Seasonal and spatial variations in activity of short- distance migrating bats in relation to weather conditions

A study of *Eptesicus nilssonii* and *Pipistrellus pygmaeus*

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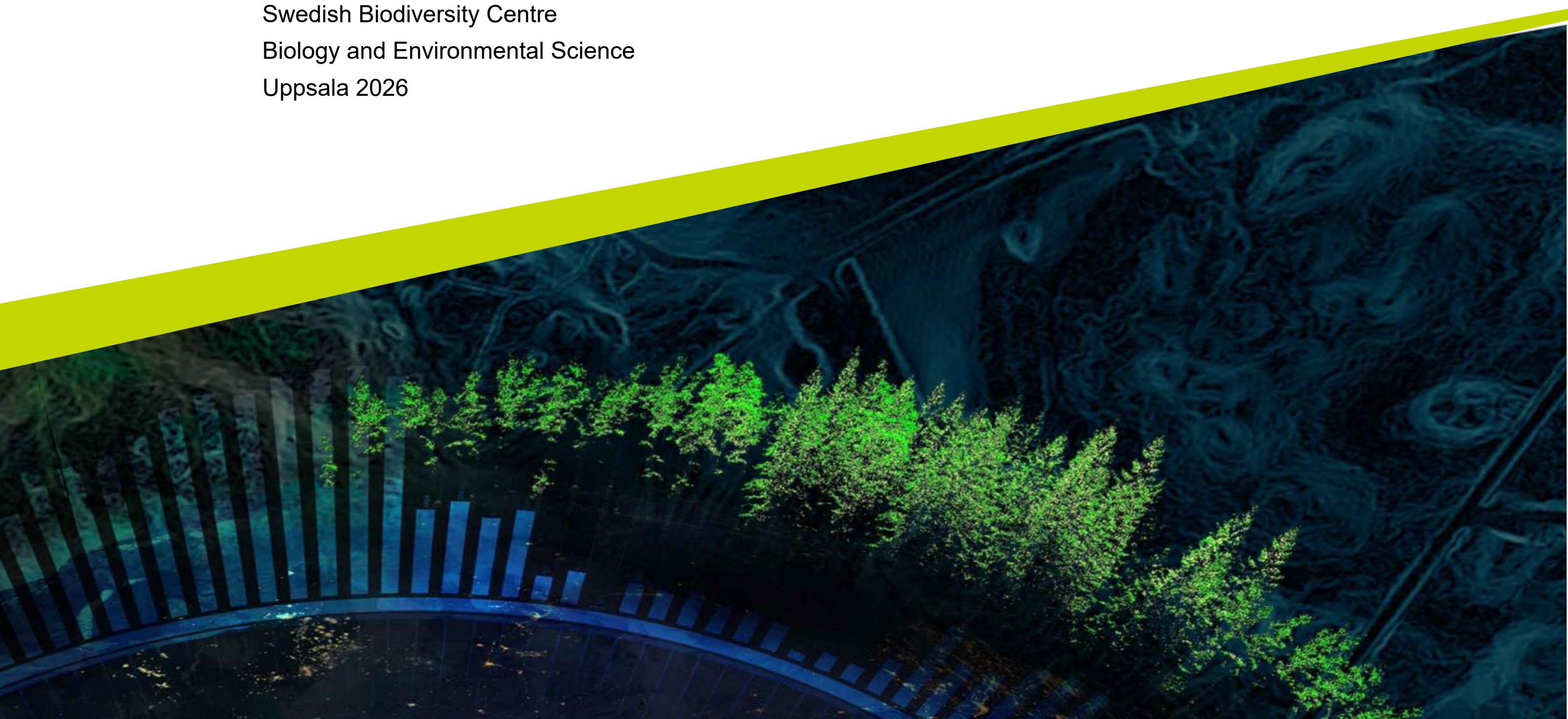

Seasonal and spatial variations in activity of short- distance migrating bats in relation to weather conditions - A study of *Eptesicus nilssonii* and *Pipistrellus pygmaeus*

Vädrets inverkan på säsongsmässig och rumslig aktivitet hos kortdistansmigrerande fladdermöss - En studie av nordfladdermus (*Eptesicus nilssonii*) och dvärgpipistrell (*Pipistrellus pygmaeus*).

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Abstract

In order to investigate the use of remote islands by short distance migratory bats in the Baltic Sea, acoustic bat monitoring was carried out in the Stockholm and Öregrund archipelago from June until November 2024 (Stockholm archipelago) from May until September 2025 (Öregrund) and May until October 2025 (Stockholm). Twenty islands within the study areas were selected for sampling, and one automatic recording unit was deployed at each site during the study period. The surveyed islands were selected to be as distant from the mainland as possible, while remaining accessible for researchers. The hypothesis was that the archipelago environments in the Baltic Sea might be of importance for bats as foraging sites, especially during the post colony period, and that spatial and weather-related variations such as distance to larger land areas from the surveyed islands, as well as unfavorable weather (strong winds, precipitation and lower temperature) could influence bat activity in these environments.

Results showed that wind speed and precipitation was the most important weather parameters negatively affecting bat activity during the study period. *P. pygmaeus* showed a decrease in bat activity of 14 % for every 1 m/s increase in wind speed. Bat activity in *E. nilssonii* declined with 17 %. Similarly, activity declined with 56 % with every 1 mm/hour increase in precipitation for *E. nilssoni*, and with 53 % for *P. pygmaeus*. In addition, bat activity decreased significantly with increasing distance to larger land areas (11.6 % for every 1 km increase), suggesting that more isolated islands are visited less frequent than islands closer to land.

These findings suggest that the presence of short distance bats on offshore islands in the Baltic Sea during the post colony period primarily reflects foraging behaviour rather than long distance migration. The study provides insight into the use of coastal environments as important foraging sites for bats, how their activity responds to different weather conditions as well as the locations of islands as foraging sites. These findings contribute to a better understanding of bat ecology during the post colony period in northern archipelago environments.

Keywords: seasonal movements, foraging behavior, island biogeography, short- distance migration, wind speed, temperature, precipitation, *Eptesicus nilssonii*, *Pipistrellus pygmaeus*.

Register

Introduction

Bat ecology

Temperate zone bats have a life cycle with significant seasonal variation (Ciechanowski 2010). Palearctic bats generally have reproductive cycles closely linked to fluctuations in insect abundance (Rydell 1989). During the maternity period, female bats loose large quantities of energy due to pregnancy and lactation and require high insect abundance to meet the demands. Therefore, lactation and weaning generally occurs in July and August, with high insect quantities present (Rydell 1989). Prior to hibernation, bats must create a fat storage to meet the increasing energy demands during hibernation. Therefore, bats undergo hyperphagia, increasing their foraging activity and creating a fat supply (Speakman and Rowland 1999, Fleming 2019).

Four of the 19 bat species occurring in Sweden are considered long distance migrants. These are: *Nyctalus noctula*, *N. leisleri*, *Vespertilio murinus and Pipistrellus nathusii* (Hutterer et.al. 2005). These species are capable of flying across large areas of open sea when moving between summer roosts and winter hibernation sites (Rodrigues 2014). Bats considered as short distance migrators usually migrate up to a few hundred kilometres, while stationary bats generally migrate from 10 up to 100 kilometres (Hutterer 2005).

