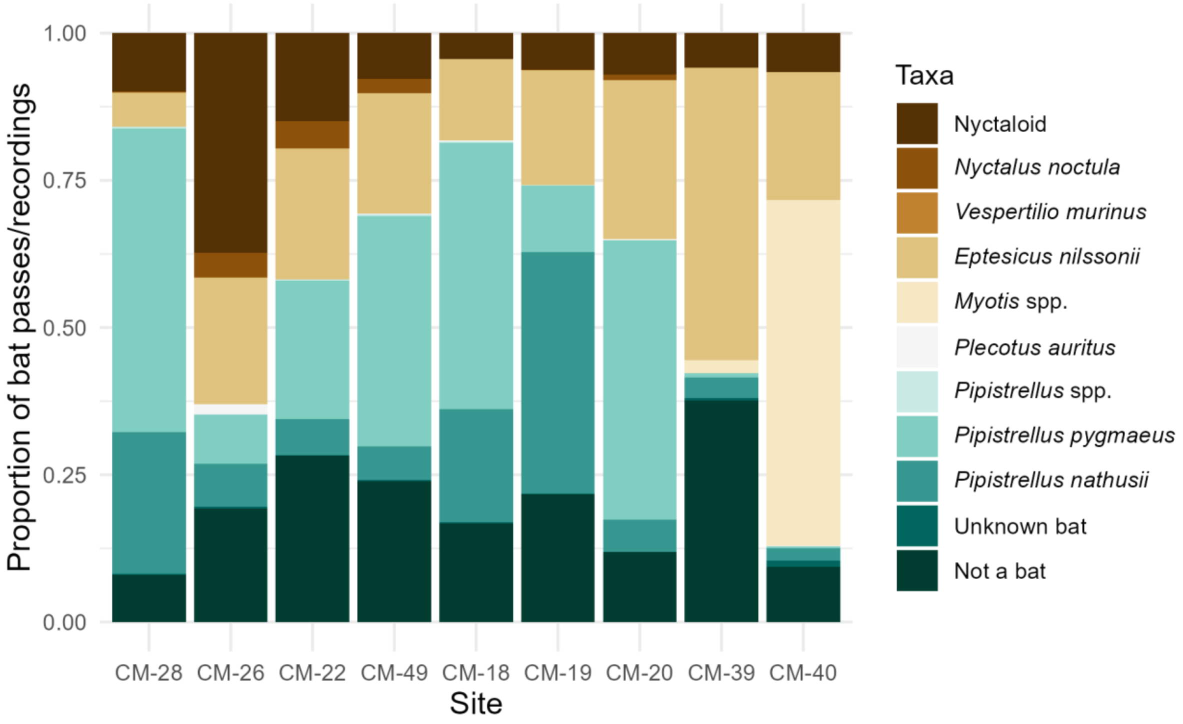

Figure 3.2. *Proportion of activity (number of bat passes) by different bat taxa throughout the study period at the nine study sites. Bat passes of Vespertilio murinus were recorded on site CM-28 (n=1 (territorial)) and site CM-26 (n=2 (territorial)). The study sites are arranged from the southernmost (CM-28) on the left to the northernmost (CM-40) on the right. 'Not a bat' are recordings of noise.*

Table 3.2. *Variables explaining the variance in bat community composition in the study area. Output from permutational multivariate analysis of variance (PERMANOVA) test based on Bray-Curtis dissimilarity, with 999 free permutations. Seasons (n = 3) were defined as Early Summer (June 27–July 26), Late Summer (July 27–August 31), and Early Autumn (September 1–October 18).*

	Df	***Sum of Squares***	***R^2 (%)***	***F***	***p***
Site	8	3.10	43.6	2.60	*0.001*
Season	2	1.62	22.8	5.43	*0.001*
Residual	16	2.39	33.6		
Total	26	7.12	1.0		

The activity of migratory bat species decreased along the south-north gradient, and sites further south showed the highest activity (Spearman’s ρ = -0.85, p = 0.006) (**Figure 3.3**). Among the migratory species, only *P. nathusii* was recorded at all sites; however, activity varied considerably, with a difference of 129 times between the site with the lowest (n = 11) and the site with the highest (n = 1420) number of bat passes recorded (**Figure 3.3**). *N. noctula* occurred at six sites, but the number of bat passes of this species was substantially lower than for *P. nathusii* (**Table 3.3**). A Wilcoxon matched-pairs signed-rank test showed a significant difference in bat pass counts between *N. noctula* and *P. nathusii* across sites (V = 0, p = 0.0039), with *P. nathusii* being consistently more abundant. The sites with the highest activity of *N. noctula* were not the same as those with the highest activity of *P. nathusii*. When including only *P. nathusii* and *N. noctula* in the PERMANOVA, the variance between the composition of the species across sites was also explained best by site-specific factors (R^2 = 45.5%, p = 0.003), while season explained 28.9% of the variation (p = 0.001) (**Table 3.4**). *V. murinus* were only confirmed occurring at site CM-28 (one bat pass) and CM-26 (two bat passes), all of which were territorial calls characteristic of the species.

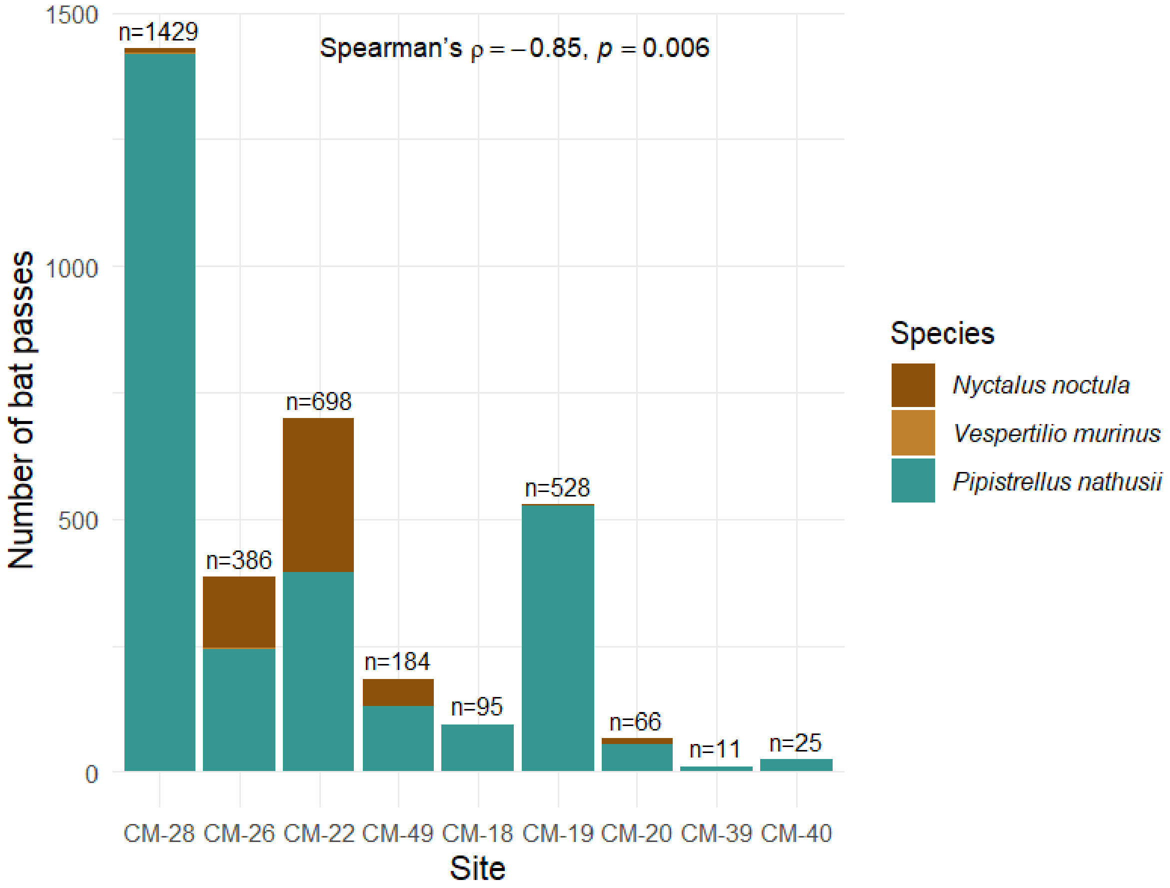

Figure 3.3. *The distribution of activity by three migratory bat species throughout the study period across the nine study sites. Bat passes of Vespertilio murinus were recorded on site CM-28 (n=1) and site CM-26 (n=2). The study sites are arranged from the southernmost (CM-28) on the left to the northernmost (CM-40) on the right.*

Table 3.3. *The distribution of the number of bat passes of Nyctalus noctula and Pipistrellus nathusii across the study sites. The study sites are arranged from the southernmost (CM-28) on the top to the northernmost (CM-40) on the bottom.*

Site	***N. noctula***	***P. nathusii***
CM-40	0	25
CM-39	0	11
CM-20	10	56
CM-19	2	526
CM-18	0	95
CM-49	55	129
CM-22	302	396
CM-26	140	244
CM-28	8	1,420
Sum	**517**	**2,902**

Table 3.4. *Variables explaining the variance in migratory bat (Pipistrellus nathusii and Nyctalus noctula) community composition in the study area. Output from permutational multivariate analysis of variance (PERMANOVA) test based on Bray-Curtis dissimilarity, with 999 free permutations. Eight site-season combinations were dropped from analysis due to zero detections of both species. Seasons (n = 3) were defined as Early Summer (June 27–July 26), Late Summer (July 27–August 31), and Early Autumn (September 1–October 18).*

	Df	***Sum of Squares***	***R^2 (%)***	***F***	***p***
Site	8	2.62	45.5	1.77	*0.035*
Season	2	1.67	28.9	4.51	*0.001*
Residual	8	1.48	25.7		
Total	18	5.78	1.0		

3.3. Seasonal patterns and activity peaks of migratory bats

There was substantial site variation of *P. nathusii* activity throughout the study season (**Figure 3.4**). No activity was recorded in June, and the activity of *P. nathusii* was low across all sites in July, while activity began to increase in late August. *P. nathusii* activity increased substantially in early to mid-September, before decreasing again in late September. Sudden activity peaks (>350 bat passes per night) occurred early to mid-September at sites CM-28 and CM-19. Peak activity nights were significantly different from non-peak nights (W = 38049, p < 0.0001), but the number of bat passes per peak night varied considerably across sites (**Table 3.5**, **Figure 3.5**). The earliest activity peak night occurred September 1st at site CM-40 (n=3), while the latest activity peak night occurred September 19th (n=371) (**Figure 3.6**).

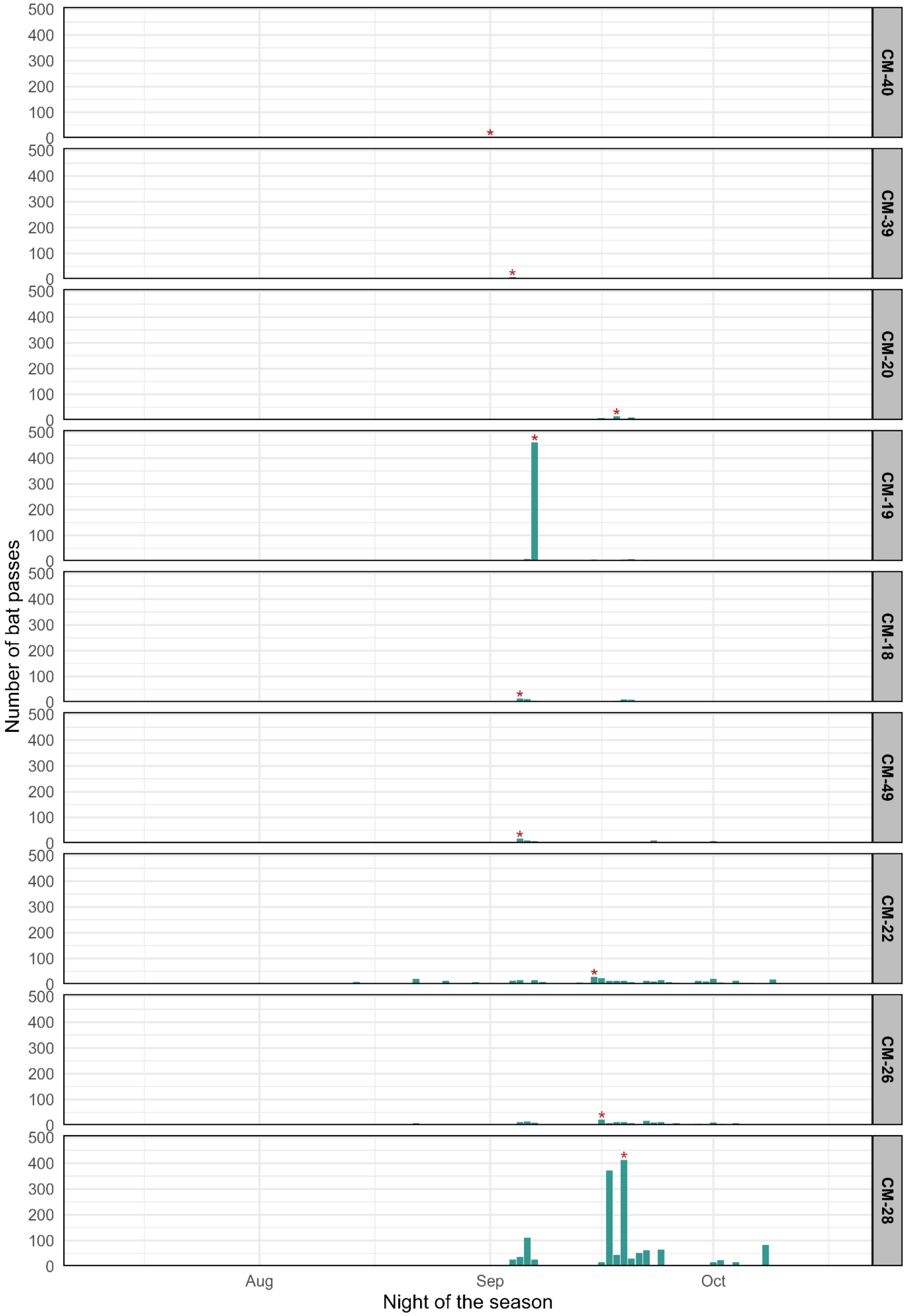

Figure 3.4. *Nightly activity of Pipistrellus nathusii across study sites throughout the study season. Each bar represents one night when the detector was actively recording. Asterisks (*) indicate nights of peak activity (i.e. the highest number of bat passes) calculated per site. Study sites are arranged from the northernmost (CM-40) on top to the southernmost (CM-28) to the bottom.*

