



Spatiotemporal occurrence of bats at the southern North Sea 2017-2020

Authors: Sander Lagerveld, Steve C.V. Geelhoed, Tony Wilkes, Bart Noort, Marinka van Puijenbroek, Jan Tjalling van der Wal, Hans Verdaat, Martijn Keur & Josien Steenbergen

Wageningen University &
Research report C031/22A

Spatiotemporal occurrence of bats at the southern North Sea 2017-2020

Authors: Sander Lagerveld, Steve C.V. Geelhoed, Tony Wilkes, Bart Noort, Marinka van Puijenbroek, Jan Tjalling van der Wal, Hans Verdaat, Martijn Keur & Josien Steenbergen

Wageningen Marine Research
IJmuiden, July 2023

Wageningen Marine Research report C031/22A

Keywords: Bats, North Sea, Spatiotemporal occurrence, Offshore wind energy, Curtailment, Bat migration

Client: RWS Water, verkeer en Leefomgeving (WVL) - WOZEP
Attn.: Mevr. D. van Nieuwpoort / Dhr. M. Platteeuw
Postbus 17
8200 AA, Lelystad

Zaaknummer 31127573.0003

This report can be downloaded for free from <https://doi.org/10.18174/571525>
Wageningen Marine Research provides no printed copies of reports

Wageningen Marine Research is ISO 9001:2015 certified.

Photo cover: René Janssen

© Wageningen Marine Research

Wageningen Marine Research, an institute within the legal entity Stichting Wageningen Research (a foundation under Dutch private law) represented by

Drs. ir. M.T. van Manen, Director Operations

KvK nr. 09098104,

WMR BTW nr. NL 8113.83.696.B16.

Code BIC/SWIFT address: RABONL2U

IBAN code: NL 73 RABO 0373599285

Wageningen Marine Research accepts no liability for consequential damage, nor for damage resulting from applications of the results of work or other data obtained from Wageningen Marine Research. Client indemnifies Wageningen Marine Research from claims of third parties in connection with this application.

All rights reserved. No part of this publication may be reproduced and / or published, photocopied or used in any other way without the written permission of the publisher or author.

A_4_3_2 V32 (2021)

Contents

Summary	4
1 Introduction	6
1.1 Background and problem definition	6
1.2 Aim of the study	7
1.3 Research questions	7
2 Material & Methods	8
2.1 Equipment	9
2.2 Monitoring periods	11
2.3 Monitoring data	11
2.4 Spatiotemporal occurrence	12
2.4.1 Data management	12
2.4.2 Analysis	14
2.5 Movement analysis	14
2.5.1 Data management	14
2.5.2 Analysis	15
3 Results	16
3.1 Monitoring effort	16
3.2 Recorded bat activity	16
3.3 Spatio-temporal analysis	20
3.4 Movement analysis	24
4 Discussion	26
4.1 Occurrence in spring	26
4.2 Spatio-temporal occurrence in autumn	26
4.3 Environmental predictors	28
4.4 Limitations of our study	29
5 Conclusions	30
6 Recommendations	31
7 Acknowledgements	32
8 Quality Assurance	33
References	34
Annex 1: monitoring locations	40
Annex 2: date-time plots	43
Annex 3: output spatiotemporal analysis	59
Annex 4: output movement analysis	62

Summary

The aim of this study is to provide policy makers with information on where, when and under which conditions bats can be expected to occur at the southern North Sea. This will enable them to take the occurrence of bats into account in marine spatial planning and when developing and implementing mitigation measures in current and future offshore wind farms.

The main research questions of this study are:

1. How is the probability of the presence distributed over space and time at the southern North Sea?
2. What is the migration speed and distance travelled per night?

To answer these questions we performed acoustic monitoring of bats at 14 locations across the southern North Sea in the years 2017-2020. In total we monitored 11,520 nights, with most effort during the active season of bats, which roughly extends from mid-March until November.

In accordance to previous studies *Nathusius' pipistrelle* was the most commonly recorded species, but occasionally Common pipistrelle and *Nyctaloids* (includes the genera *Nyctalus*, *Vespertilio*, *Eptesicus*) were noted as well. We restricted our statistical analysis to the occurrence of *Nathusius' pipistrelle* in autumn, as spring records were relatively scarce.

The *Nathusius' pipistrelle's* spatio-temporal occurrence was modelled with a Bernoulli Generalized Additive Model (GAM) to predict the presence per night as a function of the covariates Night in year, Year, Tailwind, Crosswind, Atmospheric pressure, Atmospheric pressure change, Cloud class, Rain, Lunar phase and a spatial component (Longitude x Latitude). Important predictors for the offshore occurrence of *Nathusius' pipistrelle* proved to be Night in year, Tailwind, Crosswind, Lunar cycle and the spatial component. The covariates Rain and Atmospheric pressure change were of minor importance, whereas Cloud class and Atmospheric pressure were not important.

To answer the second research question we used a Gamma Generalized Additive Model with log-link function to model the relationship between the time after sunset of positive minutes with bat activity as response variable and the covariates Distance from shore and Night in year. Distance from shore proved to be important for the timing of offshore occurrence, whereas Night in year was not important at all.

From our study we conclude that:

- *Nathusius' pipistrelle* is the most common bat species at the southern North Sea. Offshore activity of it continues till later in the year than previously thought (until the end of October). Late migrants possibly refer to adult males.
- Migration over sea occurs regularly during consecutive nights and offshore structures are used as roosts during the day. Therefore, the offshore occurrence of *Nathusius' pipistrelle* varies considerably during the night, in particular at locations further away from the coast.
- The average timing of occurrence shows a linear relationship with the distance to the coast between 30 and 60 km from shore, corresponding to an average movement speed of 25.1 km/h.
- Our study predicts an offshore distribution of *Nathusius' pipistrelle* with higher probabilities of bat presence further away offshore off the North Holland coast. This east-west gradient is caused by individuals which are detected when they continue their migration after a roost at sea during the day. The increased probability of occurrence off the coast of North Holland in comparison to that further north and south may reflect real differences in bat abundance.
- Most migration activity is to be expected with a light tailwind, although higher tail wind speeds may result in animals flying at altitudes above the detection range of our bat detectors. In addition, the offshore occurrence of bats can also be expected with light to moderate crosswinds, in particular from land, as well as with headwinds. It should be stressed that the effect of wind speed and wind direction should always be considered together.

-
- The observed relationship between the lunar phase and offshore bat occurrence may be caused by reduced migratory bat activity during higher phases of the moon to avoid predation, or by bats making use of increased insect availability over sea, or by a combination of both factors.
 - Finally, our observations show that the occurrence of bats at sea was reduced in 2020 in comparison to the previous years. Although 2017-2020 is a short period to draw firm conclusions, a decline cannot be ruled out.

When designing, developing and implementing mitigation measures to reduce the potential impact of offshore wind farms on bats, these measures should take the following elements into account:

- seasonal occurrence: autumn migration takes place between late August and late October.
- spatial distribution: the highest densities are likely present west off the coast of North Holland.
- daily temporal occurrence: bats may occur throughout the entire night, in particular at locations further away from the coast. Bat activity during daylight hours occurs occasionally.
- wind speed and wind direction: most offshore migration can be expected during light tailwind conditions (ENE). However, it seems also likely that migration can be expected during stronger tailwinds at higher altitudes. Furthermore, migration also occurs during with light to moderate crosswinds, in particular from land, as well as with light to moderate headwinds. Note that the wind speeds mentioned in this report refer to wind speeds measured at an altitude of 10 m above sea level, and that the wind speeds increases with height. Mitigation measures therefore should not be based on wind speeds measured at nacelle level when using information from this report.
- lunar phase: bat presence is decreased between full moon and last quarter, and increased just before new moon.

To answer remaining questions we recommend:

- to focus future studies on flight heights of bats in spring and autumn, since little is known about the vertical distribution of migrating bats and the effect of environmental parameters on their flight height, particularly wind speed and wind direction.
- to conduct telemetry studies data to provide information on attraction by offshore wind farms, and flight behavior within a wind farm. Furthermore, telemetry can likely provide information on spring migration more effectively than acoustic monitoring.
- to continue offshore acoustic monitoring of bats with the current monitoring network to follow the long-term trend of bat migration over the southern North Sea.