Bats use a multitude of different habitats when foraging, including forests, ravines and over open water (Ahlén 2011). The use of open water for hunting is especially important in archipelago environments, particularly in brackish water systems like the Baltic Sea, where bats can take advantage of high insect densities over open water bodies (Ahlén et.al. 2009).

A study of bat activity and migratory behaviour at sea was conducted at coastal areas of southern Sweden and Denmark and observed that 11 out of 19 species occurred in the southern Baltic Sea and Öresund (Ahlén et.al. 2009). Foraging over open water at notable distances from the coast was a common behaviour well before the onset of the migration period, with *Pipistrellus pygmaeus* (considered a short distance migrator) being the most abundant bat. It is therefore suggested that coastal environments may represent important habitats for bats in terms of foraging and migratory movements (Ahlén et.al. 2009). However, a study of island biogeography of bats in California found that bat species richness is affected by the isolation of islands. In the study, species richness declined with roughly one species per 6.25 km increase in isolation from the mainland (Winifred et.al. 2008).

Pipistrellus pygmaeus and *Eptesicus nilssonii* are two widely spread bat species in Sweden. *E. nilssonii* occurs from southern Sweden up to the mountain boarder in northern Lapland, and *P. pygmaeus* can be found in large numbers in southern Sweden, with few observations being made as far north as Umeå in northern Sweden (de Jong et.al. 2020). Both species have been observed in archipelago environments and are capable of foraging at sea despite being considered short distance migrants. Therefore, they are suitable for studying bat activity in archipelago landscapes (Ahlen et.al. 2009, Hutterer et.al. 2005).

Weather parameters

A study by Erickson (2002), studied how climate conditions affect bat activity during the summer, and found that the occurrence of low temperatures and rain was strongly correlated with declining flight activity. Possibly, bats are sensitive to unfavourable weather due to the amount of energy they consume to maintain a stable body temperature (Erickson 2002). In addition, a study on bat echolocation in relation to precipitation, observed that bats avoid rain partly because raindrops interfere with bat echolocation calling (Voigt 2011). Unfavorable weather also reduces the insect prey abundance (Racey 1987). A study by Pasek (1988) found that insect abundance declines with higher wind speeds. Similarly, insect abundance declines with decreasing temperature (Vebrová 2018) and increasing precipitation (Lawson 2019), and bats are capable of entering torpor to save strategy during adverse conditions (Racey 1987).

A study investigating bat activity patterns in relation to insect abundance at wind farms in southern Sweden observed that activity decreased with increasing wind speed, with 90 % of bat registrations made at wind speeds below 8,2 m/s (de Jong et.al. 2021). A study by McKay et.al. (2024) similarly found that bat activity declined with increasing wind speed, with 92% of bat activity recorded at <12 m/s. Interestingly, higher temperatures (above 10 °C) improved the negative effects of higher wind speed, making it possible for bats to stay active above wind speeds of 10 m/s (McKay et.al. 2024).

Bender et.al. (2015) found that bat activity increases with increasing barometric pressure, suggesting that the positive relationship was related to flight costs and available prey. Interestingly, a study on cave roosting bats (particularly *Pipistrellus subflavus*) and barometric pressure found that bats instead increased their activity during falling barometric pressure (Paige 1995). Both studies suggested that bats potentially use pressure as an indicator of insect abundance outside of the roost, possibly due to pressure being one of few environmental cues available in caves (Paige 1995, Bender et.al. 2015).

Wind farms and bats

The Swedish coastline along is one of the longest in Europe, with the majority extending along the Baltic Sea. Therefore, the expansion of offshore wind farms plays an important role in the transition towards fossil free energy production in Sweden (Swedish Energy Agency 2023). In 2023, wind farm expansions at 14 different sites were either planned or investigated in The North Sea, Baltic Sea and the Gulf of Bothnia (Swedish Energy Agency 2023). The Baltic Sea is of strong importance in the context of bat migration, although few studies have been made regarding offshore wind farms and their effects on bats in the area (Gaultier *et.al* 2020).

Aim of the study

Even though the potential impacts of wind farm on migratory bats in the Baltic Sea are overlooked, some researchers have still tackled the topic (e.g. Geidnert 2025, Seebens-Hoyer 2026, Ahlén 2009). In addition, a quantity of studies has been made regarding bat activity in relation to colony contexts (e.g. Ngamprasertwong et.al. 2014, Suominen et.al. 2023). In comparison, very few studies have focused on short-distance migrating bats and post-colony movements in the Baltic Sea archipelago. Therefore, this study aimed to explore spatial, seasonal and weather-related variations in the activity of the short distance migratory bats *Eptesicus nilssonii* and *Pipistrellus pygmaeus,* during the period before, during and after lactation (the colony period) in the Stockholm and Öregrund archipelago. Using acoustic monitoring at 20 offshore sites, bat activity passes from May to November was observed, both in relation to island size and distance to mainland, as well as environmental conditions such as wind speed (m/s), temperature (°C), precipitation (mm) and atmospheric pressure (hPa).

Material and methods

Monitoring of bats

Passive acoustic monitoring (PAM) is generally used for estimation of bat activity, as it provides the opportunity for data collection without trapping and having to be present in the field (Roemer et.al. 2025). An ultrasonic detector is deployed at a study site for more than one night, and the device may be triggered to record by the occurrence of bat echolocation calls (Roemer et.al. 2025). When estimating bat activity through acoustic monitoring, interpretation of the detections must be carefully performed (Miller 2001). Counting all recorded calls can lead to overestimation, since an individual bat can be detected multiple times during a single night. To solve the issue, researchers use a standardized activity index (from now on referred to as AI), which summarizes detections over time intervals. AI provides a more accurate measurement of bat activity and allows for comparisons between sites and times (Miller 2001).

The acoustic bat surveillance was carried out in the Stockholm archipelago and Öregrund from June until November 2024 (Stockholm archipelago) from May until September 2025 (Öregrund) and May until October 2025 (Stockholm). Twenty islands within the study areas were carefully selected for sampling, and one automatic recording unit was deployed at each site for the duration of the study period (figure 1, table 1). The selected islands were small and generally not suitable for bat colonies, and were chosen to be as distant from the mainland as possible while remaining logistically accessible, in order to better evaluate bat activities at increasing distances to the mainland. Bat activity was recorded using automatic ultrasound detectors (song Meter mini 2 Li-lon bat detector, Wildlife acoustics).