Table 3.5. *Nights (dates) of peak activity for migratory bat species across the study sites. Peak activity nights were defined as the night with the maximum number of bat passes for each site. No bat passes of Nyctalus noctula were recorded on site CM-40, CM-39, and CM-18 throughout the study season. The study sites are arranged from the northernmost (CM-40) on the top to the southernmost (CM-28) at the bottom. Date = date (yyyy-mm-dd) of peak activity night per site, Bat pass max = maximum number of bat passes per site.*

	Pipistrellus nathusii		*Nyctalus noctula*	
Site	***Date***	***Bat pass max.***	***Date***	***Bat pass max.***
CM-40	2024-09-01	3	-	-
CM-39	2024-09-04	6	-	-
CM-20	2024-09-18	14	2024-09-13	5
CM-19	2024-09-07	439	2024-09-18	2
CM-18	2024-09-05	13	-	-
CM-49	2024-09-05	15	2024-09-04	25
CM-22	2024-09-15	28	2024-07-11	31
CM-26	2024-09-16	22	2024-07-28	10
CM-28	2024-09-19	371	2024-09-18	2

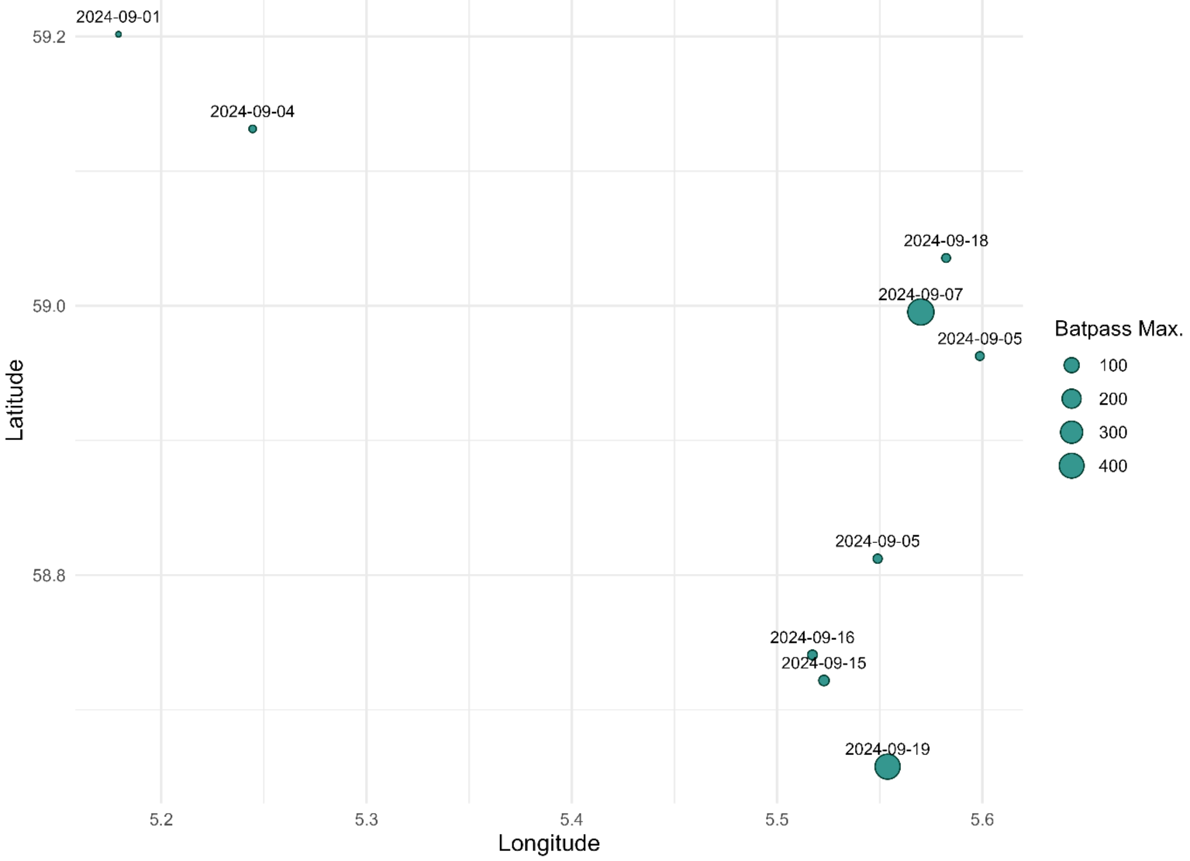

Figure 3.5. *Spatial configuration of the sites and dates of Pipistrellus nathusii peak activity (maximum number of bat passes) for each site. The size of the points represents the number of P. nathusii bat passes on the night of peak activity.*

Statistical analysis confirmed that there was a particular pattern of *P. nathusii* activity throughout the season, where activity increased in late August and peaked mid-September (**Table 3.6**, **Figure 3.6**). After the peak, bat activity decreased, but *P. nathusii* bats remained in the study area until the beginning of October. In addition, there was an apparent effect of latitude, with higher bat activity further south (**Table 3.6**, **Figure 3.6**). There was also evidence of an interaction between the date (night of the year) and latitude, where some sites further north showed an increase in bat activity earlier in the season, but most bat activity was concentrated at the site furthest south (**Figure S.2**).

Table 3.6. *Relationships between spatiotemporal variables and Pipistrellus nathusii activity. Output from a negative binomial generalized additive model (GAM) with log-link function. A smooth term of site was also included as a random effect to account for repeated measures. Analysis of 3644 observations with REML. REML-score = 1537.1, Adjusted* R^2 *= 0.040.*

Variable				
Parametric terms	**Estimate**	**SE**	**z**	***p***
Intercept	-3.48	0.54	-6.51	*<0.0001*
Smooth terms	**edf**	**Ref. df**	**X^2**	***P***
Latitude	1.0	1.0	14.32	*0.00016*
Night of the year	6.02	7.05	136.31	*<0.0001*
Latitude×Night of the year	14.73	20.11	49.50	*0.00028*
Deviance explained:	55.3%			

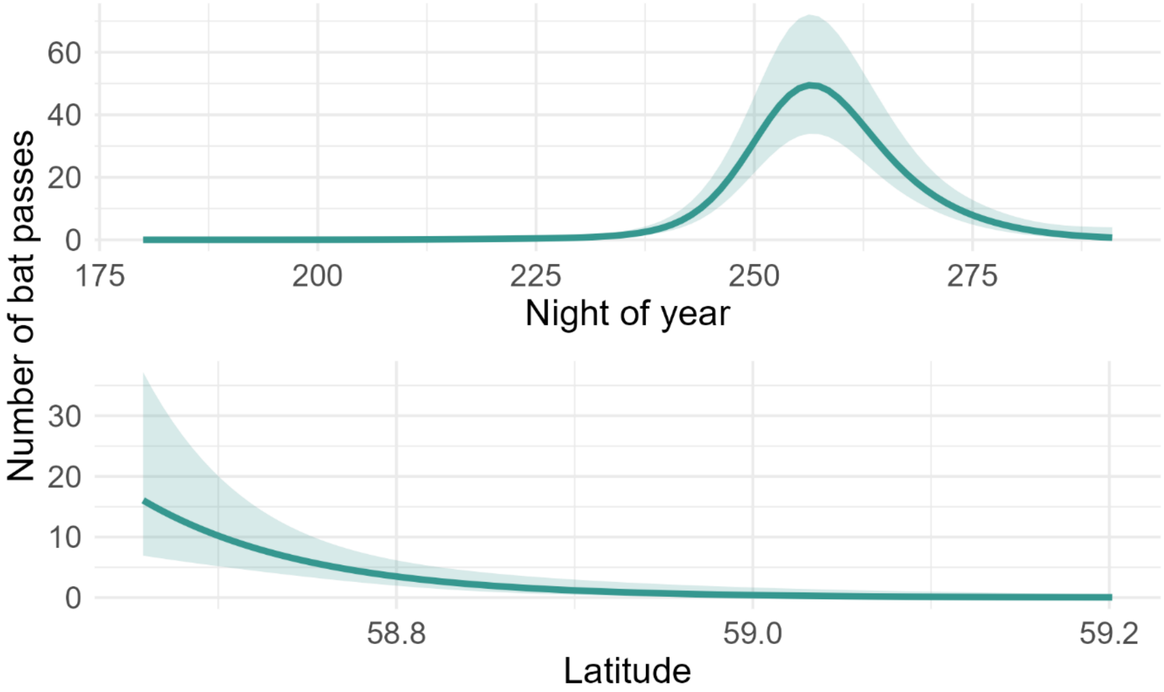

Figure 3.6. *Estimated average number of Pipistrellus nathusii bat passes (green lines), in relation to night of the year and latitude. Latitude values (n=9) were extracted from site coordinates. Night of the year represents day counts from 2024 (n=366), where 175 represents June* 23^{rd} *and 275 represents October* 1^{st}*.*

The activity of *N. noctula* was relatively evenly distributed across the study season, but activity varied considerably between sites (**Figure 3.7**). CM-22 and CM-26 had the highest number of nights with recordings of *N. noctula*, but there were some nights with higher activity in mid-September at site CM-49. Higher activity nights occurred mid-July, early August, and during the first half of September. Peak activity nights ranged from the earliest on July 11th (n=31) to the latest on September 18th (n=2) (**Table 3.5**, **Figure 3.8**). The difference in bat activity between peak nights was significantly different from non-peak nights (W = 20533, p-value = <0.0001), although the maximum number of bat passes was relatively low compared to *P. nathusii* (**Table 3.5**). As *N. noctula* was only observed on six of the study sites with relatively few observations, I did not include *N. noctula* in statistical analysis of spatiotemporal variables because of heavily zero-inflated data.

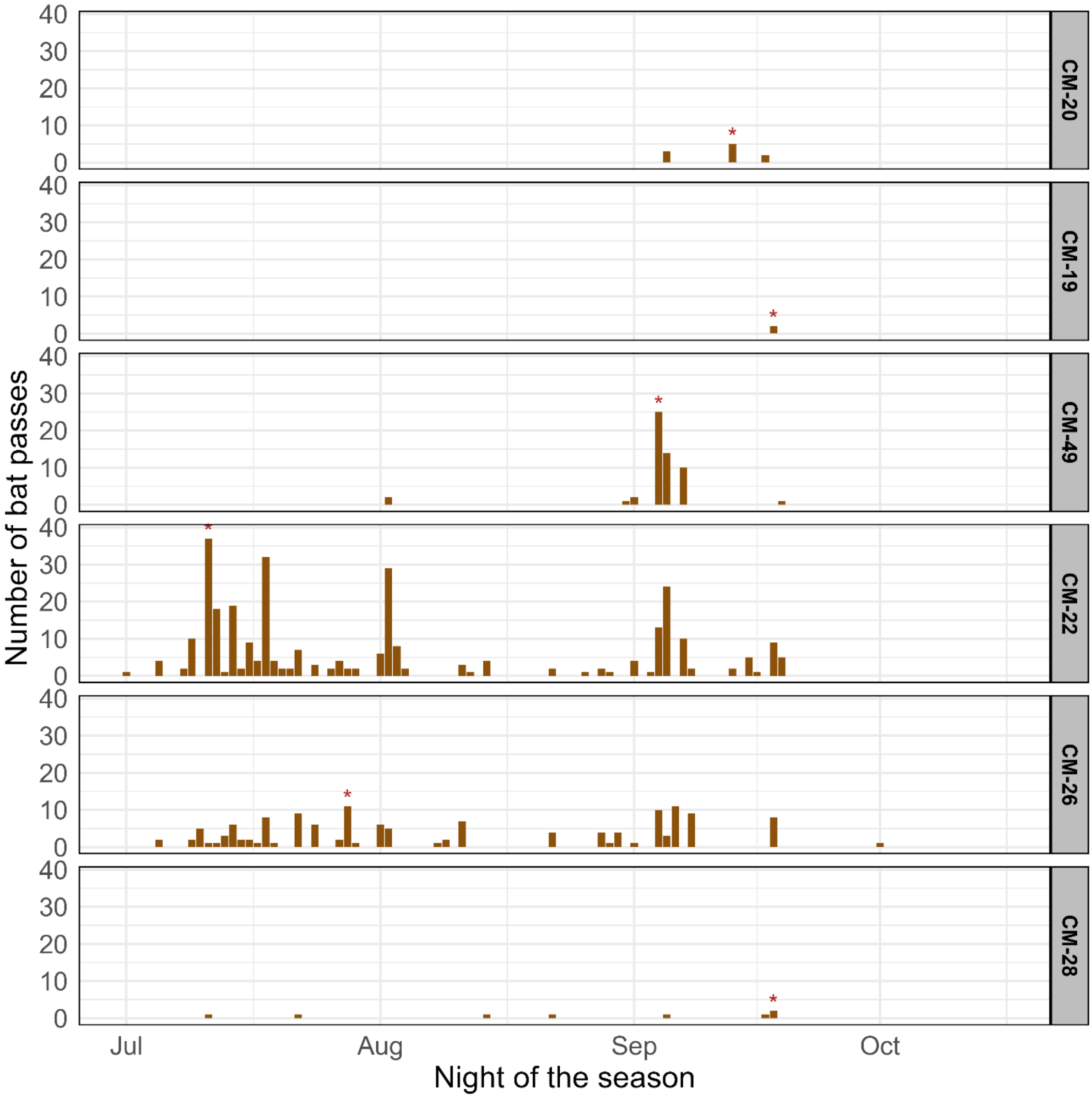

Figure 3.7. *Nightly activity of Nyctalus noctula across study sites throughout the study season. No bat passes of N. noctula were recorded at sites CM-40, CM-39, and CM-18. Each bar represents one night when the detector was actively recording. Asterisks (*) indicate nights of peak activity (i.e. the highest number of bat passes) calculated per site. Study sites are arranged from the northernmost (CM-20) on top, to the southernmost (CM-28) at the bottom.*