1 Introduction

1.1 Background and problem definition

In order to reduce carbon emissions the offshore wind sector is developing rapidly in the North Sea area. In Dutch waters, the installed capacity is around 2.5 GW in 2022 and this will increase to 11.5 GW in 2030. Despite this environmental gain, there are concerns about biodiversity at the same time. One of the main ecological issues is wind turbine induced mortality amongst bats due to collisions, and possibly barotrauma (Arnett et al 2008, Bach & Rahmel 2004, Baerwald et al 2009, Cryan et al 2014, Grodsky et al 2011, Kunz et al 2007, Lawson et al 2020, Rollins et al 2012, Rydell et al 2010). It is estimated that in Germany 250,000 bats are likely killed annually in wind farms on land (Voigt et al 2015), whilst 600,000 bat fatalities have been reported in one year in the USA (Hayes 2013). As bats behave in a similar way around offshore wind turbines in comparison to wind turbines on land (Ahlén et al 2009), it seems likely that fatalities also occur at sea.

The spatial planning of wind farms is an important determinant of the mortality (Rydell et al 2010). In addition to the location choice the number of fatalities can subsequently be reduced by operational measures. Effective mitigation has been achieved by limiting the production time of wind turbines during periods when bats are most active (Adams et al 2021, Arnett et al 2011). A further decrease of the mortality may be realized by the application of deterrents (Arnett et al 2013, Gilmour et al 2020).

Nathusius' pipistrelle *Pipistrellus nathusii* is the most frequently reported bat species at the North Sea, but Common pipistrelle *P. pipistrellus*, Common noctule *Nyctalus noctula*, Leisler's bat *N. leisleri*, Particolored bat *Vespertilio murinus*, Northern bat *Eptesicus nilssonii*, and Serotine bat *E. serotinus* have also been recorded (Boshamer & Bekker 2008, Brabant et al 2021, Hüppop & Hill 2016, Lagerveld et al 2014, 2017, 2021). Ringing recoveries from the UK show that most Nathusius' pipistrelles follow a ENE – WSW route during their migration (National Nathusius' Pipistrelle Project 2022). An analysis of its autumn occurrence in 2012-2016 at three offshore wind farms off the Dutch coast revealed that their migration over sea occurs mainly from late August until mid-October during easterly tailwinds with a distinct peak at ENE, wind speeds < 5 m/s and temperatures > 15°C (Lagerveld et al 2021). Off the Belgian coast a relationship with a relatively high atmospheric pressure was found, in addition to low easterly winds and higher temperatures (Brabant et al 2021). At a research platform in the German Bight however, most bats are recorded in overcast conditions with precipitation during southerly winds (Hüppop & Hill 2016). As different regions produce contradicting results it is urgently needed to study the offshore occurrence of bats at a larger spatial scale. Moreover, it is not known whether migrating bats cross the North Sea in a broad front, like many bird species do (Lack 1963ab), or whether spatially distinct migration patterns can be identified. If so, the suitability of areas for offshore wind developments may be identified based on relationships between bat activity, geographical location, and weather patterns.

As bats have a strictly protected status by national and international regulations, in 2017 a bat monitoring project started under the umbrella of the Dutch Governmental Offshore Wind Ecological Programme (Wozep) to reduce uncertainties about possible impacts. During this project we performed ultrasonic acoustic monitoring at 14 locations at the southern North Sea during four consecutive years, and assessed the probability of presence distributed over space and time. Furthermore, we investigated the migration speed over sea and the distance travelled per night.

1.2 Aim of the study

The aim of this study is to provide policy makers with information on when and under which conditions bats can be expected in current and future offshore wind farms. This will enable them to take the occurrence of bats into account in marine spatial planning and when designing, developing and implementing mitigation measures for offshore wind farms.

1.3 Research questions

The principal research questions of this study are:

- 1 How is the probability of the presence distributed over space and time at the southern North Sea?
- 2 What is the migration speed and distance travelled per night?

2 Material & Methods

2.1 Study area

Since wind energy production in the coming years in the Dutch Exclusive Economic Zone (EEZ) will be developed mostly west of the Dutch Provinces Noord Holland, Zuid Holland and Zeeland, most monitoring locations are located in that area. Figure 1 shows a map of the study area where acoustic bat monitoring has been taking place in the period 2017 -2020

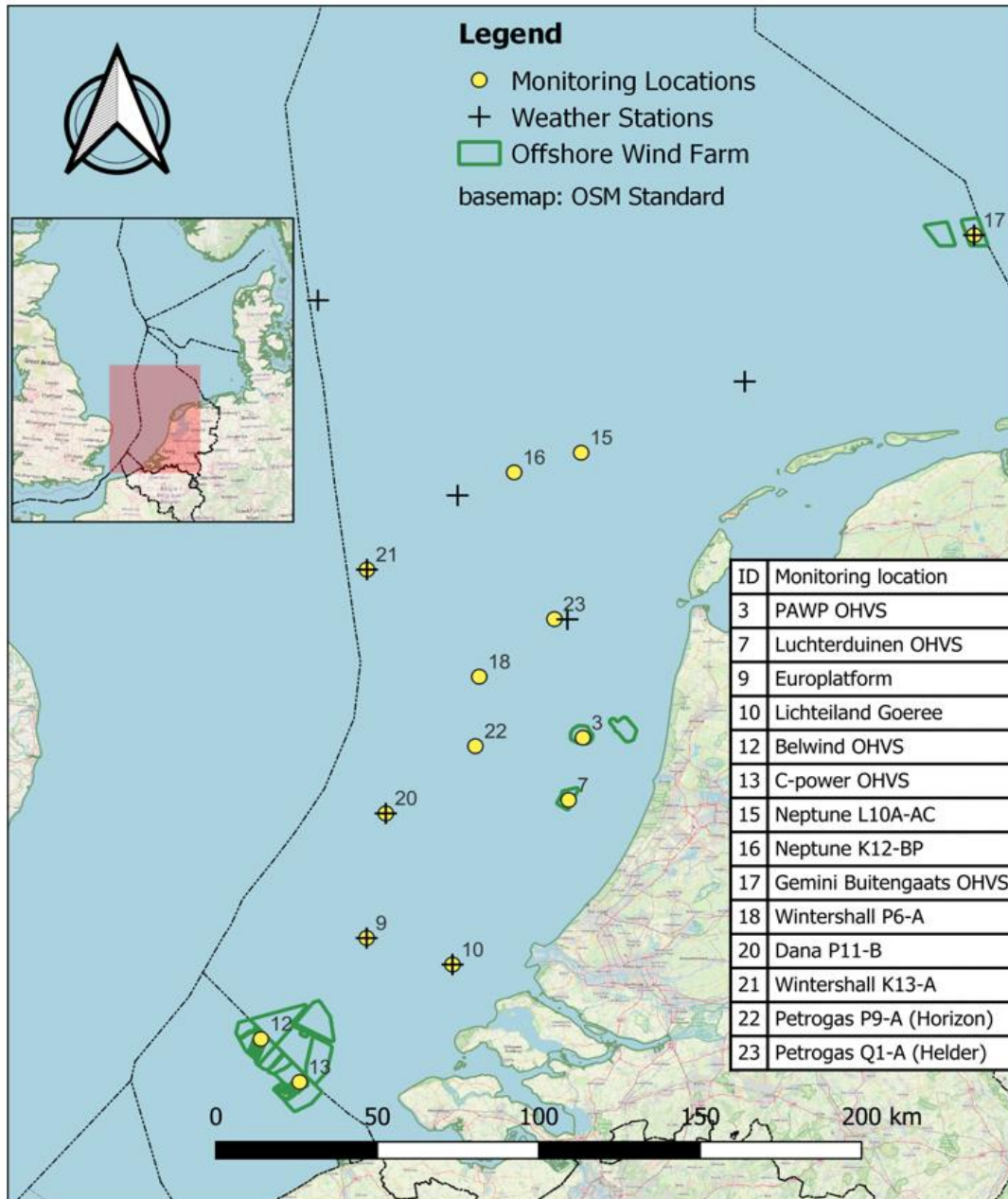


Figure 2-1. Acoustic monitoring network 2017-2020, including KNMI offshore weather stations and the operational offshore wind farms in Dutch and Belgian waters

The monitoring locations include five offshore high voltage stations (OHVS) in wind farms (PAWP, Luchterduinen, Belwind, C-Power & Gemini Buitengaats), two measurement platforms (Europlatform & Lichteiland Goeree) and seven gas production platforms (Neptune L10A-AC, Neptune K12-BP, Wintershall P6-A Dana P11-B, Wintershall K13-A, Petrogas P9-A (Horizon) & Petrogas Q1-A (Helder)). The geographical locations as well as the height and the orientation of the ultrasound microphones can be found in table 2-1. Photos of the monitoring locations can be found in Annex 1.