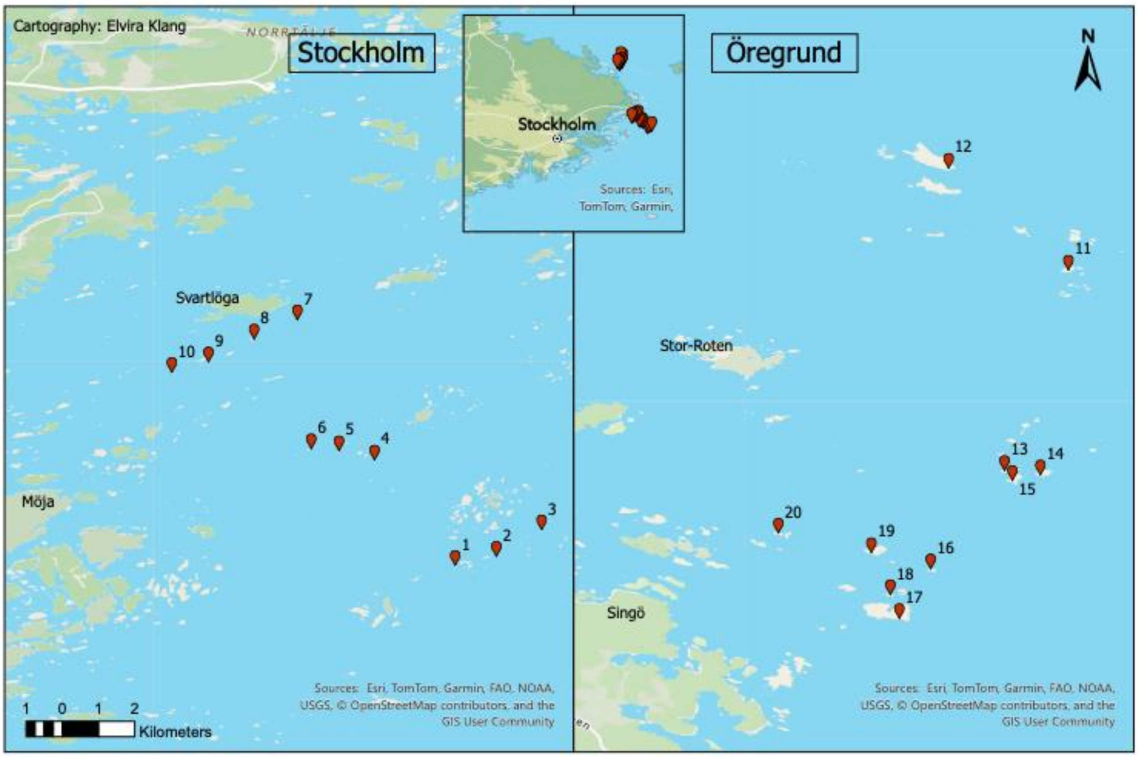

Figure 1: locations of the recording units deployed in the Stockholm and Öregrund archipelago. Map was created in ArcGIS.

Table 1: the surveyed locations within the Stockholm and Öregrund archipelago.

Site	Islands	Coordinates
Stockholm	Rönnkobben	(59°23'42"N, 19° 11'26" E)
Stockholm	Utterkobben	(59°24'4.7"N, 19°13'6.2"E)
Stockholm	Fiskeskobb	(59°25 '9.1"N, 19°14'57"E)
Stockholm	Österkobb	(59°28 '0.3"N, 19° 8'7.3"E)
Stockholm	Högkobben	(59°28' 23"N, 19° 6' 40 "E)
Stockholm	Stora rödkobben	(59°28' 28"N, 19° 5' 32 "E)
Stockholm	Östra stengrundet	(59°33' 44"N, 19° 4' 58 "E)
Stockholm	Vitgrundsfladen	(59°32' 57"N, 19° 3' 12 "E)
Stockholm	Kikarharan	(59°32'0.7"N, 19° 1' 20 "E)
Stockholm	Ägglösen	(59°31'35"N, 18° 59' 50"E)
Öregrund	Stridsbådan	(60°16’20"N, 18°53' 21"E)
Öregrund	Norrsten	(60°17’51"N, 18°51' 34"E)
Öregrund	Hållskären, norr	(60°13’21"N, 18°52' 24"E)
Öregrund	Bodskäret	(60°13’17"N, 18°52' 56"E)
Öregrund	Västerskäret	(60°13’12"N, 18°52' 31"E)
Öregrund	Måskobben	(60°11’53"N, 18°51' 18"E)
Öregrund	Måsten	(60°11’8.7”N, 18°50'50"E)

Öregrund	Lillvåna	(60°11’30"N, 18°50' 42"E)
Öregrund	Storkorsten	(60°12’7.5"N, 18°50' 25"E)
Öregrund	Storläget, västra	(60°12’25"N, 18°49' 1.9"E)

Structuring of data

The present study focused solely on short-distance migratory species, including *E. nilssonii* and *P. pygmaeus*. Long distance migratory species such as *Nyctalus noctula*, *N. leisleri*, *Pipistrellus nathusii* and *Vespertilio murinus* were therefore excluded from the analysis (Hutterer et.al. 2005). Short distance migratory species such as *Barbastella barbastellus*, *E. serotinus*, *P. pipistrellus*, *Myotis spp.* and *Plecotus spp*. did not occur in the area and files auto identified as these species was omitted from further analysis.

Acoustic files were analysed using Kaleidoscope (version 5.4, Wildlife acoustics). It was found that the higher the number of pulses in an audio file, the greater the probability that the automatic species classification was correct. To ensure that the files included in the analysis truly contained bats rather than background noise, a pulse-based threshold was established. A subset of auto identified files classified as “*No-ID*” (150 files), “*Eptesicus nilssonii*” (150) and “*Pipistrellus pygmaeus* (150) was manually reviewed in Bat Sound (Petersson Electronic) across a range of pulse counts (from 2 up to 94 pulses). The threshold was defined as the lowest number of pulse count that had at least 90% correctly identified files, as well as 90 % accuracy of the total sum of recordings with higher pulse counts. This procedure was applied separately for both species to determine species-specific threshold values (table 2-4).

Table 2: distribution of manually verified E. nilssonii- and noise files across pulse threshold. Threshold was set to 10 pulses.

Threshold_90	E. nilssonii	Noise
< 10 pulses	39	29
≥ 10 pulses	81	2

Table 3: Distribution of manually verified NoID (containing Chiroptera sp)- and noise files across pulse threshold. Threshold was set to 19 pulses.

Threshold_90	No_ID	Noise
< 19 pulses	41	59
≥ 19 pulses	45	5

Table 4: Distribution of manually verified P. pygmaeus and noise files across pulse threshold. Threshold was set to 11 pulses.

Threshold_90	P.pygmaeus	Noise
< 11 pulses	2	56
≥ 11 pulses	89	3

Each recording unit generated separate output files (containing bat recordings) corresponding to different periods of the year (for example output 1A, 1B and 1C from recording unit 1). As recording quality may vary both between different sites and periods (for example during periods with higher quantities of katydids present), a validation procedure was implemented for each output file: 20 auto identified recordings (10 per species) above the determined thresholds were randomly selected and validated in BatSound. As a result, 8 out of 93 output files didn't meet the criteria of at least 90% accuracy above the threshold and were therefore excluded from further analysis, either partially (one species) or fully (both species). In addition, 17 output files did not (partially or fully) contain the target species above the thresholds and was therefore not included in further analysis.

Even with a threshold of 19 pulses, the number of NoID-recordings remained too large for solely manual classification. Therefore, a random subsample of 100 NoID-files was manually identified to estimate species composition (table 5).