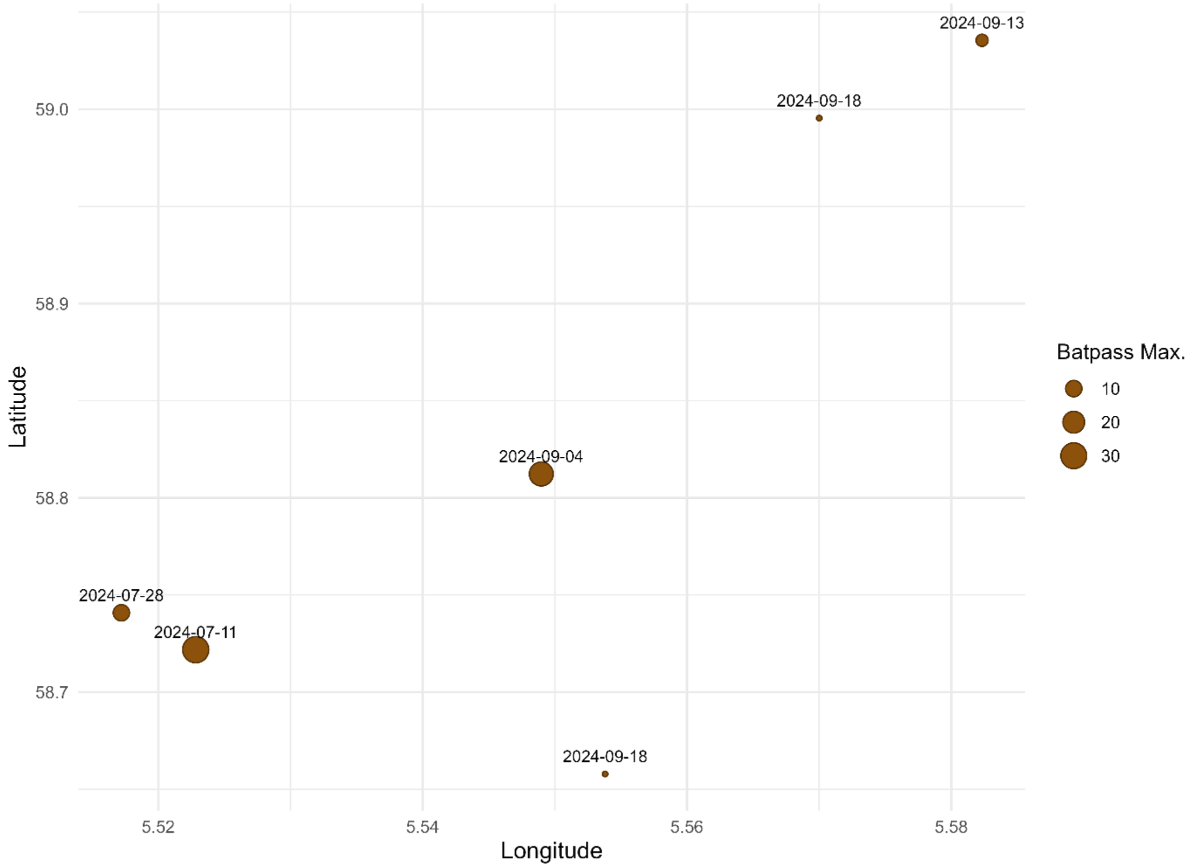

Figure 3.8. *Spatial configuration of the sites and dates of Nyctalus noctula peak activity (maximum number of bat passes) for each site. The size of the points represents the number of N. noctula bat passes on the night of peak activity. The spatial configuration of site points is at another scale from **Figure 3.5** as sites without N. noctula activity are excluded.*

3.4. Seasonal patterns in behavior

For *P. nathusii*, I found that most activity was detected in September (**Figure 3.9**). The majority of bat passes were commuting passes, with the highest number of commuting passes distributed within the period of peak activity. A relatively high number of commuting passes were also recorded later in the season (late September-early October). The number of feeding passes was considerably lower than commuting passes, but there was clear evidence of *P. nathusii* foraging both within and after the peak activity period. Social and territorial behavior observations were relatively rare, but all were recorded in August or September.

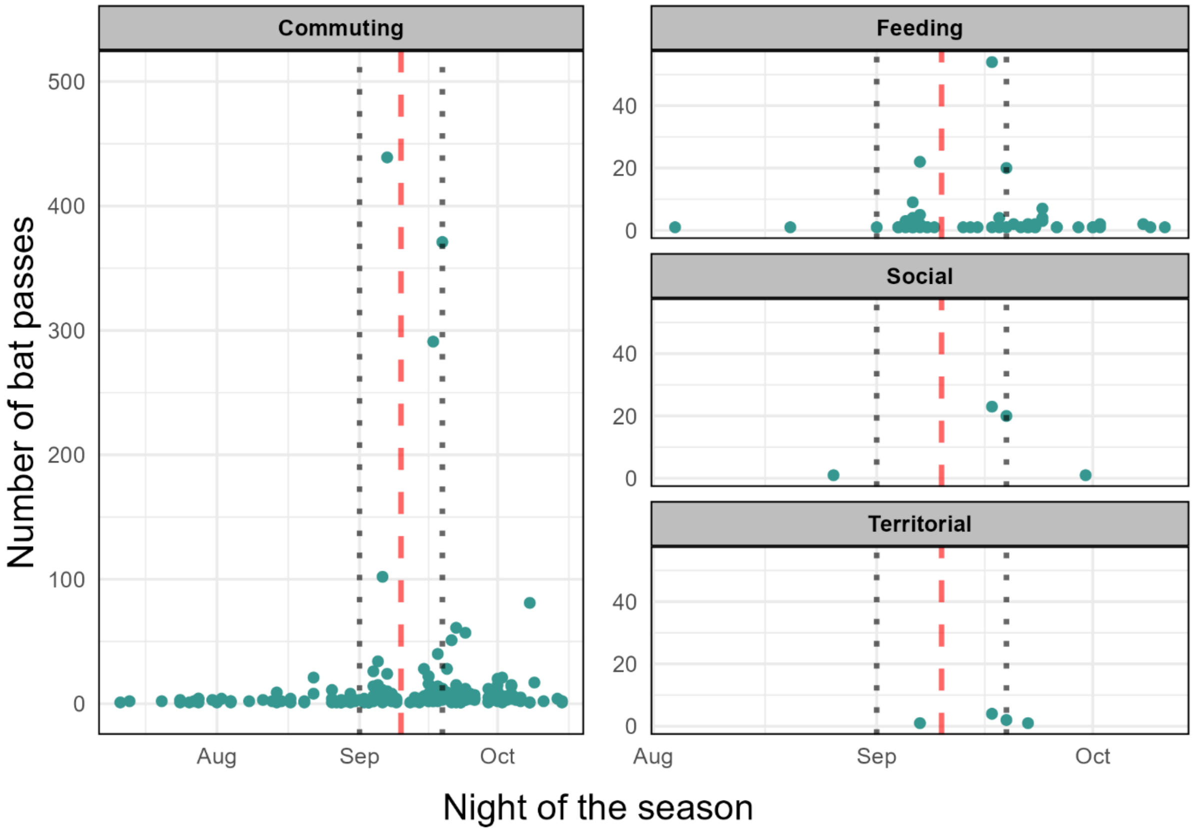

Figure 3.9. *Different behaviors of Pipistrellus nathusii throughout the season. Commuting: bat passes containing only navigational echolocation pulses (n = 2663), Feeding: bat passes containing at least one feeding buzz (n =186), Social: bat passes containing at least one social call (n = 45), Territorial: bat passes containing at least one territorial song flight call (n = 8). The red dashed line marks the average of activity peak nights across all sites, dotted black lines marks the earliest and latest peak nights.*

The overall activity of *N. noctula* was lower than *P. nathusii*, but observations were recorded earlier in the summer and were more evenly spread throughout the season (**Figure 3.10**). The highest number of *N. noctula* commuting passes was recorded in mid-July and early September. Few feeding buzzes were observed, but feeding activity coincided with the highest number of commuting passes at the earliest peak night and close to the average peak night. Only one social call was recorded in mid-September, and no territorial calls were recorded.

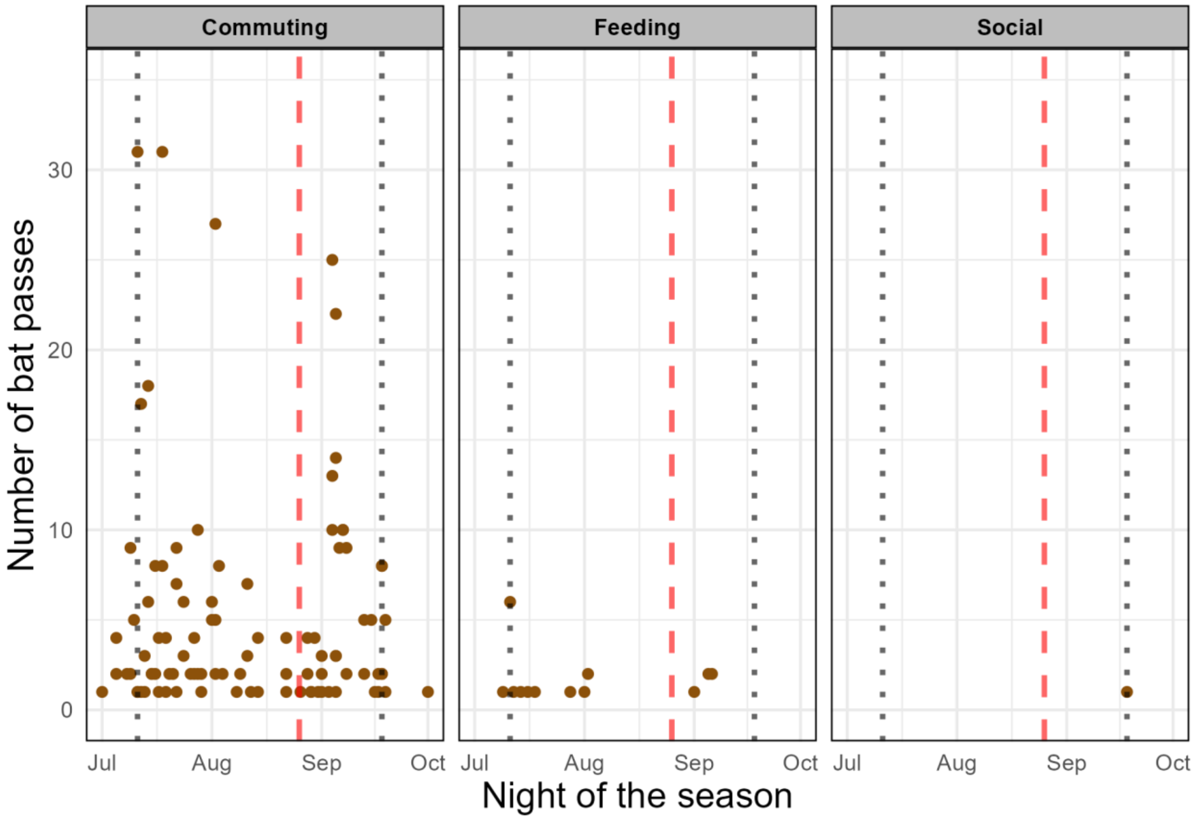

***Figure 3.10**. Different behaviors of Nyctalus noctula throughout the season. Commuting: bat passes containing only navigational echolocation pulses (n = 496), Feeding: bat passes containing at least one feeding buzz (n = 20), Social: bat passes containing at least one social call (n = 1). The red dashed line marks the average of activity peak nights across all sites, dotted black lines marks the earliest and latest peak nights.*

3.5. Influence of weather conditions on bat activity and migration

To investigate the influence of weather conditions on migratory bat activity, I focused on *P. nathusii* activity within the peak activity period (**Figure 3.11**). My rationale for focusing on the period with high overall activity is to increase the chances of detecting any influence of weather on bat activity. In other parts of the season, the overall activity of *P. nathusii* was low, irrespective of weather conditions.

I did not carry out statistical analyses of the influence of environmental conditions on *N. noctula* because of few observations and heavily zero-inflated data. The activity of *N. noctula* was therefore investigated only with exploratory analysis (see **Figure S.3-S.5**).

P. nathusii activity was mostly restricted to nights with less than 5mm of precipitation, except for a few nights during early autumn with some bat activity where precipitation was above 5 mm (**Figure S.3**). As *P. nathusii* activity was low on rainy nights and most activity occurred on nights with no rain, a subset of nights with less than 5 mm precipitation was used for further analysis and precipitation not included as explanatory variable in the models going forward (**Figure 3.11**).