Table 2.1. Geographical location of the monitoring locations, height and orientation of the microphones.

No.	Location	Longitude	Latitude	Height above sea level [m]	Orientation microphone [degrees]
3	PAWP OHVS	4.23	52.58	15	90
7	Luchterduinen OHVS	4.17	52.40	15	90
9	Europlatform	3.27	51.99	15	90
10	Lichteiland Goeree	3.66	51.92	15	90
12	Belwind OHVS	2.81	51.69	20	90
13	C-power OHVS	2.99	51.57	15	60
15	Neptune L10A-AC	4.20	53.40	17	90
16	Neptune K12-BP	3.89	53.34	20	135
17	Gemini Buitengaats OHVS	6.04	54.03	26	135
18	Wintershall P6-A	3.75	52.75	23	110
20	Dana P11-B	3.34	52.35	25	90
21	Wintershall K13-A	3.22	53.05	25	130
22	Petrogas P9-A (Horizon)	3.74	52.55	33	45
23	Petrogas Q1-A (Helder)	4.09	52.92	25	200

2.1 Equipment

Bat activity was monitored with an Avisoft - UltraSoundGate 116Hnbm in combination with an Electret ultrasound microphone FG-DT50. The settings of the UltraSoundGate recording software (Avisoft Bioacoustics RECORDER v. 4.2.29) are shown in Table 2-2.

Table 2-2. Software settings of the UltraSoundGate.

Parameter	Value	Parameter	Value
Pre-trigger	0.1 s	Buffer	0.064 s
Hold tm	0.8 s	Bat call filter	Enabled
Duration	> 0 s	Accept monotonic structures	Enabled
Syllable	> 0 s	Min sweep rate FM	-20 KHz/ms
Reject wind/rain	enabled	Min sweep rate CF	-3 KHz/ms
Trigger event level	0.501%	Max sweep rate FM	-1 KHz/ms
Trigger event range	15-100kHz	Max sweep rate CF	2 KHz/ms
Sampling rate	250000Hz	Min duration FM	1 ms
Format	16 bit	Min duration CF	2 ms

The microphone was enclosed in a waterproof box (Figure 2-2 and 2-3) and connected through a S/FTP Cat 7 Marine Approved network cable (Petrogas P9-A (Horizon) and Petrogas Q1-A (Helder) platforms) or 2Triple x 0.75mm² (CI2 TCC) RFOU(I)S1/S6 EPR/ICM/ZHAL/TCWB/ZHAL BLUE 250v cable (all other monitoring locations) with the soundgate in the computer room. In order to avoid spray during strong westerlies, the microphones were orientated in an easterly direction, if technically feasible (Table 2-1).



Figure 2-2. Ultrasound microphone at Lichteiland Goeree.



Figure 2-3. Ultrasound microphone at Gemini Buitengaats OHVS.

The performance of the equipment was checked regularly at the monitoring locations with internet connectivity (PAWP, LUD, Lichteiland Goeree, Belwind, C-Power, Neptune L10-AC and Neptune K12-B, Dana P11-B, Petrogas P9-A and Petrogas Q1-A). Checks were done once per week from week 13 until week 23 and from week 34 until week 45, and once per four weeks outside these periods. The performance of the equipment at locations without internet connection could not be checked regularly. At all locations, the microphones of the equipment were replaced twice a year; late February/early March and late July/early August, and subsequently recalibrated by the manufacturer Avisoft Bioacoustics.

2.2 Monitoring periods

We aimed to monitor throughout the active season of bats which runs roughly from mid-March until November. However, logistical problems, reduced sensitivity of microphones and PC errors caused downtime. The effective monitoring periods per location per year are shown in Table 2-3.

Table 2-3. Monitoring periods per monitoring location per year (2017 – 2020).

No.	Location	2017	2018	2019	2020
3	PAWP OHVS	02/08 - 31/12	13/01 - 31/12	01/01 - 18/10 22/11 - 31/12	01/01 - 07/02 04/03 - 31/12
7	Luchterduinen OHVS		04/04 - 18/07 15/08 - 31/12	01/01 - 31/12	06/04 - 12/06 04/08 - 03/09
9	Europlatform		06/03 - 31/12	01/01 - 31/12	18/02 - 17/05 30/07 - 25/09
10	Lichteiland Goeree	27/09 - 31/12	06/03 - 18/11	09/05 - 31/12	24/06 - 30/10
12	Belwind OHVS	02/08 - 26/12	01/03 - 31/12	01/01 - 31/12	01/01 - 30/09
13	C-power OHVS		28/02 - 31/12	01/01 - 31/12	21/06 - 27/07 10/09 - 19/09
15	Neptune L10A-AC	18/08 - 31/12	01/01 - 31/12	01/01 - 31/12	21/03 - 08/04 23/09 - 13/11
16	Neptune K12-BP	26/07 - 11/12	24/01 - 31/12	01/01 - 31/12	18/03 - 31/05 22/09 - 09/11
17	Gemini Buitengaats OHVS		16/03 - 31/12	01/01 - 31/12	13/03 - 30/06 09/09 - 31/12
18	Wintershall P6-A	31/10 - 31/12	11/03 - 21/12	01/01 - 31/12	01/01 - 04/06 13/07 - 31/12
20	Dana P11-B			25/02 - 27/06 11/07 - 31/12	15/02 - 06/06 23/07 - 31/12
21	Wintershall K13-A			01/01 - 22/08 19/09 - 27/09 01/12 - 31/12	04/08 - 16/12
22	Petrogas P9-A (Horizon)		15/11 - 31/12	01/01 - 31/12	01/01 - 08/06 25/06 - 07/07 26/07 - 16/11
23	Petrogas Q1-A (Helder)		11/09 - 31/12	01/01 - 31/12	01/01 - 31/12

2.3 Monitoring data

Echolocating bats emit ultrasonic pulses to gain information about their environment. Ultrasonic sounds are however also produced by wind gusts or by maintenance and production activities at offshore platforms. Therefore, the separation of recordings with bat calls and recordings with 'noise' needs to be done first. We used the cross-correlation function of Avisoft SASlab Pro – version 5.2.14 (Avisoft bioacoustics) to extract the recordings with bat calls from the raw monitoring data. Reference calls for the cross-correlation included 8 recordings of Nathusius' pipistrelle *Pipistrellus nathusii*, 4 recordings of common pipistrelle *Pipistrellus pipistrellus*, 4 recordings of pond bat *Myotis dasycneme*, 18 recordings of common noctule *Nyctalus noctula*, 5 recording of serotine bat *Eptesicus serotinus* and 31 recordings belonging to the Nyctaloid group (includes the genera *Nyctalus*, *Vespertilio*, *Eptesicus*). Subsequently, all recordings with bat calls were assessed individually and identified to the lowest taxonomic level as possible using the criteria provided by Barataud (2016).

All monitoring data (species, date, time, monitoring location), information on the monitoring locations (geographical location, height and orientation of the microphone) and monitoring periods (monitoring location, start date/time, end date/time) were stored in a database.

Processing of the data was done in R version 4.1.2 (R Core Team 2020) and R studio version 2021.09.2 (RStudio Team 2020), preliminary using the R-packages tidyverse (Wickham et al 2019), lubridate (Grolemund & Wickham 2011), datatable (Dowle & Srinivasan 2021), matlib (Friendly et al 2021), gstat (Gräler et al 2016, Pebesma 2004), sf (Pebesma 2018) and vmstools (Hintzen et al 2017).

In order to visualize the monitoring results, date-time plots were made in which the recorded bat activity in positive minutes is shown throughout the season and the night. Furthermore, we plotted the number of monitoring locations with recorded bat activity per night throughout the season. The plots were made using ggplot2 (Wickham 2016).