Table 5: species composition of a random subsample of 100 NoID-files.

NoID (files)	E.nilssonii	P.pygmaeus	Other
100	19	26	55

Manual validation indicated that 55 % of NoID-recordings consisted of noise or species of bats not included in the study. Of the NoID-files 45% belonged to the target species. For each hourly interval across each site during the study period, 45 % of observed NoID-recordings were therefore altered to either *E. nilssonii* or *P. pygmaeus* based on the observed species distribution among identified recordings within the same hour. The remaining 55% NoID-recordings in each hourly interval were excluded from further analysis.

Bat activity was determined using an activity index (AI) based on active minutes. Bat recordings were summarized into one-minute intervals, where any minute containing at least one detection of bat activity was counted as an individual bat, regardless of the number of recordings (from one species) within that interval. This method was chosen to reduce potential overestimation of activity caused by repeated passes of one individual bat, which can generate numerous call sequences within a short time during passive acoustic monitoring (Ijäs et.al. 2017, Miller 2001).

During earlier steps, files that did not meet the quality criteria of an approved audio file (for example files containing katydids) was with the use of manual identification and general pulse thresholds deleted from the analysis. This resulted in missing dates in the data set. Since the majority of the deleted files likely contained ”noise” instead of ”NoID-bats”, and because the recording units operated mostly continuously during the period, all missing dates was reconstructed with AI set to 0, to represent nights with ”no bats” instead of ”missing data”.

Meteorological data

Meteorological data, including wind speed (m/s), temperature (°C), atmospheric pressure (hPa) and precipitation (mm) were obtained from June to November 2024 and May to October 2025 from the Swedish Meteorological and Hydrological Institute (SMHI). Observations were collected from an active weather station nearest to the study islands. For the Stockholm archipelago, this equals “Svenska Högarna A” (59°26’32’’ N, 19°30’08’’ E), for Öregrund, the closest station is Örskär A (60° 31' 32,1594’’ N, 18° 22' 22.44’’ E).

All data was imported to the programme R (version 4.5.1). For each day during the study period, the target time for meteorological observations was set to one hour after sunset using the ”suncalc” package (Thieurmel 2025), beacuse the first hour after sunset generally corresponds to peak activity for bats (Frafjord 2021). If a measurement did not exist precisely one hour after sunset, the observation closest in time was selected. Only measurements marked as good quality by SMHI were included. This procedure resulted in one value per weather parameter for each day, which was used for examining the relationship between local weather conditions and bat activity.

Night length in the Stockholm archipelago and Öregrund varies significantly over the study period May - November, which could possibly affect bat foraging activity, as the foraging time per night varies. Night length was therefore calculated for each date using the suncalc package (Thieurmel 2025) and tested as a possible predictor of activity.

Data analysis

Statistical analysis was performed in the programme R (version 4.5.1). Full script is available in Appendix. Data was collected from Excel and imported to R using the readxl package (Wickham 2025). Data preparation was performed using dplyr (Wickham 2026). Dates were converted to day of year (DOY) using the lubridate package (Grolemund & Wickham 2011). Site, year, area and species were treated as categorical values.

Seasonal activity patterns were first visualised using ggplot2 (Wickham 2016) by plotting AI against DOY using locally smoothed regression curves (LOESS). Raw data points illustrated actual values over the study period (Cleveland 1979). Since the data showed substantial overdispersion (variance >> mean), models assuming a negative binomial error distribution were applied. Data was collected at the same sites across multiple dates. Therefore, generalized linear mixed models (GLMMs) were used (Bolker 2009), with site included as a random effect to account for non-independence of observations within sites. Models were fitted using the package glmmTMB (Brooks 2017).

Seasonal progression was first modelled using DOY, fitted as a natural spline (df = 3) using the splines package (R Core Team 2025), to allow for non-linear patterns. A multivariate model including all meteorological variables was then fitted for each species. Independent contributions of variables were tested by comparing the full model with reduced models where one variable at a time was removed. ΔAIC was calculated as AIC_reduced – AIC_full. Positive ΔAIC values suggests reduced model fit when the variable is excluded.

Model assumptions were evaluated using simulated residual diagnostics performed with the DHARMa package (Hartig 2024). Multicollinearity among predictor variables was assessed using variance inflation factors (VIF), performed with the car package (Fox 2019). Model estimates are presented as regression coefficients (log scale) with standard errors and p-values. Coefficients were exponentiated to obtain incidence rate ratios (IRR) for biological interpretation. Predicted relationships were visualised based on model estimates with 95% confidence intervals.

To examine how bat activity varied between the surveyed islands, land area and distance to mainland was determined. Land area of the 20 islands was measured using ”Min Karta” (Lantmäteriet), and distance to mainland was calculated in R (version 4.5.1). Coastline data was collected from the Natural Earth dataset (scale 1:10m) which represents the highest resolution available in the dataset (1:10 000 000), including main coastline and larger islands, larger than approximately 300 ha (figure 2). Coastline layer was imported with the rnaturalearth package (Masicotte 2026) and processed using the sf package (Pebesma 2023).

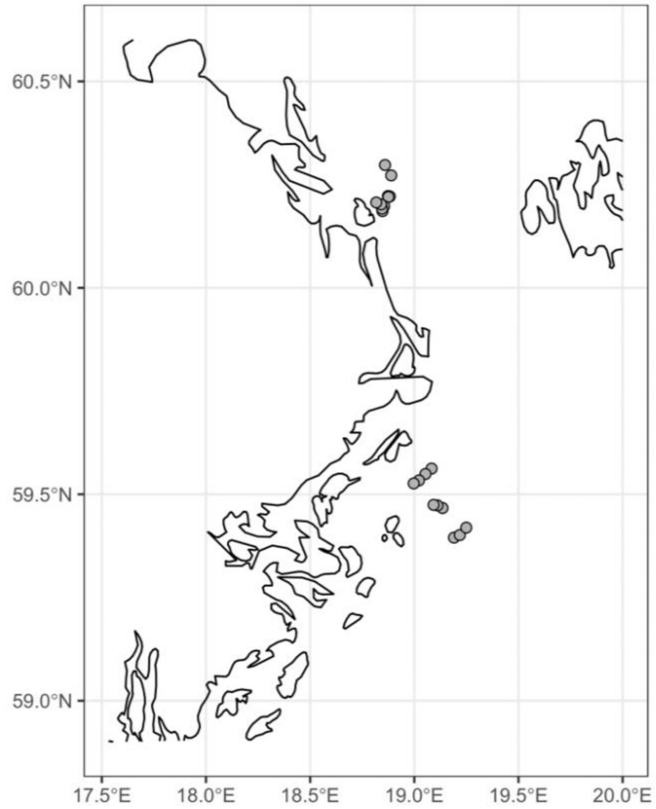

Figure 2: Natural Earth coastline dataset (scale 1:10 000 000), grey points represent study islands.