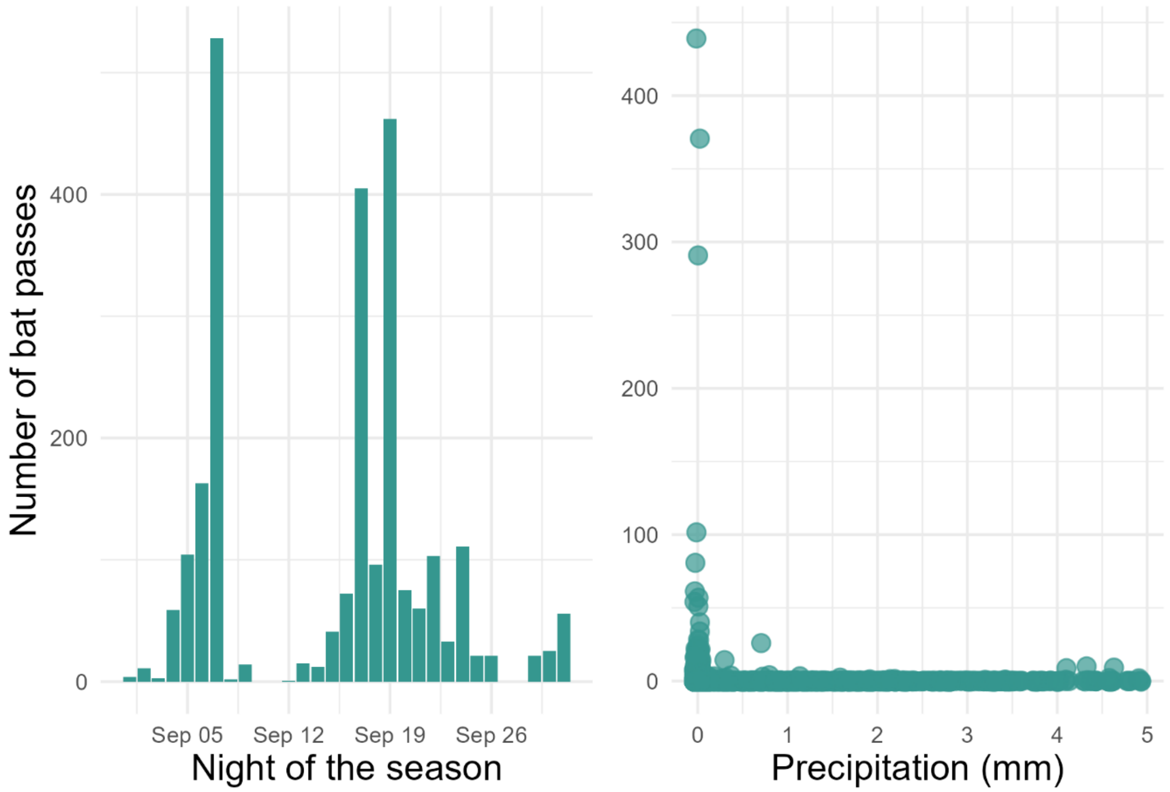

Figure 3.11. *Subset of Pipistrellus nathusii bat passes used in analysis of the influence of weather conditions on P. nathusii activity.*

The correlation between air temperature and wind speed was weak (Pearson's *r* = -0.11), and these were therefore included as explanatory variables in the same model. Wind direction was transformed from numeric (0-360°) to categorical values (north, west, south, east), and Kruskal-Wallis tests were used to test for multicollinearity with wind speed and temperature. The average temperature did not change considerably among wind directions (~1.05°C); temperature and wind direction were therefore included as explanatory variables in the same model. But the average wind speed varied considerably (3.00 to 6.94 m/s) across the categories of wind direction and was not used in the initial model with wind direction.

3.5.1. Wind speed and temperature

I found a significant negative influence of wind speed on *P. nathusii* presence, and the probability of bat activity was considerably lower in wind speeds above 7 m/s compared to lower wind speeds (**Table 3.7, Figure 3.12**). *P. nathusii* bats were more active during nights with higher temperatures (**Table 3.7, Figure 3.13**). There was moderate variation between sites, but night-to-night variation within sites was minimal (**Table 3.7**).

Table 3.7. *Analysis of the influence of variables on the probability of Pipistrellus nathusii activity. Output from binomial generalized linear mixed model (GLMM) with a logit-link function. Night nested within site and Site was added as random effects to account for night-to-night variation within sites and among-site variation. Analysis of 1068 observations at nine sites, with 267 night-to-night within site combinations.*

Variable	**Estimate**	**Std. Error**	**z**	***p***
Fixed effects				
Intercept	-2.006	0.438	-4.582	*<0.0001*
Wind speed	-0.260	0.046	-5.650	*<0.0001*
Temperature	0.096	0.025	3.799	*0.00015*
Random effects	**Variance**	**St.Dev**		
Night nested within Site	2.99×10^{-9}	5.47×10^{-5}		
Site	0.496	0.705		

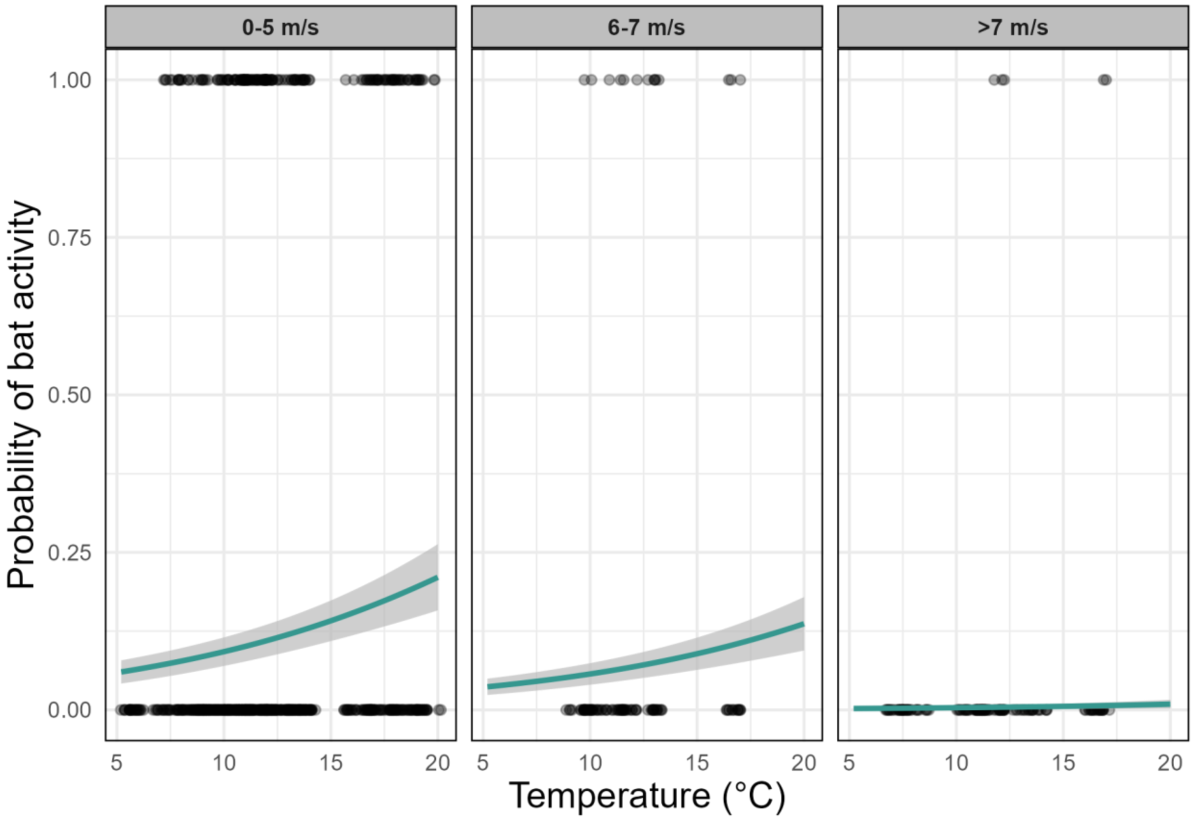

Figure 3.12. *Estimated average probability (green line) of Pipistrellus nathusii activity as a function of temperature (°C) at three levels of wind speed (m/s). The grey shaded polygon represents 95% confidence limits. Points where y = 1 are nights where P. nathusii bats were active, and points where y = 0 are nights where no P. nathusii bats were recorded.*

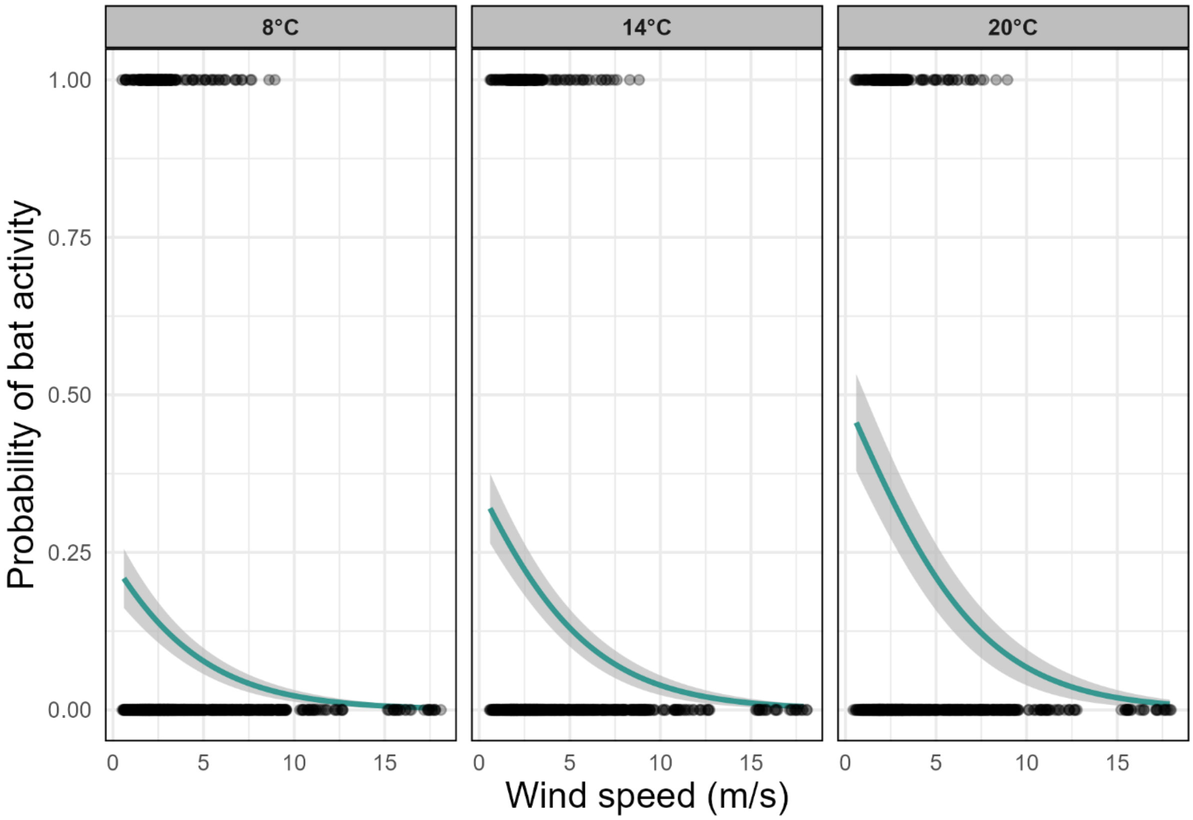

Figure 3.13. *Estimated average probability (green line) of Pipistrellus nathusii activity as a function of wind speed (m/s) at three levels of temperature (°C). The grey shaded polygon represents 95% confidence limits. Points where y = 1 are nights where P. nathusii bats were active, and points where y = 0 are nights where no P. nathusii bats were recorded.*

3.5.2. Wind direction and temperature

I found evidence of increased probability of *P. nathusii* activity at northern and eastern wind directions (**Table 3.8**, **Figure 3.14**), while bats were less likely to be active at southern or western wind directions. Higher temperatures also increased the likelihood of *P. nathusii* being active (**Table 3.8**, **Figure 3.14**). The random variation between sites was modest, while there was minimal night-to-night variation within sites (**Table 3.8**).