2.4 Spatiotemporal occurrence

2.4.1 Data management

Since bats are nocturnal we analysed their occurrence per night instead of per calendar day. A night was defined as the period between 16:00 UTC on a particular calendar day until 16:00 UTC the next calendar day. We only included *Nathusius' pipistrelle* in the analysis as this is the most frequently recorded species in our data set (92% of the positive minutes with bat activity).

Due to the low number of nights with bat activity in spring we limited the analysis to autumn from night number 230 (17 or 18 August, depending on the year) till night number 321 (16 or 17 November, depending on the year). We excluded monitoring location 17 (Gemini Buitengaats OHVS) from the analysis because of its isolated northeasterly location. The time frame considered consisted of 3255 monitoring nights in total of which bats were recorded in 251 of the nights (7.7% of the data).

Offshore weather data per hour of various offshore weather stations (203, 204, 207, 211, 212, 214, 252, 321, 320) were obtained from the Royal Dutch Meteorological Institute (https://www.knmi.nl/nederland-nu/klimatologie/uurgegevens_Noordzee), retrieved at 15 July 2021. Weather variables used are: wind direction averaged over 10 minutes, wind speed averaged over 10 minutes measured at an altitude of 10 m above sea level, temperature at 1.5 m height, atmospheric pressure at sea level, cloud cover in octants and rain. For the latter variable a 1 indicates rain occurred in the preceding hour or at the time of observation, 0 indicates it did not. Cloud class 9 (sky invisible) and wind directions with values of 0 (no wind) and 990 (variable direction) were set to NA.

The main migration direction in autumn off the Dutch coast likely runs from east-north-east to west-south-west (National *Nathusius' Pipistrelle* Project 2022, Lagerveld et al 2021). We used this presumed migration direction to derive the average tailwind and crosswind components per night (Hüppop & Hilgerloh 2012):

- 1) Tailwind component = $\text{COS}(\text{average wind direction [rad]} - \text{migration direction [rad]}) * \text{windspeed}$
- 2) Crosswind component = $\text{SIN}(\text{average wind direction [rad]} - \text{migration direction [rad]}) * \text{windspeed}$

Positive values of the tailwind component indicate supportive wind conditions in the migration direction, whereas negative values indicate headwind. The crosswind component is the wind vector perpendicular to the migration direction. Positive values of the crosswind component indicate wind from the right (from the north-north-west) and negative values indicate wind from the left (from the south-south-east).

In case of missing data we used the data of the two closest weather stations to impute the missing values. Finally, each monitoring location was allocated to the nearest weather station (Table 2-4). In addition to the

weather data, we included lunar phase as an extra covariate. The lunar phase was calculated using the R-package lunar (Lazaridis 2014).

In order to obtain the weather data averaged per night we removed the data before sunset and after sunrise at each weather station. We averaged the temperature, atmospheric pressure, cloud cover and rain for each night, with missing data ignored in averaging. In order to obtain an average wind speed per night and an average wind direction per night, we decomposed the hourly wind direction and speed values into "North" and "East" vector components. These vector components were averaged per night, and then were used to calculate the average wind speed using Pythagorean theorem. The angle of these vectors was used to calculate the average wind direction (see matlib (Friendly et al 2021) R-package). The atmospheric pressure change was calculated based on the average atmospheric pressure from a particular night minus the average atmospheric pressure from the previous night. Table 2-5 summarizes the covariates included in the analysis.

The codetools R-package (Tierney 2018) was used to check for scoping issues in R-functions, when applicable.

Table 2-4. Geographical locations of the weather stations, the nearest weather stations used for missing data, as well as the allocated monitoring locations.

STN	Location	Longitude	Latitude	Nearest weather stations	Allocated to monitoring location (Table 2-1)
203	Dana P11-B	3.34	52.35	321 / 204	7, 20
204	NAM K14-FA-1C	3.63	53.27	212 / 252	15, 16, 18
207	NAM L9-FF-1	4.96	53.61	204 / 214	
211	Spirit Energy J6-A	2.95	53.82	252 / 204	
212	Hoorn-Alfa	4.15	52.92	204 / 203	1,2,3, 22, 23
214	Gemini Buitengaats OHVS	6.04	54.03	207 / 212	17
252	Wintershall K13-A	3.22	53.05	204 / 211	4,21
321	Europlatform	3.27	51.99	203 / 321	9,12,13
320	Lichteiland Goeree	3.66	51.92	203 / 320	10

Table 2-5. Covariates used in the analysis.

Covariate	Definition
Night in year	Each night starts at 16:00 on day 1 and continues to 16:00 on day 2. 1 January starts with night number 1
Year	Calendar year
Tailwind	The nightly averaged wind vector from ENE to WSW [m/s]
Crosswind	The nightly averaged wind vector from NNW to SSE [m/s]
Atmospheric pressure	The nightly averaged pressure [hPa]
Atmospheric pressure change	The change in atmospheric pressure compared to the previous night [hPa]
Temperature	The nightly averaged temperature [°C]
Cloud class	The nightly averaged cloud class [octants]
Rain	The nightly averaged proportion of hours with rain [%]
Lunar phase	The period of lunar cycle is a lunar month (29.53 days) divided into 360°
Longitude	Longitude of the monitoring location
Latitude	Latitude of the monitoring location

2.4.2 Analysis

The correlation and linearity between the numerical covariates was assessed with a correlogram and pairs plot, using the R-packages `corrgram` (Wright 2021) and `GGally` (Schloerke et al 2021), respectively. Night in year appeared to be collinear with Temperature and the latter covariate was excluded from the analysis. The relationships between the response variable and the continuous covariates were checked graphically.

A Bernoulli Generalized Additive Model (GAM) with a logit link function was used to model the presence per night as a function of the covariates, using the `mgcv` R-package (Wood 2017). Longitude and latitude were entered together in a tensor product smoother to model spatial (auto)correlation. Night number was entered as a low-rank thin-plate smoother to model the seasonal-temporal pattern. Atmospheric pressure and Rain were entered as linear covariates. Cloud class, Atmospheric Pressure change, Tailwind and Crosswind were entered as low-rank thin-plate smoothers. Lunar phase was entered as a cyclic cubic regression smoother with boundary knots at 0 and 360 degrees and Year was entered as a categorical covariate. The linear covariates were centred when applicable. The `emmeans` R-package (Lenth 2022) was used to aid the factor level comparisons.

The Bernoulli GAM model was inclined to predominately predict zeros, due to the extensive zero-inflation (93.3%). In a presence-absence model, sensitivity is a measure of how well a test can identify true positives and specificity is a measure of how well a test can identify true negatives. The specificity (true negative rate) was found to be very high (nearly 1), but the sensitivity (true positive rate) was very low. By adding a small positive constant to the linear predictor after the model is fit, one can sacrifice a little bit of specificity to increase the sensitivity. This post-model constant is referred to as α . Values between 0 and 2, with increments of 0.025, were tried out for α , and the value for α was chosen in such a way that it maximized both sensitivity and specificity, and minimized the 0/1-loss, leading to $\alpha = 2$.

Thus the model can be formulated as follows:

$$y \sim \text{Bernoulli}(p)$$
$$\text{logit}(p) \sim \text{Intercept} + \text{Covariates} + \alpha$$

where y is the response variable (0= no bat activity recorded in a night, 1 = bat activity recorded in a night).

Dunn-Smyth residuals (Dunn & Smyth 1996) were used in residual diagnostic plots to check for violations of the model assumptions, using the R-package `DescTools` (Singorell et al 2021). The model fit (the accuracy of predicted means) of the model was checked by computing the specificity (true positive rate), sensitivity (true negative rate), and the 0/1-loss.

2.5 Movement analysis

2.5.1 Data management

In this analysis we considered the same monitoring period as in the previous analysis from night number 230 (17 or 18 August, depending on the year) till night number 321 (16 or 17 November, depending on the year). Again, a night was defined as the period between 16:00 UTC on a particular calendar day until 16:00 UTC the next calendar day.