Island coordinates and coastline data was projected to the Swedish national Coordinate system SWEREF99 TM to allow for distance measurements in meters. For each island, the shortest distance from the surveyed islands to the coastline were calculated. The number of surveyed nights, total AI, mean AI and median AI were also calculated and compared to area and distance to mainland. The relationship between mean activity index (AI) and distance to mainland was visualised using the ggplot2 package (Wickham 2016).

Results

Activity index

When applying AI, the total amount of files dropped from 104 622 files from 30 463 active minutes, meaning that approximately 70 % of the files was multiple registrations within the same minute.

Night length and DOY

When activity was visualised against night length within the duration of the study period, clear differences in activity were observed for each species. *E. nilssonii* displayed highest activity levels at night lengths of approximately 4 - 6 hours, while *P. pygmaeus* showed gradually increasing activity with increasing night length.

Night length was strongly correlated with day of year (DOY; r = 0,86). When bat activity was visualised against DOY (figure 3), both species showed seasonal variation in activity. *E. nilssonii* reached peak activity in late July to early August, followed by a decline towards autumn. For *P. pygmaeus,* activity increased progressively throughout the summer and peaked in mid-September. Interestingly, a remarkable peak in activity was observed in early November (site 8, 24-11-01, AI = 269 and 24-11-02, AI = 244), however, this pattern was based on only two observations and should be interpreted with caution. reliable activity levels were observed in late September and early October.

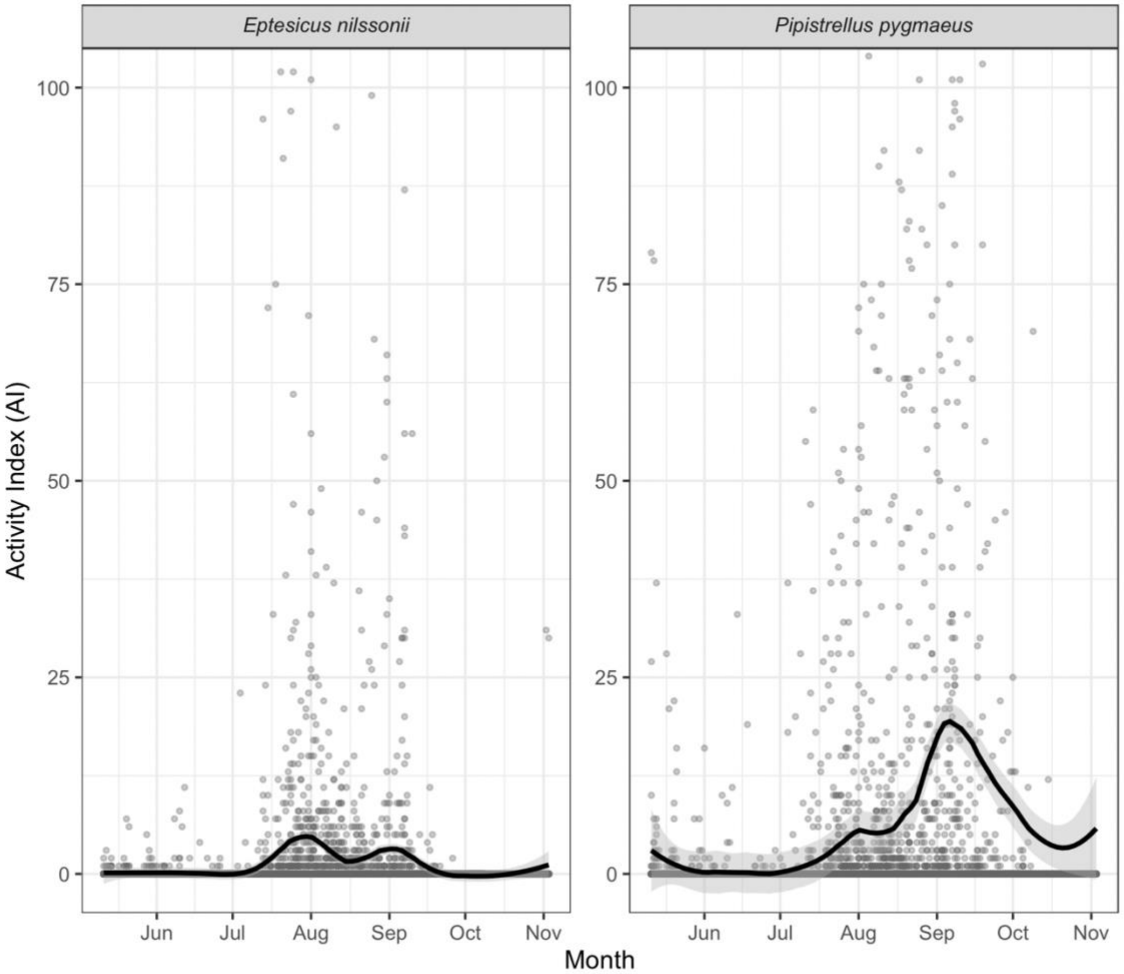

Figure 3: Seasonal variation in bat activity (AI) of E. nilssonii and P. pygmaeus from May to November. Curves represent LOESS-smoothed trends based on all observations from Stockholm (2024-2025) and Öregrund (2025). Shaded area shows 95% confidence intervals. AI represents active minutes per night. Y-axis is cut for clarification.

Multivariate weather models

Results from the multivariate model (which included all meteorological variables) are presented below for *E. nilssonii* and *P. pygmaeus* (table 8 and 9, figure 4 and 5). Independent contributions of variables were determined by comparing the full model with reduced models (models with one variable removed). ΔAIC was calculated as (AIC_reduced – AIC_full), where positive ΔAIC values indicate reduced model fit when the variable is excluded. Estimate determines the direction of the effect, with negative coefficients indicating reduced activity with increasing variable values. IRR = $e^{estimate}$ (table 8 and 9).

Results from the multivariate model shows that wind speed had the most influence on activity for *E. nilssonii* (P < 0.001, ΔAIC = +57.01) with a decrease

in bat activity with 17 % for every 1 m/s increase in wind speed (estimate: -0.181, $(e^{-0.181}) = 0.834$, 1– 0.834 ~ 0.17 (figure 4).
Precipitation showed a significant negative trend (P < 0.001, ΔAIC = +15.71), with bat activity declining by ~ 56 % with every precipitation increase in mm/hour (figure 5). The effect of temperature was slightly weaker but still significant (P = 0.012, ΔAIC = + 4.44), with an increase of bat activity by 9 % with every + 1 °C increase. Absolute pressure showed weak effects (P = 0.003, ΔAIC = + 7.17) indicating a decline with ~ 3 % for every increase in hPa (table 8).

For *P. pygmaeus*, wind speed similarly had the most influence on bat activity (P < 0.001, ΔAIC = +44.82, figure 3), with a decrease in activity with 14 % for every 1 m/s increase in wind speed (estimate -0.156 $(e^{-0.156})$ = 0.856, 1 – 0.856 ~ 14 %). *P. pipistrellus* also showed a significant relationship with precipitation (P < 0.001, ΔAIC = +17.57), with bat activity reduced by ~ 53 % with every precipitation increase in mm/hour (figure 4). The effects of temperature and absolute pressure was not significant (table 9).