Table 3.8. *Analysis of the influence of variables on Pipistrellus nathusii presence. Output from binomial generalized linear mixed model (GLMM) with a logit-link function. Wind direction west (W) is reference level. Night nested within site and Site was added as random effects to account for night-to-night variation within sites and among-site variation. Analysis of 1068 observations at nine sites, with 267 night-to-night within site combinations.*

Variable	**Estimate**	**Std. Error**	**z**	***p***
Fixed effects				
Intercept	*-3.831*	*0.465*	*-8.238*	*<0.0001*
Wind direction (N)	*1.074*	*0.297*	*3.611*	*0.00031*
Wind direction (E)	*0.900*	*0.301*	*2.987*	*0.00282*
Wind direction (S)	0.304	0.379	0.801	0.42312
Temperature	*0.109*	*0.025*	*4.377*	*<0.0001*
Random effects	**Variance**	**St.Dev**		
Night nested within Site	5.24×10^{-9}	7.24×10^{-5}		
Site	0.424	0.665		

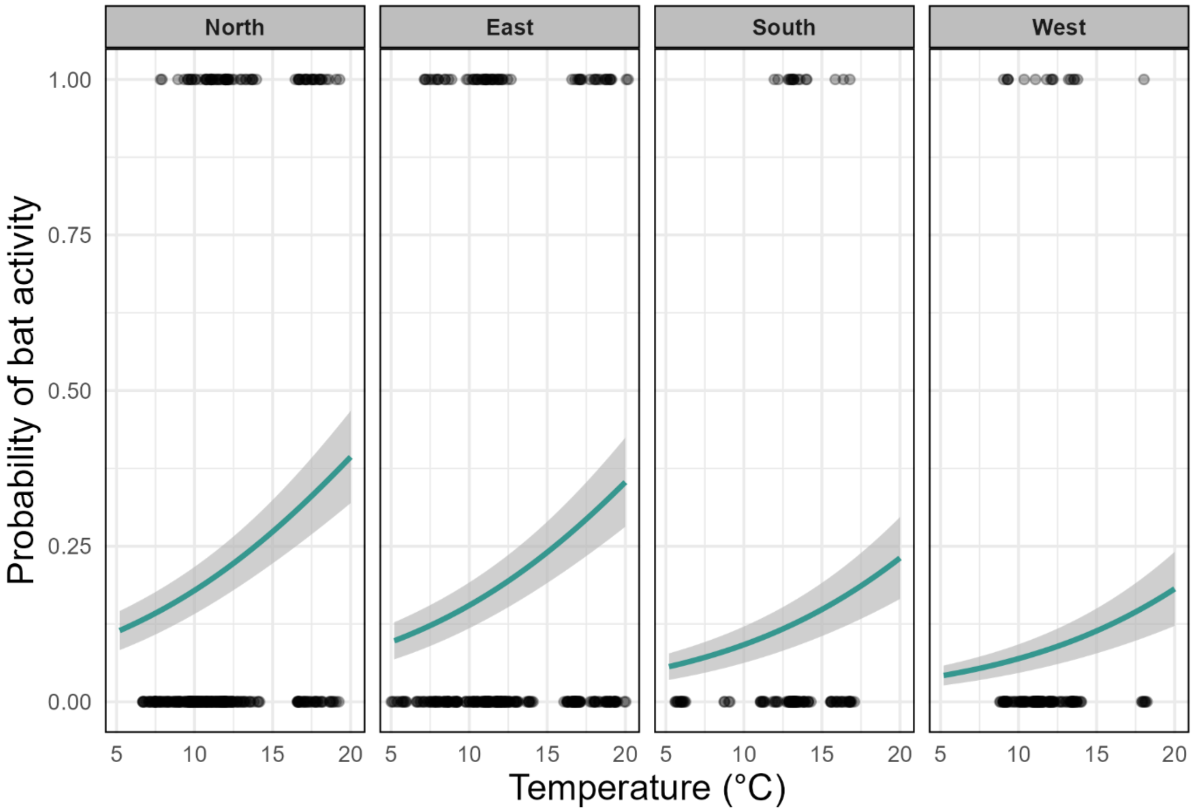

Figure 3.14. *Estimated average probability (green line) of Pipistrellus nathusii presence as a function of temperature (°C) at different wind directions. The grey shaded polygon represents 95% confidence limits. Points where y = 1 are nights where P. nathusii bats were active, and points where y = 0 are nights where no P. nathusii bats were recorded.*

When I used the number of *P. nathusii* bat passes rather than bats' presence or absence as the response variable, I found that bats were significantly more active at northern and eastern wind directions and temperatures over 10 °C (**Table 3.9**, **Figure 3.15**). Night-to-night variation was moderate, but variation between sites explained more of the random variation in bat activity (**Table 3.9**).

Table 3.9. *Analysis of the influence of variables on Pipistrellus nathusii bat passes. Output from negative binomial generalized linear mixed model (GLMM) with a logit-link function. Wind direction west (W) is reference level. Night nested within site and Site was added as random effects to account for night-to-night variation within sites and among-site variation. Analysis of 1068 observations at nine sites, with 267 night-to-night within site combinations.*

Variable	**Estimate**	**Std. Error**	**z**	***p***
Fixed effects				
Intercept	-3.644	0.775	-4.702	*<0.0001*
Wind direction (N)	1.651	0.429	3.851	*0.00012*
Wind direction (E)	1.133	0.424	2.671	*0.00757*
Wind direction (S)	0.666	0.549	1.214	0.22484
Temperature	0.181	0.045	4.014	*<0.0001*
Random effects	**Variance**	**St.Dev**		
Night nested within Site	0.269	0.518		
Site	1.517	1.232		

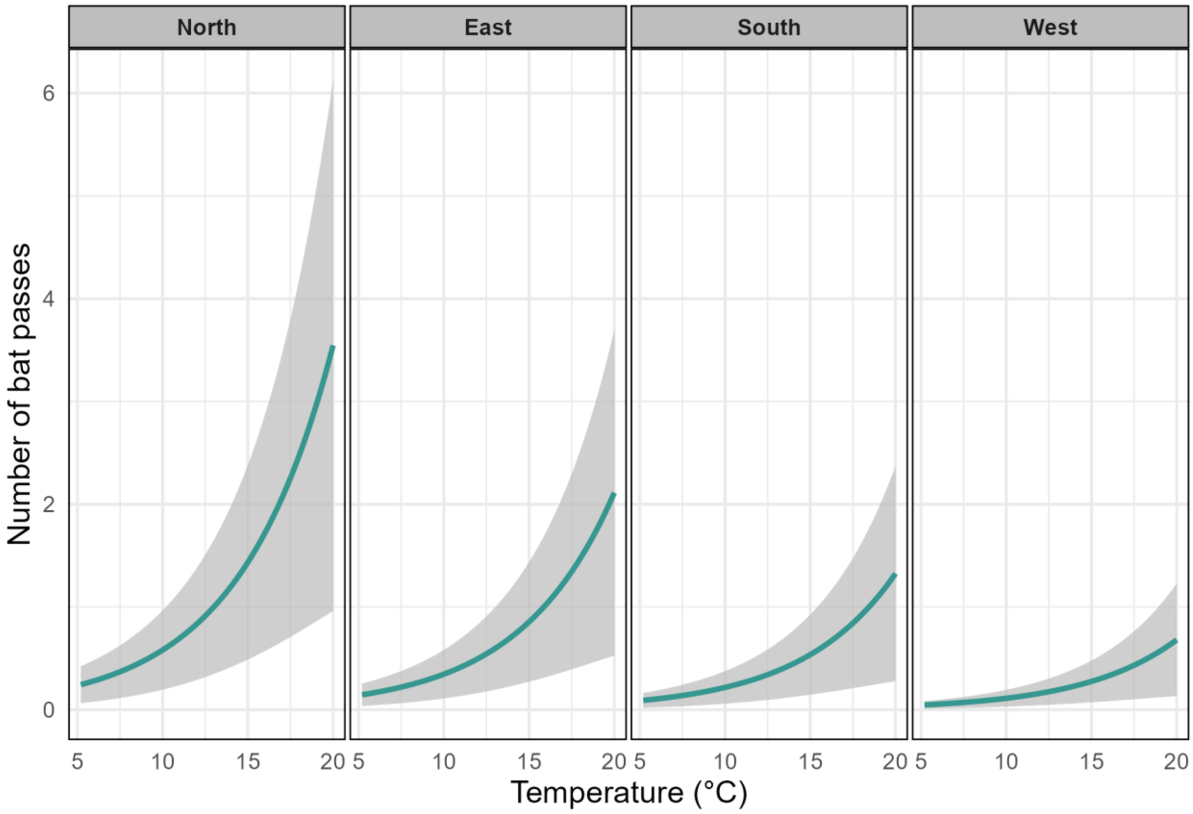

Figure 3.15. *Predicted number of Pipistrellus nathusii bat passes (green line) as a function of temperature (°C) at different wind directions. The grey shaded polygon represents 95% confidence limits. Points where y = 1 are nights where P. nathusii bats were active, and points where y = 0 are nights where no P. nathusii bats were recorded.*

3.5.3. Wind speed and temperature at northern wind directions

Further analysis with only northerly winds showed that *P. nathusii* were most active at wind speeds between 2-3 m/s, while bat activity decreased substantially at increasing wind speeds (**Table 3.10**, **Figure 3.16**). Average bat activity increase with temperature (**Table 3.10**).

Table 3.10. *Relationships between Pipistrellus nathusii activity, wind speed and temperature at northern wind directions. Output from a negative binomial generalized additive model (GAM) with a log-link function. Model predictions were limited to wind speeds between 0.6 and 7 m/s to avoid extrapolation and to represent the observed range of bat activity. Random effects from site and night were excluded from the model, due to the introduction of residual issues. Analysis of 392 observations. Adjusted* R^2 *= 0.00392, REML-score = 474.31, Scale estimate = 1.*

Variable				
Parametric terms	**Estimate**	**SE**	**z**	***p***
(Intercept)	0.08188	0.53526	0.153	0.878
Smooth terms	**edf**	**Ref. df**	**X^2**	***p***
Wind speed	3.405	4.276	22.447	*0.00023*
Temperature	2.853	3.566	6.344	0.14083
Deviance explained:	25.4%			

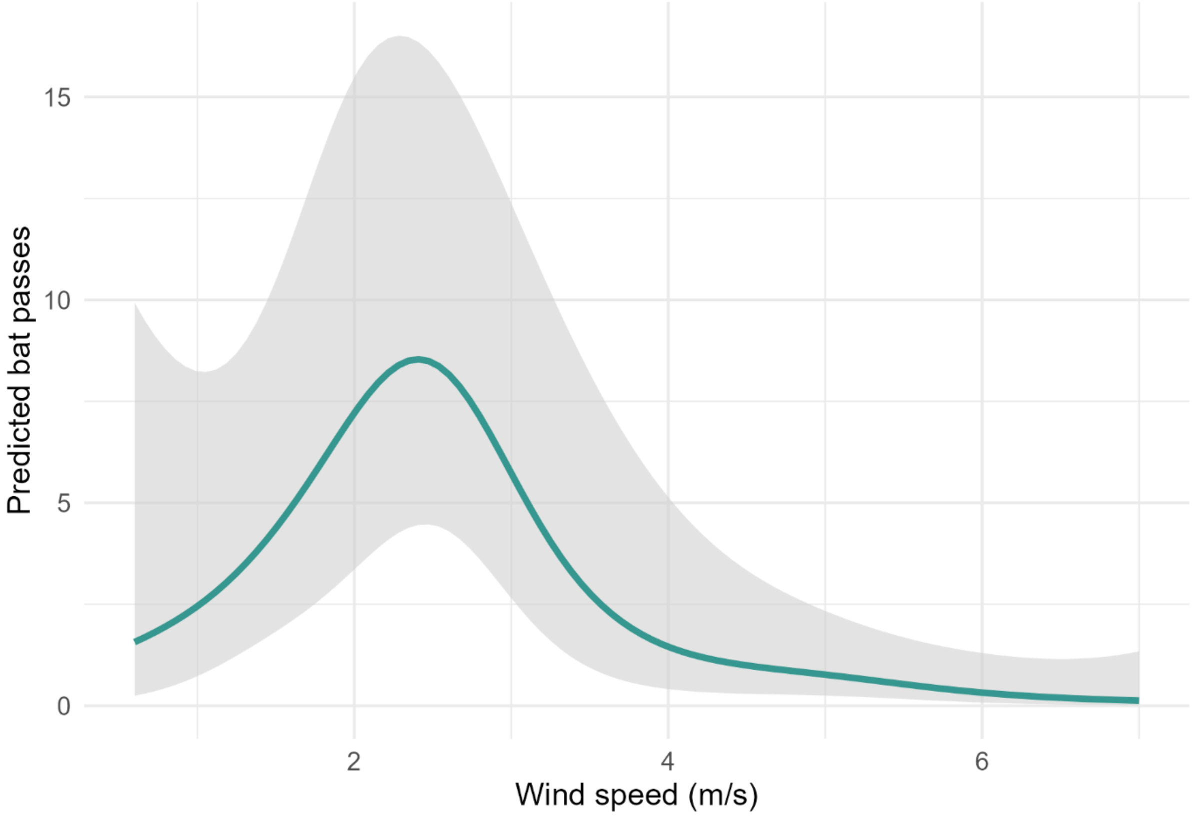

Figure 3.16. *Estimated average number of Pipistrellus nathusii bat passes (green line) in relation to wind speed (m/s) at average temperature and northern wind directions. The grey shaded polygon represents 95% confidence limits.*

4. Discussion

4.1. Main findings

In my findings, both migratory and sedentary taxa showed clear variation in overall activity across different sites. Detections mainly consisted of aerial-hawking bat species, both migratory and sedentary, which aligned with my predictions. The differences in community composition were explained mainly by site and by seasonality. Notably, *P. nathusii* was one of the most common taxa along the coast and was the most frequently observed migratory species. As I predicted, *P. nathusii* displayed distinct seasonal activity patterns, peaking in early to mid-September. In contrast, the activity of *N. noctula* was more evenly distributed throughout the season, with notable peaks occurring in July and mid-September. While peak activity nights varied between sites for both species, *P. nathusii* showed more synchronized timing of its peaks. Bat feeding behavior generally coincided with the peak activity periods of both species, which was anticipated; however, *P. nathusii* continued to forage by the coast later in the autumn. Interestingly, *N. noctula* foraged more frequently along the coast in July than expected. Finally, I found that the presence of *P. nathusii* during the migration period was positively correlated with high temperatures, low wind speeds, and north-easterly winds, consistent with my predictions. Notably, *P. nathusii* activity increased most significantly at northern wind directions during the autumn, suggesting that these bats may utilize tailwinds to aid a southward journey.

4.2. Activity of migratory and resident bats across the study sites

I found that the overall bat activity varied considerably among sites, with higher activity recorded at southern locations. As expected in the open coastal landscape, most bat taxa recorded consisted of open- and edge-space foraging bats such as *Pipistrellus*, *Eptesicus*, and *Nyctalus* spp. The spatial differences in bat activity are unlikely to be explained by latitude, given the relatively short distances between sites and the presence of observed species in more northern regions of Norway (Artsobservasjoner, 2025). For instance, site CM-18 exhibited relatively low activity, despite its proximity to known bat habitats such as Litle Stokkavatnet and Mosvatnet. This suggests that local habitat suitability may better explain site variation than location in relation to latitude.