For each positive minute with *Nathusius' pipistrelle* activity we assessed the time after sunset using the R-package `suncalc` (Thieurmel & Elmarhraoui 2019). From each monitoring location the distance to shore in a direction of 67.5 degrees was assessed using Google Earth. This corresponds with the likely main migration direction of *Nathusius' pipistrelle* over the North Sea from ENE to WSW (Lagerveld et al. 2021, National *Nathusius' Pipistrelle* Project 2022). Using this direction, the distance to the Dutch coast could not be assessed from the monitoring locations 15 (Neptune L10A-AC), 16 (Neptune K12-BP) and 17 (Gemini Buitengaats OHVS) located in the northern part of the study area (Figure 2-1). These monitoring locations were therefore excluded from the analysis.

The codetools R-package (Tierney 2018) was used to check for scoping issues in R-functions, when applicable.

2.5.2 Analysis

The time after sunset of positive minutes with bat activity was chosen as response variable. Covariates included in the analysis are Distance from shore to investigate the flight speed over sea, and Night in year to capture potential seasonal patterns. Note that the distance from shore was assessed along the likely main migration direction from ENE to WSW.

The correlation and linearity between the numerical covariates was assessed with a correlogram and pairs plot, using the R-packages corrgram (Wright 2021) and GGally (Schloerke et al 2021), respectively. The relationships between the response variable and the continuous covariates were checked graphically.

We used a Gamma Generalized Additive Model with log-link function to investigate the relationship between the response variable and the covariates, using the mgcv R-package (Wood 2017). Both covariates were included in the analysis in low-rank thin-plate smoothers.

Dunn-Smyth residuals (Dunn & Smyth 1996) were used in residual diagnostic plots to check for violations of the model assumptions. The model fit (the accuracy of predicted means) of the model was checked by computing the mean absolute deviation (MAD) and by determining the slope of the linear relation between the fitted and observed response values (should be close to 1). Checking the model diagnostics relied in part on the DescTools R-package (Signorell et al 2021).

3 Results

3.1 Monitoring effort

In total we monitored 11,520 nights during four consecutive years at 14 different locations. Table 3-1 shows the number of monitoring nights per location per year. The effort varied between locations and years, caused by logistical constraints, reduced sensitivity of microphones and PC errors. Note that monitoring frequently took place throughout the year (Table 2-3), thus also outside the active season of bats, which runs roughly from mid-March until November.

Table 3-1. Monitoring nights per location per year. See Table 2-3 for the monitoring periods.

No.	Location	2017	2018	2019	2020	Total
3	PAWP OHVS	151	352	329	339	1171
7	Luchterduinen OHVS	0	243	364	97	704
9	Europlatform	0	300	364	146	810
10	Lichteiland Goeree	95	257	236	128	716
12	Belwind OHVS	146	305	364	273	1088
13	C-power OHVS	0	306	364	45	715
15	Neptune L10A-AC	135	364	364	69	932
16	Neptune K12-BP	138	341	364	122	965
17	Gemini Buitengaats OHVS	0	290	364	222	876
18	Wintershall P6-A	61	285	364	326	1036
20	Dana P11-B	0	0	295	273	568
21	Wintershall K13-A	0	0	271	134	405
22	Petrogas P9-A (Horizon)	0	46	364	284	694
23	Petrogas Q1-A (Helder)	0	111	364	365	840
	<i>Total</i>	726	3200	4771	2823	11,520

3.2 Recorded bat activity

Figure 3-1 shows an example of the recorded bat activity offshore. In this figure the dots refer to positive minutes with acoustic activity throughout the monitoring season and during the nights (time interval between sunset and sunrise is represented by grey). Different colours represent different species or species groups; Pnat = *Nathusius' pipistrelle*, Ppip = Common pipistrelle, Nyctaloid = species group, includes genera *Nyctalus*, *Vespertilio* and *Eptesicus*. The effective monitoring effort is indicated by a white background, whereas a pink background indicates no monitoring due to equipment failures or logistical problems.

The recorded bat activity at PAWP in 2019 is a typical example of offshore bat activity off the Dutch west coast with *Nathusius' pipistrelle* as the most commonly recorded species and occasional records of Common pipistrelle and Nyctaloids. The offshore occurrence of *Nathusius' pipistrelle* is generally characterized by a few records in spring and multiple records in autumn. Most activity is recorded during the night, but sometimes also during daylight hours. Here, an individual arrived more than one hour after sunrise on 23 May 2019 and (likely the same individual) was recorded again the same evening just after sunset. Frequently, multiple records occur during one particular night which may refer to a single individual spending a prolonged time at the monitoring location, or multiple individuals passing through.

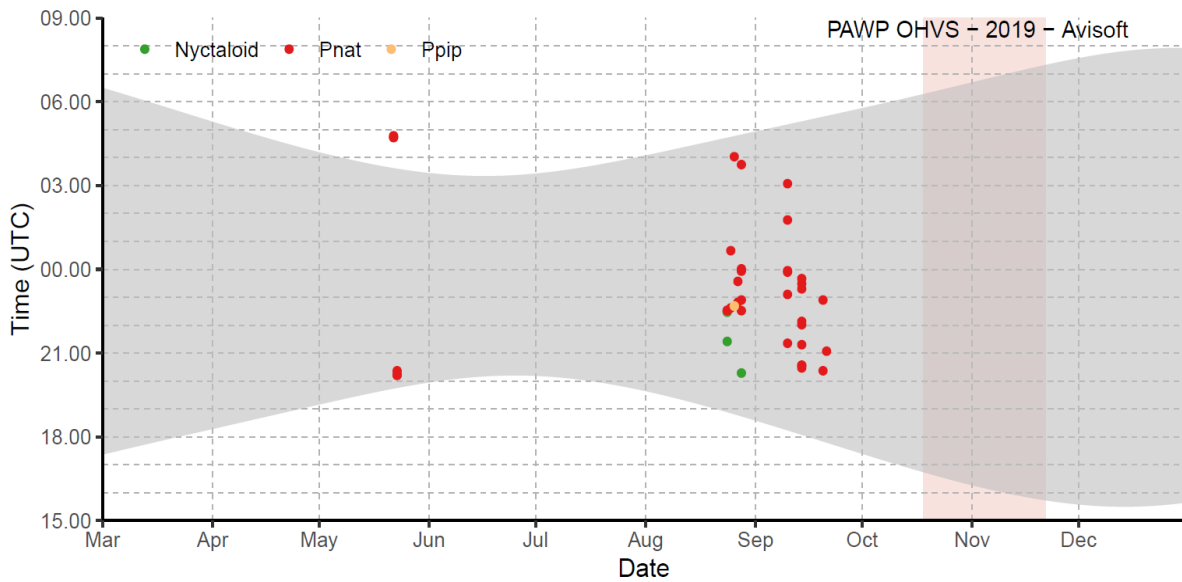


Figure 3-1. Acoustic bat activity in positive minutes at PAWP in 2019.

Figures 3-2 – 3-5 show the number of nights with recorded bat activity of *Nathusius’ pipistrelle* for each monitoring location in subsequent years (2017-2020). The header shows the effective monitoring effort per monitoring location, a white background indicates operational monitoring and a pink background indicates no monitoring. Note that *Nathusius’ pipistrelles* are frequently recorded at multiple monitoring locations during the same night. The spring migration season runs from late March until early June and peaks in April and May. The autumn migration season starts late August and the last individuals have been recorded early December. Most activity in autumn is recorded from late August until late October.