Table 8: Independent effects of weather variables on activity index (AI) in E. nilssonii.

Variable removed	**P-value**	**ΔAIC**	**Estimate**	**IRR**
Wind speed	< 0.001	+ 57.01	- 0.181	0.834
Temperature	0.012	+ 4.44	+ 0.087	1.091
Precipitation	< 0.001	+ 15.71	- 0.820	0.440
Absolute pressure	0.003	+ 7.17	- 0.033	0.967

Table 9: Independent effects of weather variables on activity index (AI) in P. pygmaeus.

Variable removed	**P-value**	**ΔAIC**	**Estimate**	**IRR**
Wind speed	< 0.001	+44.82	-0.156	0.856
Temperature	0.561	-1.66	0.017	1.017
Precipitation	<0.001	+17.57	-0.759	0.468
Absolute pressure	0.442	-1.41	-0.007	0.993

Mean activity index

Mean activity index (MAI) declined with increasing wind speed (figure 4), with highest activity levels observed at wind speeds of 0-4 m/s for both species, after which MAI gradually decreased. *E. nilssonii* reached MAI = 0 at around 8-9 m/s. *P. pygmaeus* showed a significant decline in activity from 4-6 m/s, but maintained marginally higher activity levels at higher wind speeds than *E. nilssonii*, Overall, both species showed similar trends.

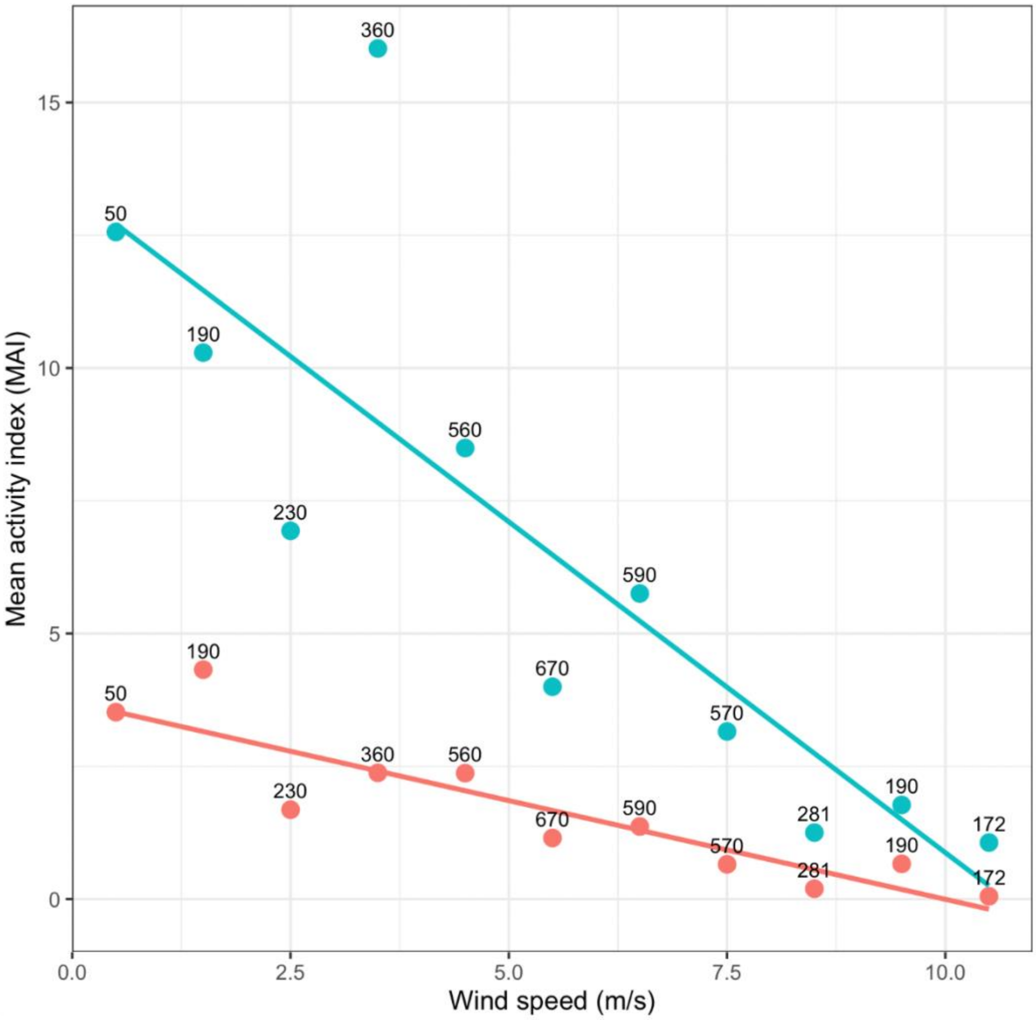

Figure 4: Visualisation of mean activity index (MAI) across wind speed intervals (0-1, 1-2…) for E. nilssonii (red) and P. pygmaeus (blue). MAI was calculated across all observations (number above each point) within each interval (one observation = AI per species, site and night).

MAI declined with increasing precipitation, and activity was highest at intervals of 0-1 mm for both species (figure 5). Both *E. nilssonii* and *P. pipistrellus* reached MAI = 0 at precipitation levels of ~ 4-5 mm rainfall. Number of observations were largest at low precipitation values and decreased with increasing rainfall.