The southernmost sites, which showed the highest bat activity, were located in coastal grass dunes near nutrient-rich lakes and wetlands, key foraging habitats for many bat species (Wilson & Mittermeier, 2019). In contrast, the more northern sites were characterized by rockier terrain, dense urban and residential infrastructure, and intensively managed agricultural land, factors that likely reduce their suitability as bat habitats (Jung & Threlfall, 2016; Williams-Guillén et al., 2016).

My findings also indicated significant variation in community composition among sites and across the seasons. Similar to overall activity, these site differences are likely to be driven primarily by habitat suitability rather than latitude. Seasonal changes were likely influenced by the arrival of migratory species in late summer and autumn, and possibly by shifts in habitat use by resident bats. Several studies in Scandinavia have documented seasonal changes of bat activity in coastal areas, higher activity in late summer and autumn (Ahlén et al., 2007, 2009; Bach et al., 2015). Both migratory and sedentary bats have been observed feeding at sea on insects and crustaceans on the ocean's surface (Ahlén et al., 2009; Boshamer & Bekker, 2008). The availability of these resources is likely affected by wind and ocean currents, which affect food abundance over space and time (Ahlén et al., 2009). Additionally, Ahlén et al. (2007) suggested that the increase of activity later in the season could be related to the timing of volancy, where mothers likely forage closer to maternity colonies early in the summer when pups are most dependent. Later in the summer, these bats may extend their foraging trips as the pups become volant and more independent (Ahlén et al., 2007). However, I did not investigate the seasonal variation of sedentary bat species or food resources along the coast, but this remains an interesting avenue for future research.

The most frequently detected species were *P. pygmaeus*, *E. nilssonii*, and *P. nathusii*. This was expected, as *P. pygmaeus* and *E. nilssonii* are considered some of the most common bats in Norway (Eldegard et al., 2021b, 2021a). While *P. nathusii,* is considered relatively rare throughout Norway, it has been regularly observed along coastlines and valleys during late summer and early autumn (Artsdatabanken, 2025b; Eldegard et al., 2021d). Observations of *N. noctula* were few, which was also anticipated, as this species is quite rare in Norway and can be challenging to differentiate acoustically from *V. murinus* (Russ, 2021). Since I manually analyzed only a subset of recordings, some activity from non-target taxa (like *E. nilssonii*, *Myotis* spp.) may have gone undetected. Nonetheless, *E. nilssonii* was one of the most commonly occurring species in the study area, indicating its abundance and regular presence along the coast.

Surprisingly, I detected species typically associated with forest interiors, such as *P. auritus* and *Myotis* spp., in these open coastal areas. While I did not expect to find them in this landscape, other studies have made observations of *P. auritus* and *Myotis* spp. at sea previously, including *Myotis daubentonii* and *Myotis dasycneme*, (Ahlén et al., 2009; Boshamer & Bekker, 2008). Although I did not identify *Myotis* spp. to the species level during acoustic analysis, I suspect my observations were most likely of *M. daubentonii,* as other studies indicate that they frequently forage along coastlines and archipelagos (Ahlén et al., 2007, 2009).

4.3. Seasonal patterns and activity peaks of migratory bats

The seasonal activity patterns of migratory bats clearly differed between the species. While the temporal activity patterns and sudden activity peaks of *P. nathusii* could indicate migratory behavior, the activity of *N. noctula* was less interpretable as migratory activity. As there were fewer observations of *N. noctula* overall and the species was not present at all sites, no statistical analysis was done on its seasonal and spatial activity patterns.

I found that *P. nathusii* was predominantly absent in coastal areas during the summer months, but a substantial increase in activity was observed in September. As this aligns with the species' typical migration period, I interpret this as indicative of migratory behavior. There was a clear seasonal influence on *P. nathusii* activity patterns, indicating that the species migrates along the coast of Norway between late August and mid-October. The activity of *P. nathusii* began to increase in late August, followed by activity peaks in September. Bats continued to be active along the coast in October, which could be individuals migrating later in the season. A significant activity peak for bats was observed further north in early September, followed by later observations further south. This pattern may suggest that bats are moving in a north-south direction, aligning with my expectations during active migration periods and the general direction of travel of *P. nathusii* during autumn migration (Russ, 2023). In other countries, the autumn migration period of *P. nathusii* follows the same temporal pattern as I've observed: bats initiate migration in mid-August, migratory activity peaks in mid-September, and continues to October (Bach et al., 2015; Fritzén, 2015; Lagerveld et al., 2021, 2023). The similarity of these patterns highly suggests that the seasonal activity pattern observed in my study represents migration. The sudden peaks of high activity could be interpreted as groups of individuals who travel together, as *P. nathusii* have often been reported to fly in large groups along shorelines during migration (Ahlén, 1997; Gerell & Lundberg, 2018). I encountered *P. nathusii* bat passes that included several individuals during manual acoustic analysis. However, as I did not keep records of the number of individuals in each recording, I cannot be certain of whether these peaks originate from one, a few, or a group of individuals.

While a few observations in Rogaland indicate that some individuals occur in the area during summer, this is a relatively rare occurrence in Norway (Artsdatabanken, 2025b). So far, no maternity colonies have been found within Norway (Eldegard et al., 2021b), suggesting that the high autumn activity originates mostly from individuals migrating from other parts of Scandinavia. The summer breeding areas of *P. nathusii* are mainly located in the northeastern parts of Europe, stretching out to Russia (Russ, 2023). In the autumn, many individuals migrate from Finland to Sweden, following the Swedish coastline to later cross the Baltic Sea (Fritzén, 2015; Ijäs et al., 2017; Kurvits et al., 2011). Some of these bats might choose a different route, as two radio-tagged individuals have been detected by Motus stations in southern Norway (Hellström, 2025). Additionally, observations of *P. nathusii* along valleys in mid-Norway suggest a potential migratory corridor through the mainland of Sweden and Norway (T. Michaelsen, personal communication; Eldegard et al., 2021d). However, it remains unclear which routes the bats from Finland have taken to reach southern Norway, and whether they travelled through the mountains or not. Further investigation of the spatial movements of *P. nathusii* in Norway and other Scandinavian countries is needed to identify specific migratory routes.

Although *N. noctula* was active along the coast in September, where migratory activity would be expected, *N. noctula* was also active during the summer. Nights of peak activity were significantly different from non-peak nights (W = 20533, p-value = <0.0001), but with much fewer observations than for *P. nathusii*. However, the peaks of activity in September, followed by an absence of activity in October, could indicate migratory behavior of *N. noctula* in this area. Similar seasonal activity patterns have been observed in coastal areas of southern Sweden, with activity both during summer and the autumn migration (Ahlén et al., 2009; Bach et al., 2015). Coastal activity may be bats seeking foraging opportunities along the coast and out at sea, a behavior observed in both migratory and sedentary bats in Sweden (Ahlén et al., 2009). The coastal activity of *N. noctula* in July could also be males searching for territories adjacent to migratory routes along the coast. Petit & Mayer (2000) proposed that *N. noctula* males could be dispersing to migratory routes earlier in the summer to establish territories and gain a reproductive advantage as females initiate migration. However, the low number of observations and the seasonal distribution of activity make it challenging to conclude on the migratory status of *N. noctula* based purely on acoustics. Nonetheless, documenting the presence of this rare and endangered species in this area is notable, as few observations of *N. noctula* have been registered in Rogaland previously (Artsdatabanken, 2025a).

There is also a possibility that the coastal movements of these bats during the autumn reflect regional movements to hibernation areas within Norway. *P. nathusii* and *N. noctula* usually hibernate in roosts above ground, such as tree holes, rock crevices, and buildings (López-Baucells & Burgin, 2019). The preference to roost above ground is considered the primary driver of migratory behavior in these species, as they provide little protection against temperature fluctuations (Fleming et al., 2003; Popa-Lisseanu & Voigt, 2009). However, none of the species has been firmly confirmed to overwinter in Norway so far (Eldegard et al., 2021c, 2021d). Hibernating individuals (*N. noctula*) or winter activity (*P. nathusii*) have been documented in southern Sweden and Finland, respectively (Ahlén, 2011; Blomberg et al., 2021; Lindecke et al., 2020). Fleming et al. (2003) state that *N. noctula* and *P. nathusii* primarily hibernate in areas where average winter temperature remains above 0°C, and travel from breeding areas where minimum temperatures drop below -10°C. The Norwegian southwest coastal areas experience significantly milder winter temperatures than other regions of Norway (**SOURCE**), and in theory, the climatic conditions could support the hibernation requirements of these species. Bats may also find suitable hibernation roosts in urban areas, as heated buildings can provide a more stable roost temperature throughout the winter (Sachanowicz et al., 2019). This makes it reasonable to suggest that some individuals may be hibernating in Norway's more temperate coastal areas. Additionally, due to climate change, temperatures are increasing, and winters are getting shorter; shifts or expansions in the hibernation range of these species are expected (Kravchenko et al., 2025).

However, the regular observations of *P. nathusii* in the North Sea and remote islands (Eldegard et al., 2021d; Petersen et al., 2014) strongly suggest that at least some individuals of this species cross the North Sea, migrating from Norway. While individuals of *N. noctula* have also been observed in these areas, *N. noctula* appear to be rarer in the Norwegian North Sea and northern British Isles than *P. nathusii* (Petersen et al., 2014). Both of these species may be partially migratory in Norway, but *P. nathusii* appears to be a more prominent migrant in coastal Norway and the northern North Sea.

4.4. Seasonal patterns in behavior

My findings of behavioral patterns offer further insights into the behavior of migratory bats throughout the season. I found that *P. nathusii* primarily foraged along the coast during the migration period in September, continuing well into October, with very few feeding buzzes recorded earlier in the summer. This was in line with my predictions regarding behavior during migration. In contrast, *N. noctula* was observed feeding in coastal areas throughout the season, although few feeding buzzes were recorded for this species. My findings indicate that *P. nathusii* mainly forage along the coast during the autumn, while *N. noctula* forage by the coast continuously throughout the season. During the breeding season, both species are typically associated with terrestrial habitats, such as wetlands, lakes, and meadows, mostly in forested landscapes (Lindecke et al., 2020; Russ, 2023). However, migratory bats commonly follow coastlines during migration and may opportunistically forage in alternative habitats along their travels (Krüger et al., 2014; Šuba et al., 2012). Krüger et al. (2014) discovered that the diet of *P. nathusii* differed slightly between breeding and migrant individuals, and proposed that a shift in foraging habitat might be the reason. Other studies have found that *N. noctula* take regular foraging trips at the coast and out at sea, not only during migration, but also throughout the summer (Ahlén et al., 2007, 2009; Bach et al., 2015).

Although I did not investigate the spatial distribution of behavioral observations, I suspect that most observed feeding calls originate from sites near the coastal dunes at Jæren, where most bat activity was recorded. The vegetated dunes likely provide food resources, as *P. nathusii* forage in a similar habitat during migration along the Baltic coast (Šuba et al., 2012). Additionally, kelp and seaweed regularly get washed ashore and accumulate at these beaches, which are typically rich with insects that can be attractive to foraging bats. Large groups of *P. nathusii* bats have previously been observed above these kelp wracks in the autumn, likely feeding on kelp flies (Coelopidae) (E. Nyfors, personal communication). Collective feeding during the autumn migration period has also been observed in Sweden (Gerell & Lundberg, 2018). However, foraging behavior in coastal areas is not exclusive to migrants, as several studies in southern Sweden have observed both migratory and sedentary species feeding along the coast and at sea (Ahlén, 1997; Ahlén et al., 2007, 2009). Ahlén et al. (2007) noted that insects and other invertebrates were locally abundant during calm weather in coastal areas, attracting several species of foraging bats.

Similar dynamics between insect abundance, weather conditions, and bat activity are likely to occur in coastal Norway, but further investigation on food availability along the coast is needed to confirm.

I found relatively few social and territorial calls overall, although such behaviors were notable for *P. nathusii*. Observations of social and territorial calls indicate that there are several individuals present, most likely interacting with conspecifics. The territorial mating calls of *P. nathusii* are particularly noteworthy, as they confirm that mating is occurring in this region. In addition to acoustic observations, the field crew observed two females roosting with a male in a bat box at Litle Stokkavatnet in mid-September, which is located near my coastal study sites (Artsdatabanken, 2025b). I only detected territorial calls in September, which aligns with the typical mating display of *P. nathusii* males during migration (López-Baucells, 2019; Russ, 2023). The mating period of *P. nathusii* coincides with the autumn migration period, where males defend territories along routes that migrating females traverse (McKracken & Wilkinson, 2020, as cited in Fleming, 2019; López-Baucells & Burgin, 2019). But since *P. nathusii* males also display mating calls at hibernation areas (López-Baucells, 2019), I cannot confirm whether this behavior is strictly related to a potential migratory corridor. Territorial behavior along migration routes is similarly observed in *N. noctula* (Lindecke et al., 2020). However, while *N. noctula* typically emits mating calls stationary in a roost (Lindecke et al., 2020), *P. nathusii* males may also produce territorial calls in flight (Russ, 2023). Since my study sites were located in open areas with few roosting opportunities, the probability of recording male *N. noctula* advertisement calls was low.

4.5. Influence of weather conditions on bat activity and migration

My results demonstrated that weather conditions significantly influenced the activity of *P. nathusii* during autumn migration. However, as *P. nathusii* activity was primarily restricted to nights with low or no precipitation (<5 mm accumulated over three hours), precipitation was excluded from models analyzing the influence of weather on migratory bat activity. Due to collinearity between the wind variables, wind speed and wind direction were modelled separately alongside temperature.