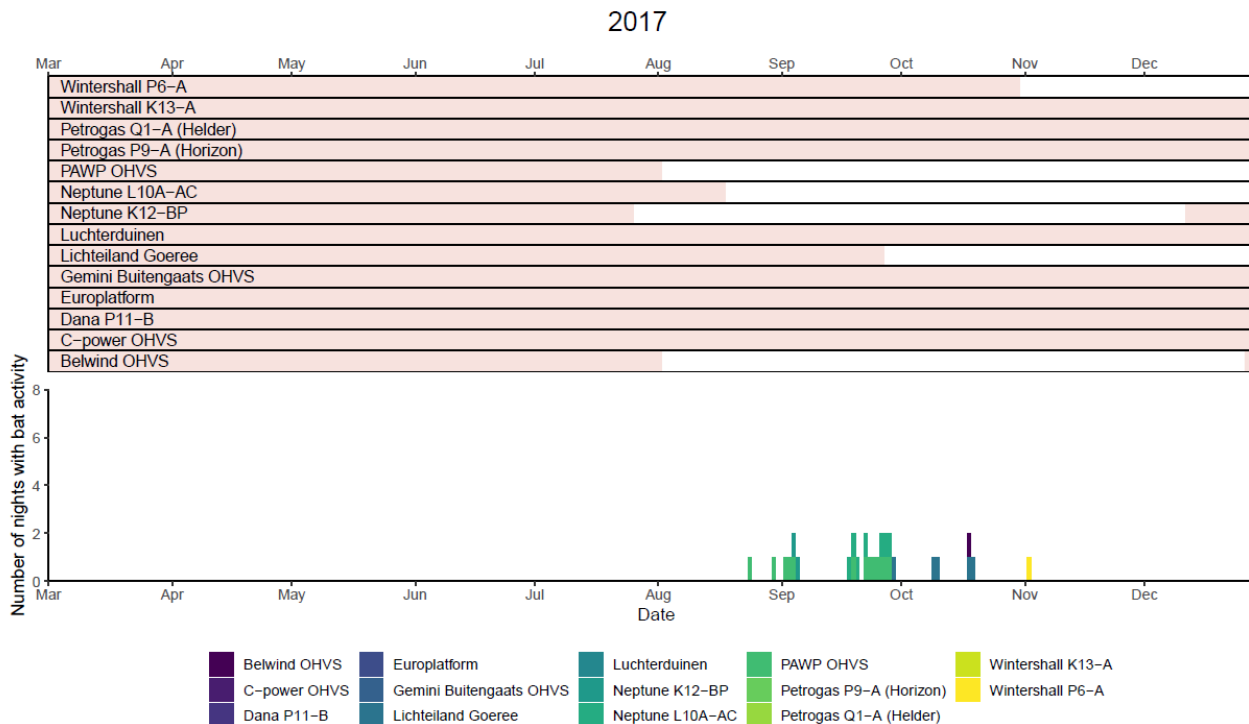


Figure 3-2. Number of nights with recorded bat activity of *Nathusius’ pipistrelle* in 2017. See Figure 2-1 for a map of the monitoring locations.

2018

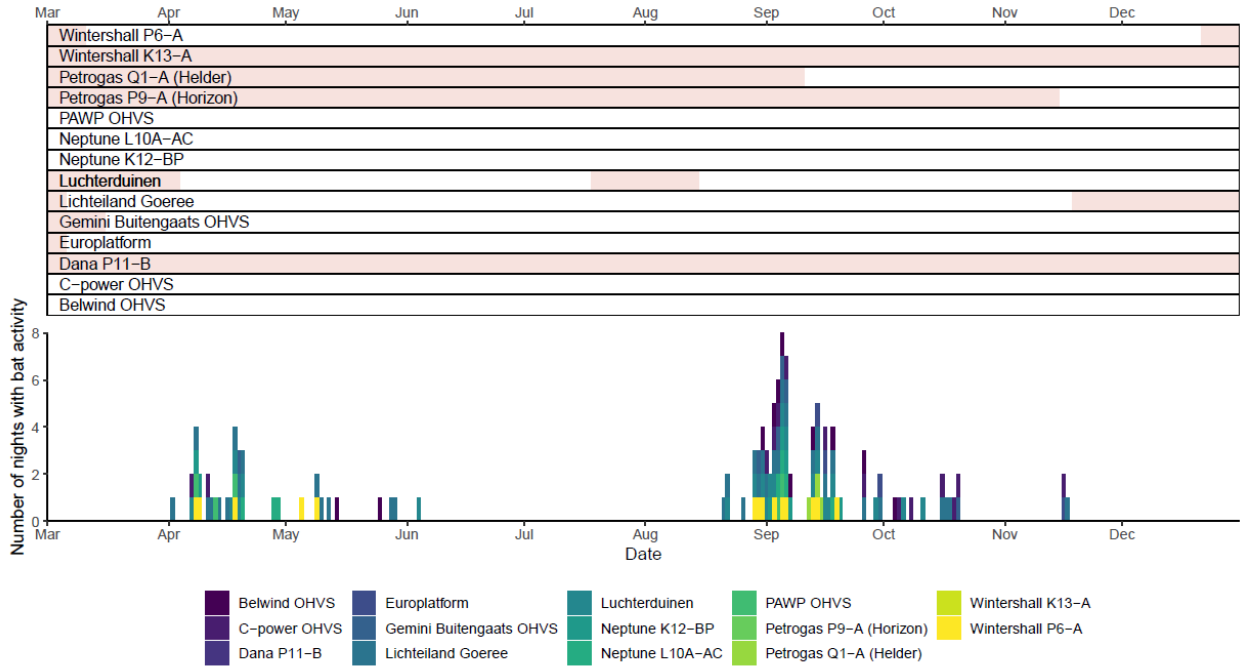


Figure 3-3. Number of nights with recorded bat activity of *Nathusius' pipistrelle* in 2018. See Figure 2-1 for a map of the monitoring locations.

2019

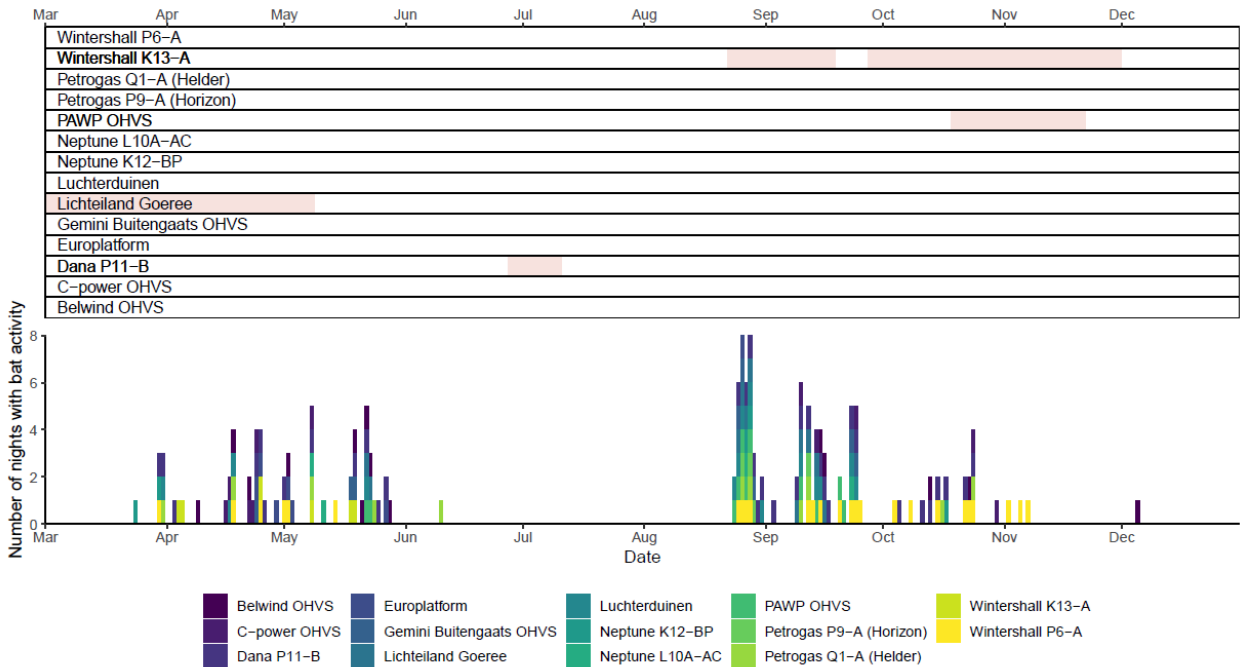


Figure 3-4. Number of nights with recorded bat activity of *Nathusius' pipistrelle* in 2019. See Figure 2-1 for a map of the monitoring locations.