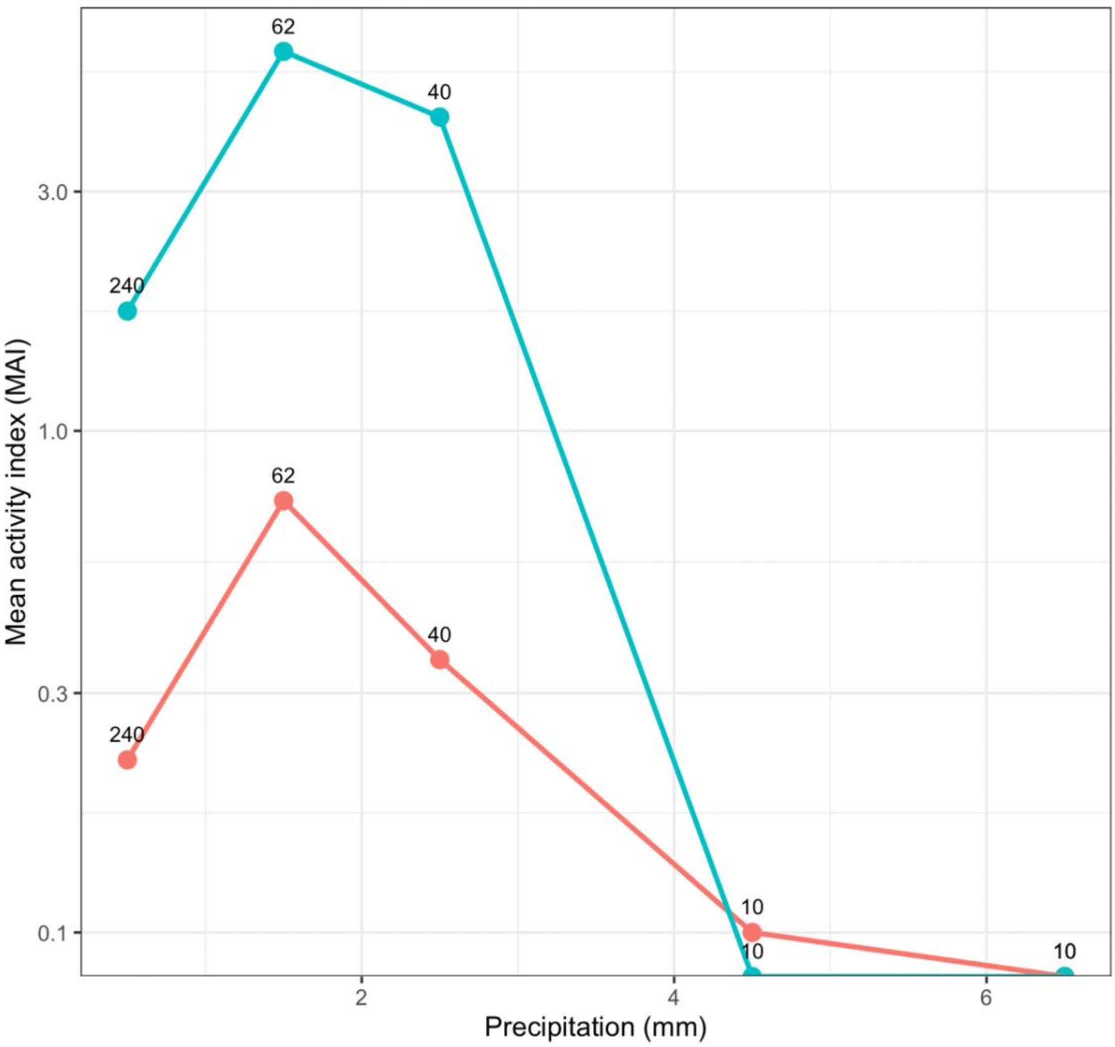

Figure 5: Visualisation of mean activity index (MAI) across precipitation intervals of 1 mm/hour for E. nilssonii (red) and P. pygmaeus (blue). MAI was calculated across all observations (numbers above each point) within that interval (one observation = AI per night, site and species).

Site comparison

Bat activity varied remarkably between different sites, with total AI varying from 7-13 881 active minutes. Mean AI varied from 0.02 to 47.9 active minutes per night (table 10). Median AI was zero for all sites except Vitgrundsfladen, indicating that more than half of all surveyed nights on these islands had no measured activity. Bat activity decreased with increasing distance to larger land areas islands in both study areas, with a decline in bat activity with ~ 11.6 % for every 1 km increase to larger land areas (figure 6). Islands located closer to larger land areas showed significantly higher values of AI than islands located further away. No significant connection between island area and bat activity could be made for Öregrund nor Stockholm (P = 0.204).

Table 10: Comparison of AI in relation to recorded nights, island area and distance to mainland for all surveyed islands.

Name	Site nr	Study period(days)	Tot. AI	Mean AI	Median AI	Area (ha)	Distance to coast (m)
Rönnkobben	1	290	483	1.67	0	2.6	13876
Utterkobben	2	290	7	0.02	0	1.7	15516
Fiskekobben	3	290	389	1.34	0	3.3	17534
Österkobb	4	290	307	1.06	0	2.6	12312
Högkobben	5	290	449	1.55	0	1.6	11180
Stora rödkobben	6	290	1103	3.80	0	3.8	10230
Östra stengrundet	7	290	1530	5.28	0	0.74	8862
Vitgrundsfladen	8	290	13881	47.9	7	1.7	9192
Kikarharan	9	290	1809	6.24	0	1.5	8627
Ägglösen	10	290	2988	10.3	0	2.2	8201
Stridsbådan	11	131	109	0.83	0	2.7	10309
Norrsten	12	131	80	0.61	0	21.6	11428
Hållskären	13	131	233	1.78	0	1.3	6210
Bodskäret	14	131	485	3.70	0	3.5	6555
Västerskäret	15	131	29	0.22	0	4.6	6157
Måskobben	16	131	711	5.43	0	1.2	3872
Måsten	17	131	2329	17.8	0	24.8	2803
Lillvåna	18	131	1889	14.4	0	1	3016
Storkorssten	19	131	458	3.50	0	5.1	3485
Storläget, västra	20	131	1194	9.11	0	2.4	2701

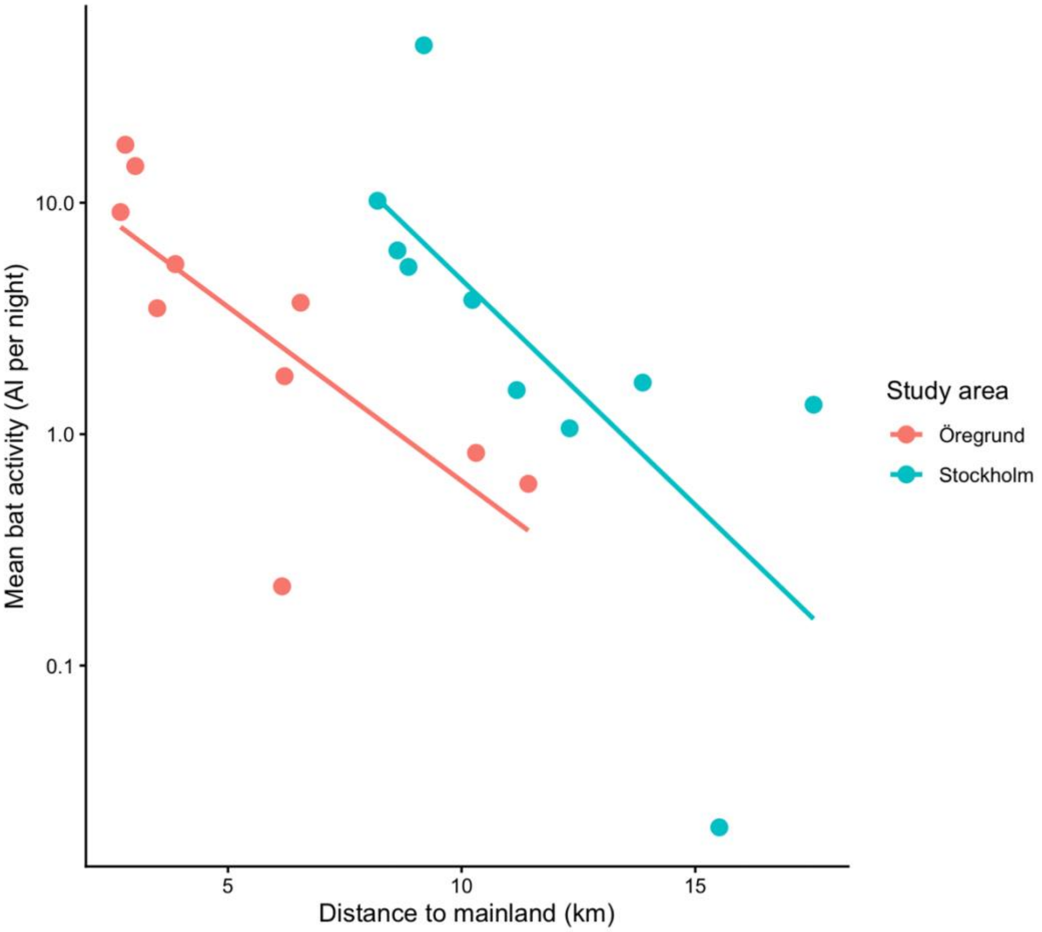

Figure 6: Mean bat activity (MAI) in relation to distance to coast (km) for all sites in the Stockholm archipelago and Öregrund. Each point represents mean AI per night for each islet. Y-axis is on log scale for clarification.