During the migration period, I found that *P. nathusii* activity was negatively influenced by high wind speeds, and bats were rarely active at wind speeds above 7 m/s. Temperature had a positive influence on bat activity, with a higher probability of bat presence at higher temperatures. This was consistent with my expectations and results from many other studies on bat migration in coastal areas (Ahlén et al., 2007; Hüppop & Hill, 2016; Lagerveld et al., 2021; Pettit & O'Keefe, 2017). As travelling long distances exerts high energetic costs, bats will benefit from being active mainly during favorable weather conditions (Fleming et al., 2003; Popa-Lisseanu & Voigt, 2009). Higher activity on warm, calm nights may reflect that low winds are less energetically demanding to fly in or a potential increase in food availability. In general, the activity of insectivorous bats is highly associated with food availability, as more insects are active during warm, calm weather (McKay et al., 2024; Rydell, 1989). Because migrating bats must cover long distances and refuel during their nocturnal journey, feeding along the way is essential (Fleming, 2019; Šuba et al., 2012).

Due to the many observations of *P. nathusii* in the northern North Sea and the British Isles (Petersen et al., 2014), migrant bats are suspected to depart from the southwestern coastline of Norway (Eldegard et al., 2021d; Russ, 2023). However, specific departure points from the Norwegian coast have not yet been identified. Along many confirmed migratory routes, *P. nathusii* fly long distances while crossing the open sea (Lagerveld et al., 2024; Rydell et al., 2014). Nonetheless, the distance from Norway to Great Britain would represent a considerably longer flight route, with no land masses in sight for several hundred kilometers. Migrant bats crossing the northern North Sea must find other roosting opportunities at sea. Several studies have observed or found acoustic evidence suggesting that migrating bats roost at offshore installations, such as oil and gas platforms, and even wind turbines (Ahlén et al., 2007, 2009; Lagerveld et al., 2023). As accumulations of insects have been observed nearby offshore installations, these structures may also serve as food resources for bats at sea (Ahlén et al., 2007). In the North Sea, there are numerous offshore structures where migrating bats can find a rest and refuel (Martins et al., 2023; Petersen et al., 2014). However, since offshore wind turbines also appear to be attractive to bats, this can also put them at significant risk.

In my findings, wind direction also significantly influenced the activity of *P. nathusii*. The probability of bat presence increased particularly during warmer nights with northerly and easterly winds. However, when I used the number of *P. nathusii* bat passes as the response variable, results showed a significantly higher activity at nights with northerly winds and elevated temperatures. Assuming that my observations represent migrating individuals following the coastline southwards, northern wind directions would represent tailwinds. If bats depart to cross the sea in Rogaland, easterly winds would be in the bats' favor. The activity was also significantly higher in easterly winds, although less prominent. *P. nathusii* and other migrating bat species have frequently been shown to take advantage of tailwinds during migration (Hurme et al., 2025; Lagerveld et al., 2024; Pettit & O'Keefe, 2017). When crossing the southern North Sea to reach Great Britain in autumn, *P. nathusii* migration appears to be most concentrated at east-northeasterly winds (Lagerveld et al., 2023). If the activity I observed during autumn represented a south-westerly migration of *P. nathusii* in Norway, my results reflect those of other studies. Although acoustic evidence limits my conclusion, I suggest my findings strongly indicate migratory activity.

My findings have revealed distinct spatiotemporal patterns of potentially migratory species along the coast and how weather conditions may influence their activity. However, it is important to acknowledge that acoustics has its limitations. Unfortunately, distinguishing individual bats solely from acoustic evidence is not possible, and one single bat can generate many recordings, thereby creating a false indication of high bat activity. For the same reason, it is equally challenging to determine directional patterns. However, the seasonal and spatial activity patterns I have revealed may guide future studies on where, when, and under what environmental conditions research efforts should be aimed. To firmly confirm the migratory status of these bats in Norway, future studies should aim to provide more evidence on travel direction, potential departure sites, and destination points. Techniques such as banding, radiotelemetry, visual observations in combination with acoustics, and stable isotope analysis of fur samples have been successful in other bat migration studies (Ahlén et al., 2009; Fleming, 2019; Krauel & McCracken, 2013; Popa-Lisseanu & Voigt, 2009), and can provide valuable information to confirm whether or not these bats are migrating from Norway.

4.6. Implications for management

Bats that migrate across national boundaries represent a significant conservation challenge and require coordinated international efforts (Fleming, 2019). To address this issue, Norway and many other European countries have ratified the *Agreement on the Conservation of Populations of European Bats* (EUROBATS), established under the Convention on Migratory Species (CMS). The EUROBATS agreement works to develop legislation, education, and conservation measures to protect bats and facilitate cooperation between the member states (EUROBATS, 2025). As wind energy poses a significant risk to both migratory and resident bats, EUROBATS has developed guidelines for the consideration of bats during the planning and development of wind farms, as well as mitigation measures to avoid negative impacts on bats (Rodrigues et al., 2014). Although research on the impact of wind energy on bats in Norway has so far been scarce (but see McKay et al., 2024), Norwegian wind farms likely have similar negative impacts.

My research indicates that not only migrant bats, but also sedentary bat species are active in coastal areas. Many of these species are listed as threatened or near threatened on the Norwegian Red List (Artsdatabanken, 2021). This includes *P. nathusii*, *V. murinus*, *E. nilssonii*, and *N. noctula*. Since they are all aerial-hawking bats foraging in open habitats, they are particularly vulnerable to collisions with wind turbines (Rodrigues et al., 2014; Rydell et al., 2010). To avoid such impacts, Norwegian wind energy should adhere to the guidelines of EUROBATS (Rodrigues et al., 2014) and take them into consideration for both existing and planned future wind farms.

Based on the EUROBATS guidelines, I have some general suggestions for wind energy in coastal Norway. So far, wind energy projects are not legally obliged to include pre- and post-construction surveys considering bats in Norway. Implementing pre- and post-construction bat surveys will be crucial to assessing the potential impact on bats. As a minimum, this should include acoustic monitoring during active periods of bats to identify areas of high activity, foraging habitats, and seasonal variations in activity. This is particularly important since the knowledge of bat movements and important bat habitats in Norway is poor. Future wind farms should avoid areas with high bat activity, including coastal areas adjacent to important foraging habitats (e.g., lakes, wetlands, forested areas). Migratory and sedentary bat species may also be foraging at sea, and offshore wind farms should therefore be installed at least two kilometers from the coastline. At wind farms where considerable bat mortalities occur, mitigation measures, such as blade feathering and temporary shut-down, should be implemented in high-activity periods (e.g., low wind speeds, migration periods).

My findings highly suggest that *P. nathusii* is migrating along the coast. Considering the evidence on offshore occurrences of *P. nathusii* in the North Sea (Petersen et al., 2014; Russ et al., 2001), seasonal movements over the northern North Sea are most likely occurring. As Norway plans to develop offshore wind in these areas, acoustic monitoring of bats should also be implemented offshore. Post-construction surveys at offshore wind farms will be critical, as other studies have shown that structures offshore can have an attractive effect on bats (Ahlén et al., 2007; Lagerveld et al., 2023).

5. Conclusion

My research has provided valuable insights into the spatial and seasonal patterns of migratory bats along the coast of Norway, with a particular focus on the species *P. nathusii*. The seasonal trends in *P. nathusii* activity aligned with expected autumnal migration along the coastline. Nonetheless, more evidence is needed to confirm whether and where they depart to cross the North Sea. However, the migratory status of *N. noctula* remains uncertain due to limited detections and considerable observations during the summer. Environmental factors, such as wind speed, wind direction, and temperature, were confirmed to affect bat activity significantly during early autumn. Weather conditions may act as predictors of bat activity along the coast, but further investigation at more sites should be conducted. Additionally, I have demonstrated that coastal areas are important not only for migrating species but also for the local bat fauna. This highlights the need to consider bats in coastal wind energy planning. Specifically, the presence of species at high risk of turbine collisions needs to be considered and addressed. To fulfill its commitments under the EUROBATS Agreement and ensure a sustainable coexistence of coastal bats and renewable energy, Norwegian wind energy must carefully plan the placement of future wind farms and implement mitigation measures during peak activity periods.

Supplementary material

Table S.1. *Overview of sampling period and location of study sites. Deployment date = date (yyyy-mm-dd) of bat detector deployment. Retrieval date = date (yyyy-mm-dd) of bat detector retrieval. Sites are arranged from the northernmost site (CM-40) at the top to the southernmost site (CM-28) at the bottom. Site coordinates are in decimal degrees (WGS84 datum), rounded up to six decimal places.*

Site	Deployment date	Retrieval date	Latitude	Longitude
CM-40	2024-07-10	2024-10-10	59.20163	5.17920
CM-39	2024-07-10	2024-10-18	59.13136	5.24453
CM-20	2024-06-28	2024-10-16	59.03549	5.58233
CM-19	2024-06-28	2024-10-07	58.99543	5.57001
CM-18	2024-06-28	2024-10-07	58.96270	5.59877
CM-49	2024-07-15	2024-10-16	58.81229	5.54898
CM-26	2024-07-05	2024-10-08	58.74083	5.51721
CM-22	2024-07-01	2024-10-16	58.72184	5.52283
CM-28	2024-07-05	2024-10-16	58.65786	5.55381

Table S.2. *Detailed overview of Song Meter Mini Bat 2 Li-ion (Wildlife Acoustics) detector settings. Abbreviations: h = hours, kHz = kilohertz, secs = seconds, dB = decibels.*

Firmware	4.4
Time zone	UTC+2
Schedule	5h before sunset – 1h after sunrise
Recording format	Full-Spectrum
Full spectrum sample rate	256 kHz
Non-triggered recording	Off
Min. trigger frequency	16 kHz
Max. recording length	15 secs
Trigger window	3 secs
Save noise files	On
Left channel gain	12 dB

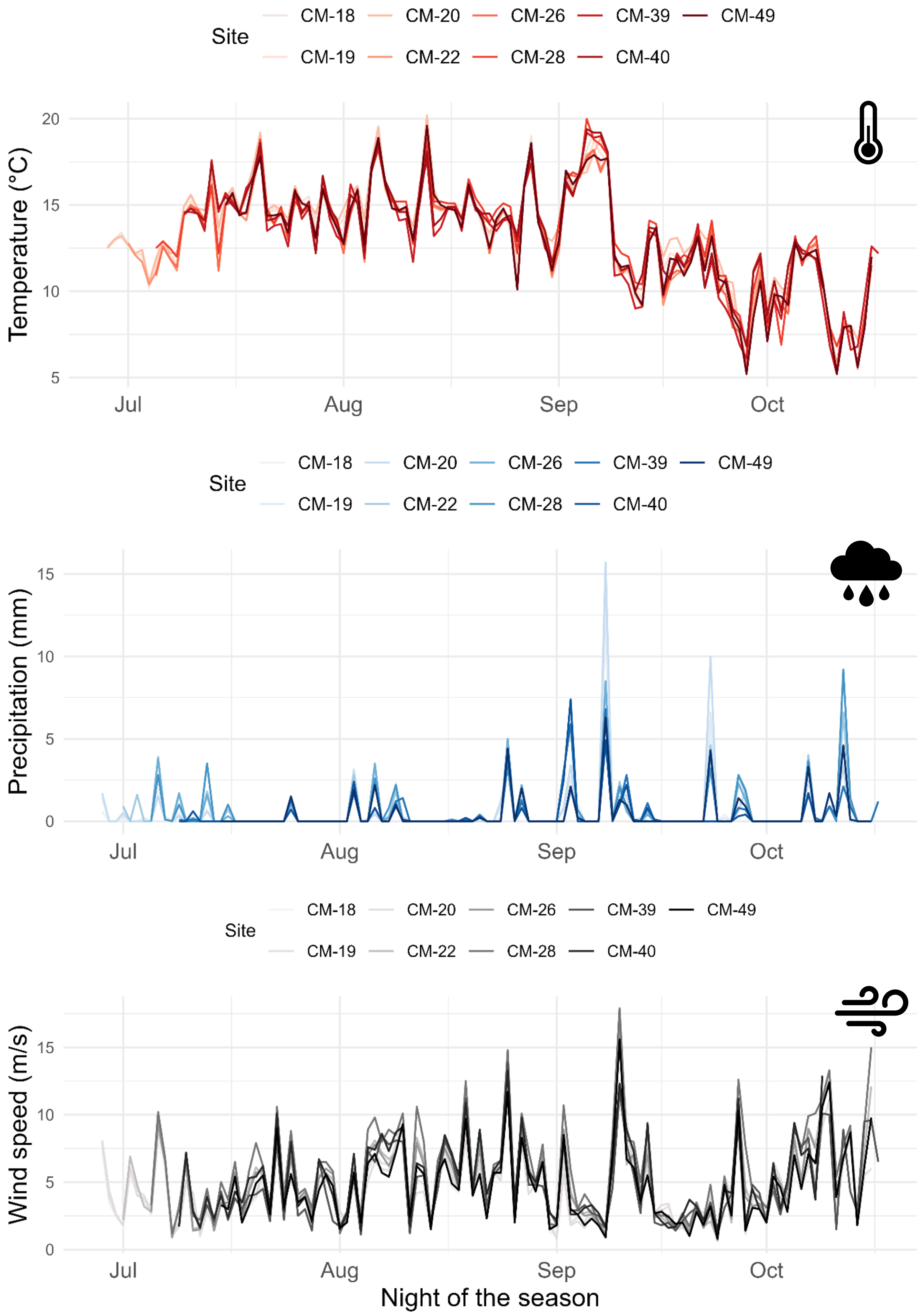

Figure S.1. *Nightly measures of a) temperature (°C), b) precipitation (mm), and c) wind speed (m/s) for each study site throughout the study season.*