2020

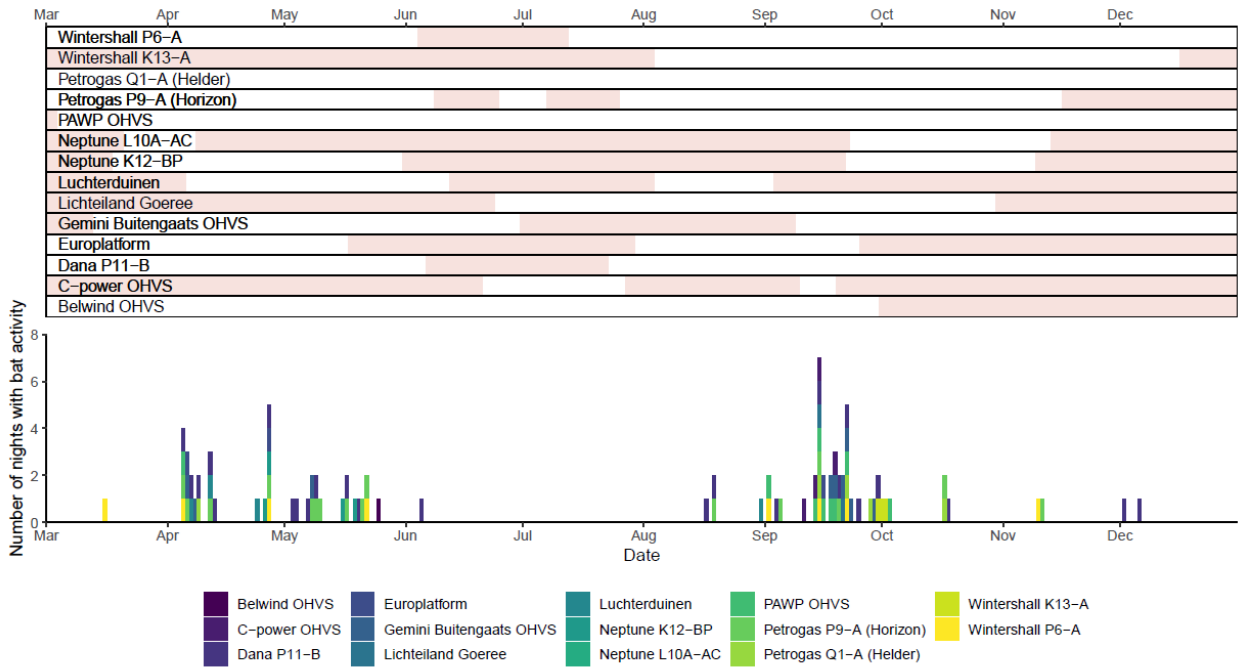


Figure 3-5. Number of nights with recorded bat activity of *Nathusius' pipistrelle* in 2020. See Figure 2-1 for a map of the monitoring locations.

3.3 Spatio-temporal analysis

Diagnostic plots of the model showed that the model fitted well. Some slight heteroskedasticity was found, but this was considered to be of little influence. The true positive rate was found to be 74.7%, the true negative rate 84.8%, and the 0/1-loss was 16%.

Annex 3 shows the output of the analysis. The linear covariate atmospheric pressure proved to be not important, and Rain was found to be of little importance (almost significant). A significant difference was found between the year 2020 and the previous years. Coefficient plots of the smoothers showed that Night in year, Lunar phase, Tailwind and Crosswind proved to be important predictors for bat activity at sea. Cloud class was not important and pressure change was found to be of minor importance. The tensor smoother for longitude and latitude showed that areas in the west had a higher probability of bat presence, while areas in the south, east and north had a lower probability (within the boundaries of the monitoring locations). Moreover, the areas with a low probability of bat presence also had the highest standard errors of the estimates.

In order to visualize the influence of individual covariates, we calculated their predicted values from the model. The predictor effect plots of the important covariates are shown in Fig. 3-6 and 3-7. In each plot, only the term of interest varies, while the spatio-temporal effects are ignored (they average out to zero) and all other covariates are fixed at their mean values. The solid line represents the expected value of the predictions, and the red dashed lines indicate the 95% confidence interval. In the case of the year categories, the black points indicate the mean estimates, the grey shades indicate the 95% confidence intervals of the means, and the red crossbars indicate the (Tukey-corrected) confidence intervals for pairwise differences. Cloud class, Atmospheric Pressure, Atmospheric pressure change and Rain are not presented in this plot as they were considered not significant or of minor importance. Note the different Y-axis scales.

Night in year proved to be an important predictor for bat activity at sea (Figure 3-6). In autumn the first *Nathusius' pipistrelle* was recorded 17 August 2020 and the last on 5 December 2019, with the majority passing through in September and October, with a peak from early September to the end of September and a possible smaller second peak at the end of October.

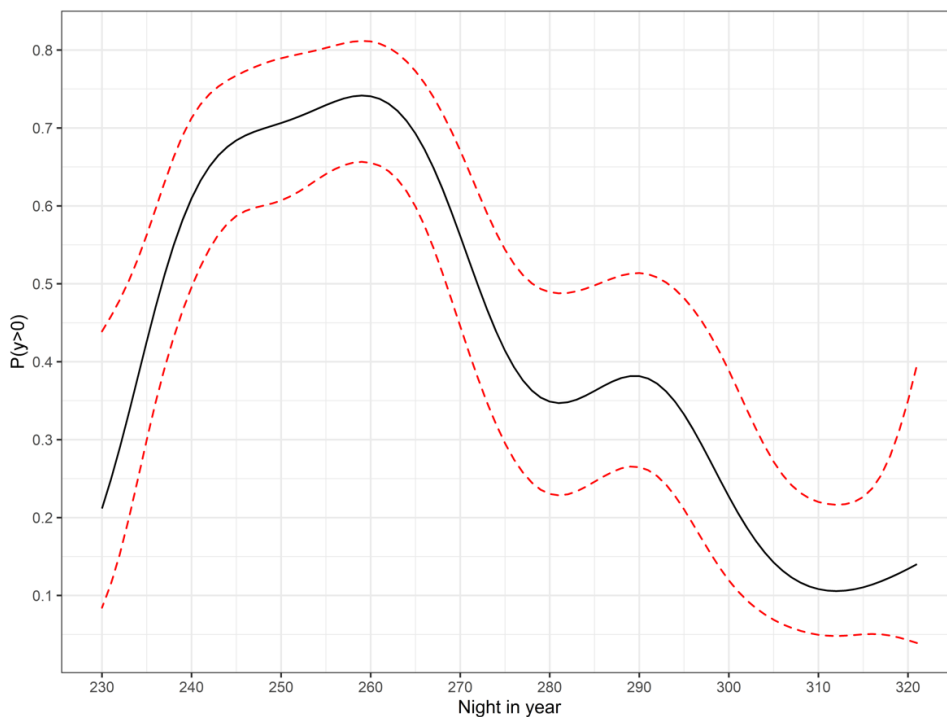


Figure 3-6. Predictor effect plot of the covariate Night in Year

Both tailwind and crosswind (Figure 3-7 & 3-8) were found to be important covariates. The highest probability of presence occurs during tailwind conditions (from ENE) of approximately 2 m/s. A further increase in wind speed does not coincide with higher probability of presence. In headwind conditions the probability of presence is still positive. The probability of presence during crosswind (CWC) peaks at a wind speed of 1 m/s from the SSE. Increasing crosswinds (from either SSE or NNW) decreased the probability of presence.