Discussion

Seasonal movements

When bat activity was visualised against DOY, a clear difference in seasonal activity was shown between the two species. *E. nilssonii* reached peak activity in late July- early August, with a decline towards autumn, while *P. pygmaeus* reached highest activity numbers in early September. Both species had a steep decline in activity throughout September with very few active minutes in October, suggesting a gradual transition to hibernation places at that time. Results suggests that *P. pygmaeus* generally stay in the Stockholm and Öregrund archipelago for a longer period of time during the autumn, while *E. nilssonii* migrate earlier towards hibernation sites. The late observations of activity in especially *P. pygmaeus* as well as the activity peak in early November reflect previous research, suggesting increasing bat activity as a result of foraging prior to hibernation (Fleming 2019, Speakman and Rowland 1999).

Effects of spatial variation

Bat activity differed significantly between different islands, with mean activity per night varying from 0.02 to 47.9 active minutes. These results correlated strongly with distance from each site to the mainland, with a decrease in bat activity with ~ 11.6 % for every 1 km increase to larger land areas. The observed decline in activity with increasing distance to land areas suggests that the observed activity patterns reflect foraging behaviour rather than migration. If the activity reflected migratory behaviour, bat activity would regardless of distance be expected to occur more evenly across the recorded islands, as migrating bats are capable of crossing large water bodies when migrating to hibernation sites (Hutterer et.al. 2005, Rodrigues 2014).

The decrease in activity with increasing distance to mainland instead indicate that bats (originating from bigger land areas) make shorter foraging trips to the archipelago, and with increasing distances to larger land areas, the amount and frequency of bats occurring on more distant islands is limited (Winifred et.al. 2008). Median AI values were zero for all surveyed islands except Vitgrundsfladen, supporting the idea that most offshore islands were visited more occasionally. Island area did not have a significant relationship with bat activity, indicating that island size does not have a clear individual effect. Instead, results indicate that island location plays a greater role in attractiveness to bats.

Effects of weather parameters

The result show that the two mainly weather parameters affecting short term bat activity patterns in Stockholm and Öregrund archipelago during the study period were wind speed and precipitation. Wind speed was the significantly strongest affecting weather parameter, with activity decreasing with 14 and 17 % for every 1 m/s increase in *P. pygmaeus* and *E. nilssonii,* and AI close to 0 at wind speeds above 8-9 m/s for both species. In addition, precipitation was an important affecting parameter, with a decline in activity with more than 50 % with occurring rainfall for both species. The effect of temperature was weak but significant for *E. nilssonii*, with an increase of bat activity with 9 % for every 1 °C increase.

The observed preference for lower wind speeds and low precipitation is suggested to reflect a balance of cost versus benefit between the costs of flight and the gains in energy obtained from insect prey. This relationship could partly be explained by the fact that insect abundance generally declines with increasing wind speed, precipitation, and declining temperature (Racey 1987, Pasek 1988, Lawson 2019) and partly due to the higher cost of flight for bats in unfavourable weather conditions (Erickson 2002, Racey 1987). A possible explanation to reduced activity during precipitation might be that rain interferes with bat echolocation calls, making it harder for bats to navigate and forage during such circumstances (Voigt 2011).

Implications for conservation

The expansion of offshore wind farms play an important role in the transition towards fossil free energy production in Sweden (Swedish Energy Agency 2023). Although, offshore wind farms can be a threat to migratory bats as seen in previous studies (Geidnert 2025, Seebens-Hoyer 2026, Ahlen 2009). However, previous studies have focused primarily on the effects on long distance migrating bats, and increased knowledge about other bat activity patterns (such as foraging behaviour) in archipelago environments is necessary to make successful curtailment models for offshore wind farms in the area. The results of this study highlight the importance of coastal archipelagos as foraging environments for bats during the post-colony period and can be of importance for offshore wind energy facilities when modelling curtailment schemes in similar environments.

Future research

The two species were not equally represented in the dataset, due to the fact that *P. pygmaeus* accounted for 81 % of the target species bat activity. Future studies could improve the representation of these less common species by extending the study period to create more credible comparisons. Spatial comparisons between

Stockholm and Öregrund archipelago could also favour from more evenly distributed monitoring periods across the different study areas. Also, by increasing the amount of manually validated recordings from 150 files per species, the reliability of automatically identified audio files included in the analysis would improve. Furthermore, future studies could if possible collect weather parameters directly from monitoring sites to obtain more accurate weather data from each site. A relevant extension of the study would be to investigate how insect abundance varies among different islands and during varying weather conditions (possibly with the use of a suction trap), and how this influences bat activity. Lastly, research regarding wind direction as a potential influence on bat activity across different locations in the archipelago could be performed. Strong winds in certain directions could potentially drive bats greater distances offshore or prevent them from flying into the archipelago and could therefore possibly work as an indicator of where bat abundance will increase or decrease in the near future.

Conclusions

This study demonstrates seasonal, spatial and weather-related activity patterns of the short distance migrating bats *E. nilssonii* and *P. pygmaeus* in the Stockholm and Öregrund archipelago. Results suggests that *P. pygmaeus* generally stay in the archipelago for longer periods during the autumn, while *E. nilssonii* migrate earlier towards hibernation sites. Furthermore, wind speed and precipitation were the most important factors negatively affecting bat activity during the study period, possibly due to a mixture of increasing flight cost and declining prey abundance. In addition, bat activity decreased significantly with increasing distance to the mainland, arguing that more isolated islands are visited less frequent than islands closer to larger land areas. These findings suggest that the presence of *E. nilssonii* and *P. pygmaeus* on offshore archipelago islands in the Baltic Sea area during the post colony period primarily reflects foraging behaviour rather than migration movements.

The results highlight the importance of coastal archipelagos as foraging environments for regionally migrating bats during the post-colony period. The understanding of how bats use these coastal habitats, and how their activity responds to different weather conditions, contribute to a better understanding of bat ecology in northern archipelago environments.

Declaration of the use of AI

AI (ChatGPT version 5.3) was used in the creation of the scripts used in R for the statistical analysis of the data. During the process, the generated script was rewieved, controlled and edited to ensure credibility. Full script is available in Appendix.

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Appendix

Full script used for statistical analysis and creation of all figures in the report: https://drive.google.com/file/d/1YKuomklbcqf-15bUBMKBQS3jtvDwoyF-/view?usp=sharing

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