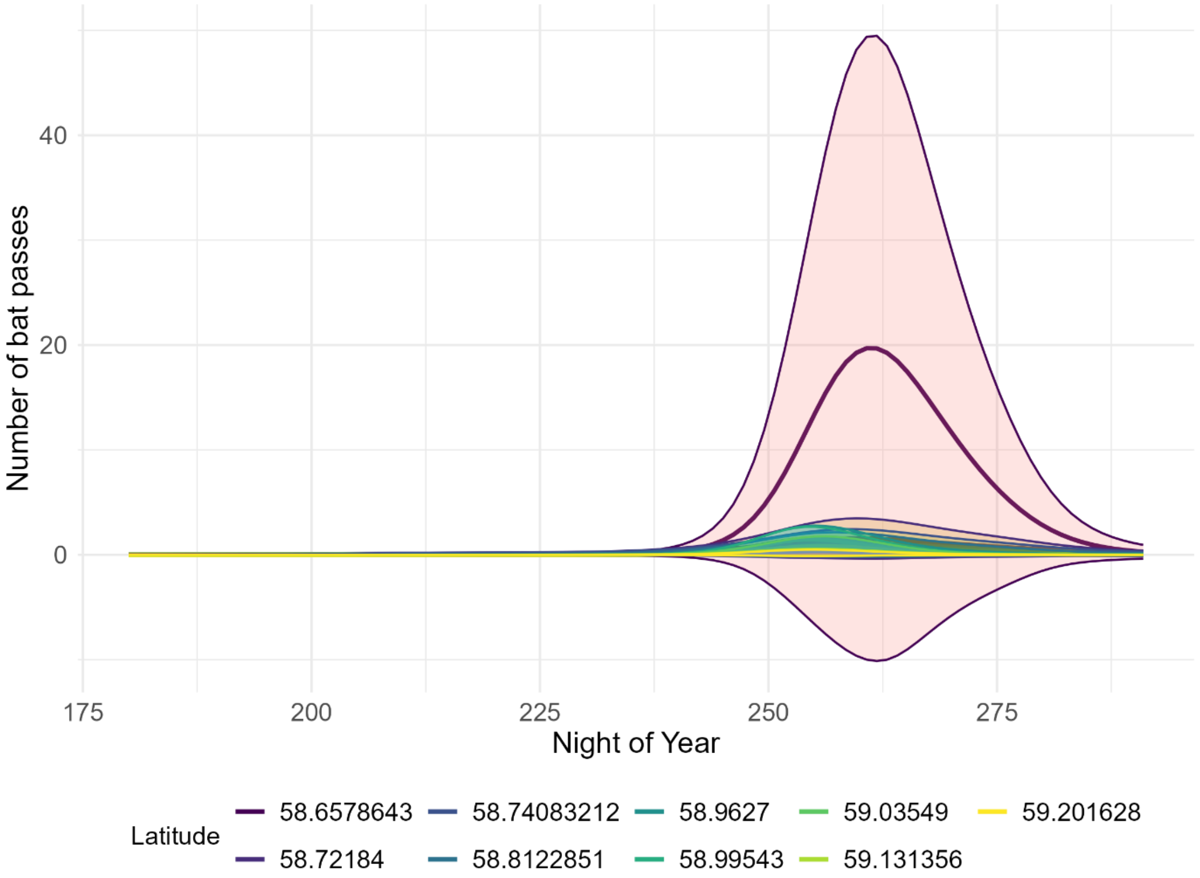

Figure S.2. *Estimated average number of Pipistrellus nathusii bat passes as a function of night of the year on different latitudes, related to results presented in* ***Table 3.6****. The shaded polygons represent the 95% confidence limits. Latitudes were extracted from site coordinates. Night of the year represents day counts from 2024 (n=366), where 175 represents June 23rd and 275 represents October 1st.*

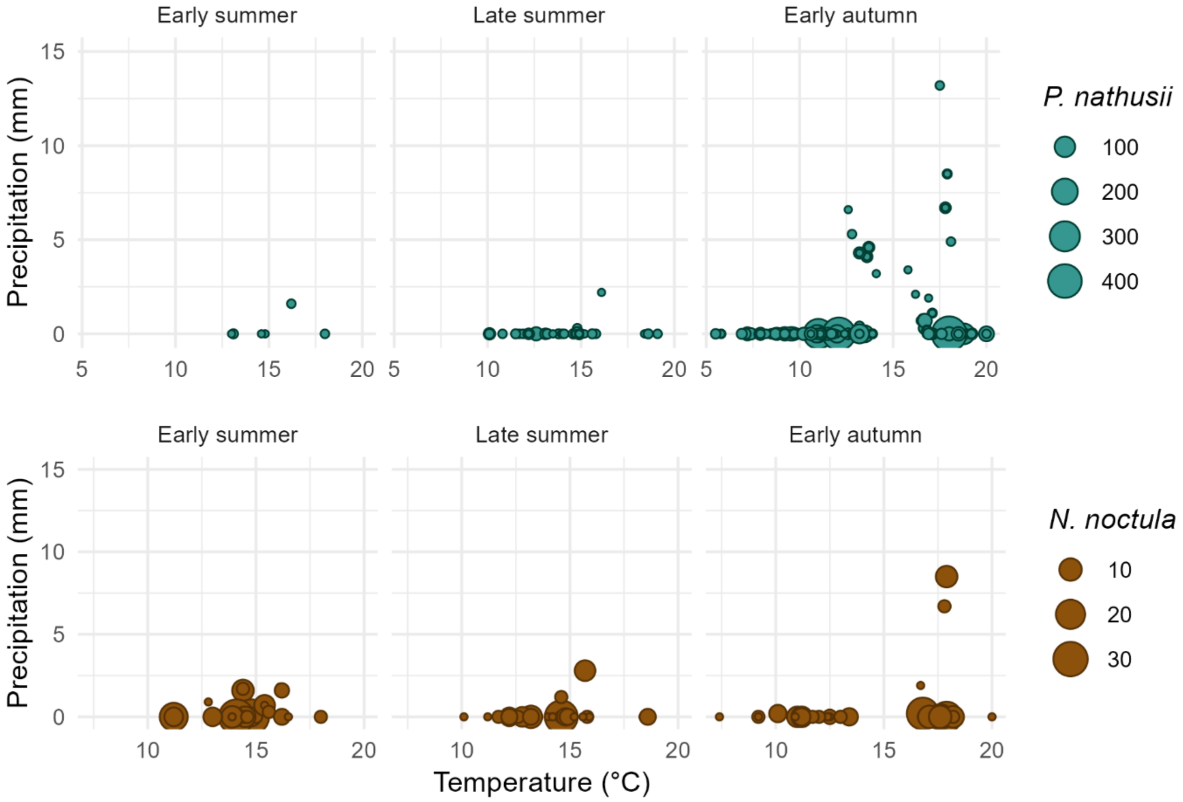

Figure S.3. *Migratory bat activity in relation to precipitation (mm) and temperature (°C). The size of the points represents the number of bat passes per night. Green = Pipistrellus nathusii, Brown = Nyctalus noctula. Seasons were defined as: Early Summer = June 27–July 26, Late Summer = July 27–August 31, Early Autumn = September 1–October 18.*

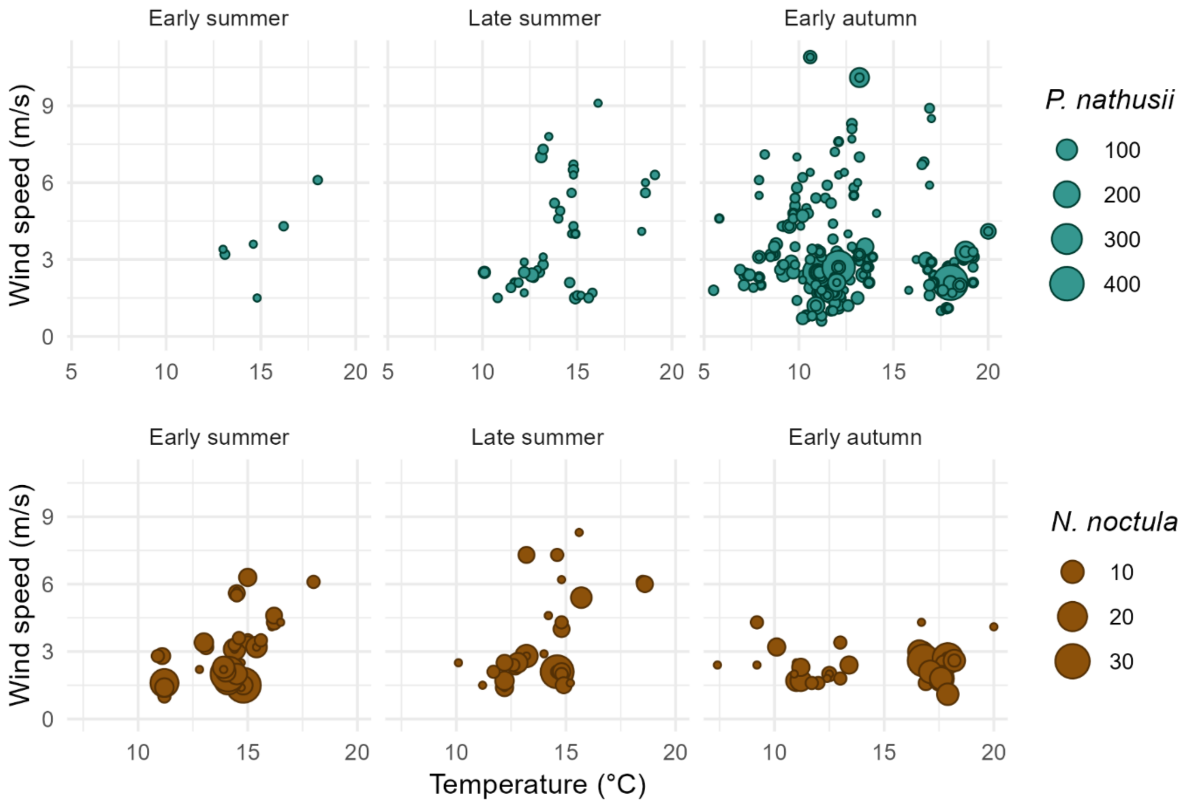

Figure S.4. *Migratory bat activity in relation to wind speed and temperature (°C). The size of the points represents the number of bat passes per night. Green = Pipistrellus nathusii, Brown = Nyctalus noctula. Seasons were defined as: Early Summer = June 27–July 26, Late Summer = July 27–August 31, Early Autumn = September 1–October 18.*

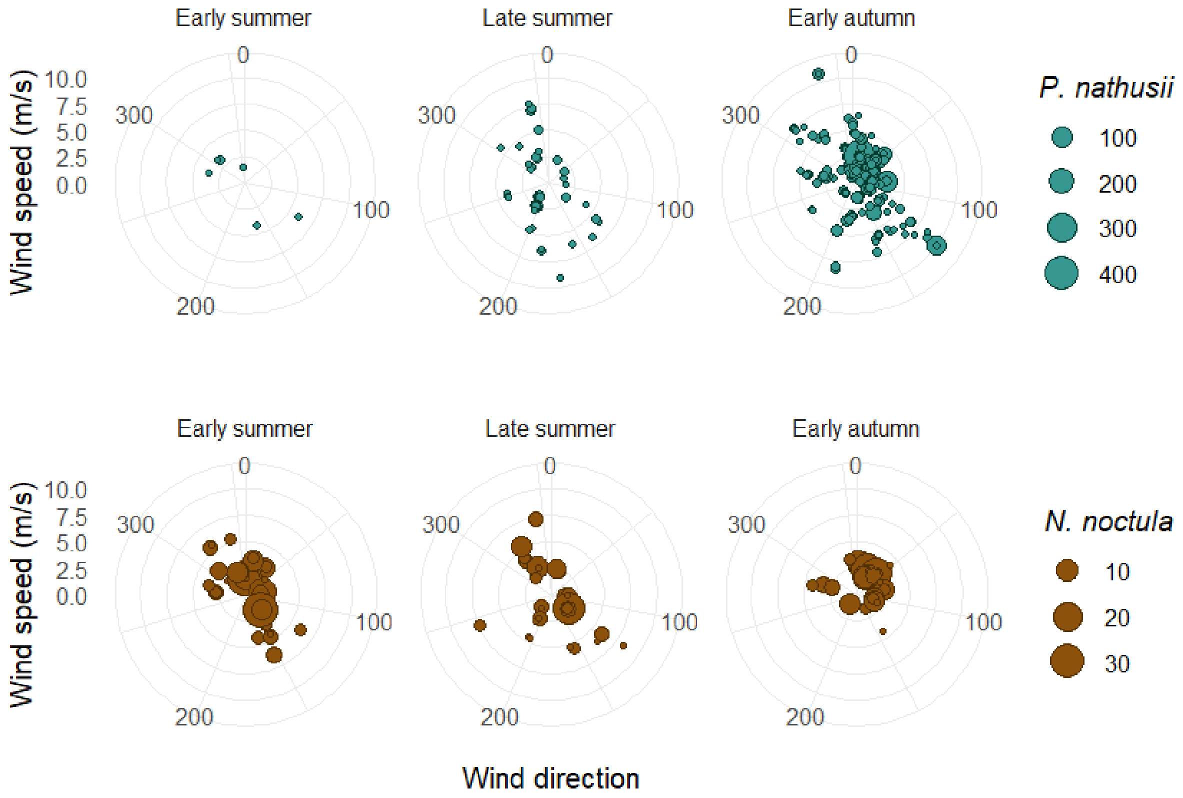

Figure S.5. *Migratory bat activity in relation to wind speed (m/s) and wind direction (degrees). The size of the points represents the number of bat passes per night. Green = Pipistrellus nathusii, Brown = Nyctalus noctula. Seasons were defined as: Early Summer = June 27–July 26, Late Summer = July 27–August 31, Early Autumn = September 1–October 18.*

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