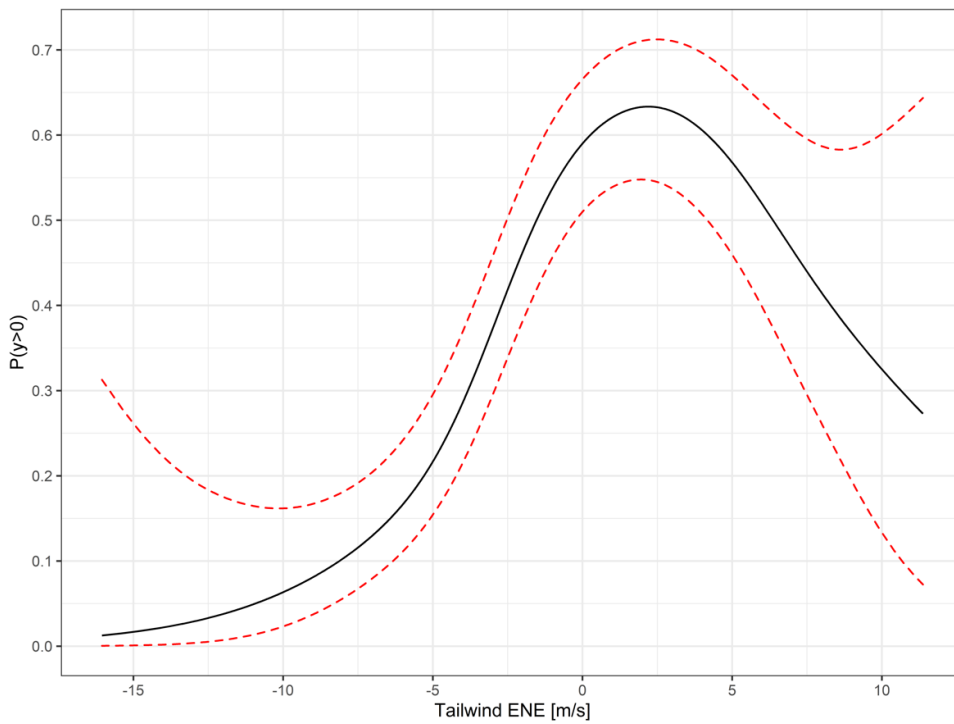


Figure 3-7. Predictor effect plot of the covariate Tailwind

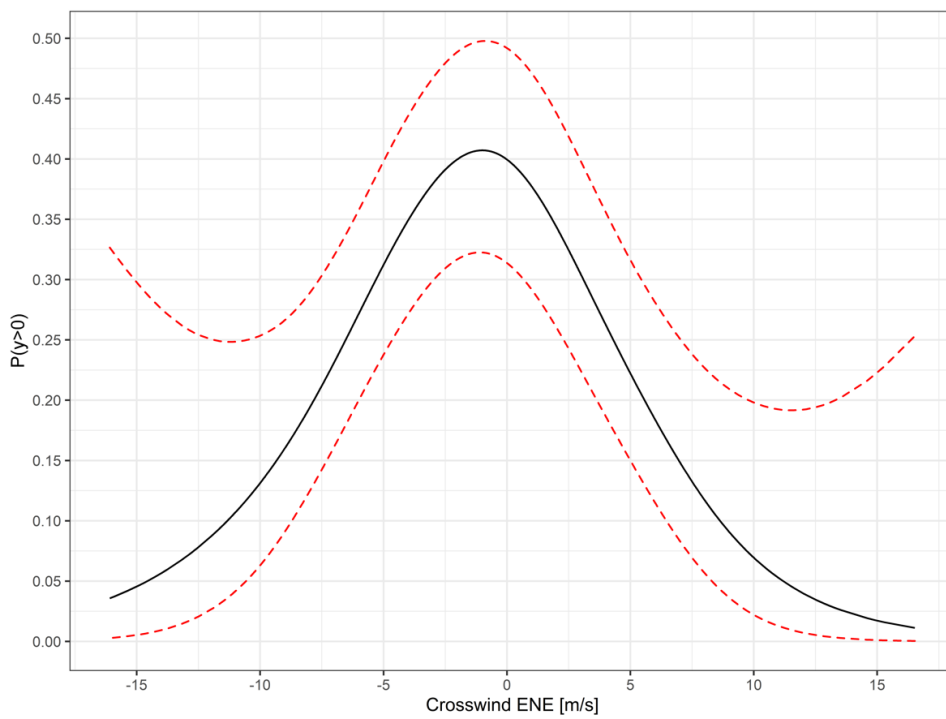


Figure 3-8. Predictor effect plot of the covariate Crosswind

Next to tail- and crosswinds we found lunar phase to predict the probability of offshore presence of *Nathusius' pipistrelle* (Figure 3-9). Bat presence decreased between full moon and last quarter, and increased just before new moon.

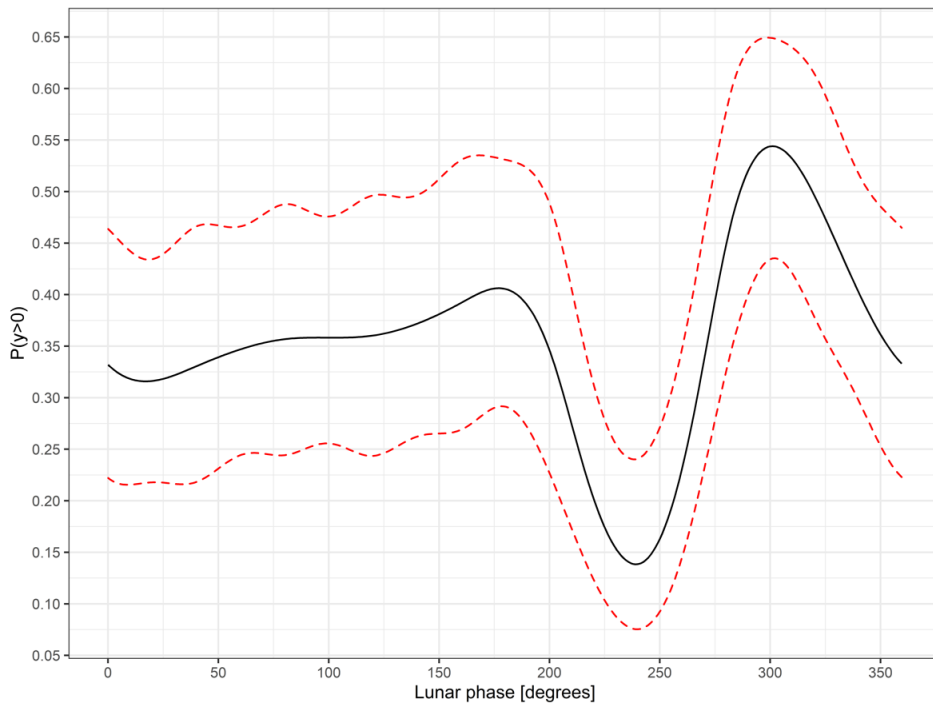


Figure 3-9. Predictor effect plot of the covariate Lunar phase; 0 and 360 degrees represent new moon, 90 degrees first quarter, 180 degrees full moon and 270 degrees third quarter

The probability of presence showed a decrease in 2019 and 2020, a significant difference was found between 2020 and the previous years (Figure 3-10).

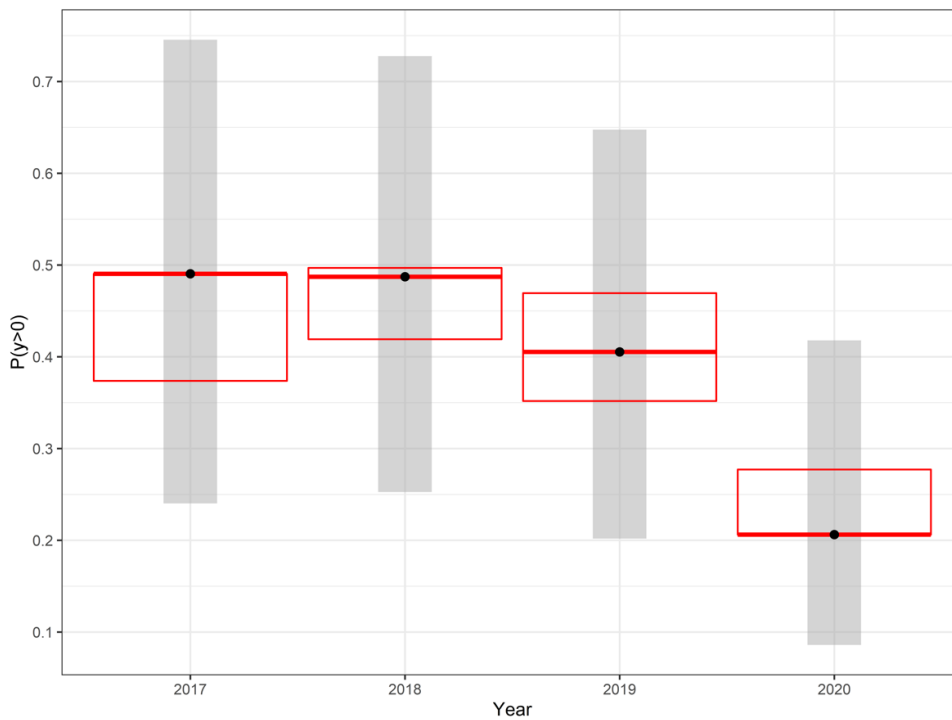


Figure 3-10. Predictor effect plot of the covariate Year

The predictor effect plot of the spatial smoother for longitude and latitude (Figure 3-11) showed that areas in the west had a higher probability of bat presence, while areas in the south, east and north had a lower probability.

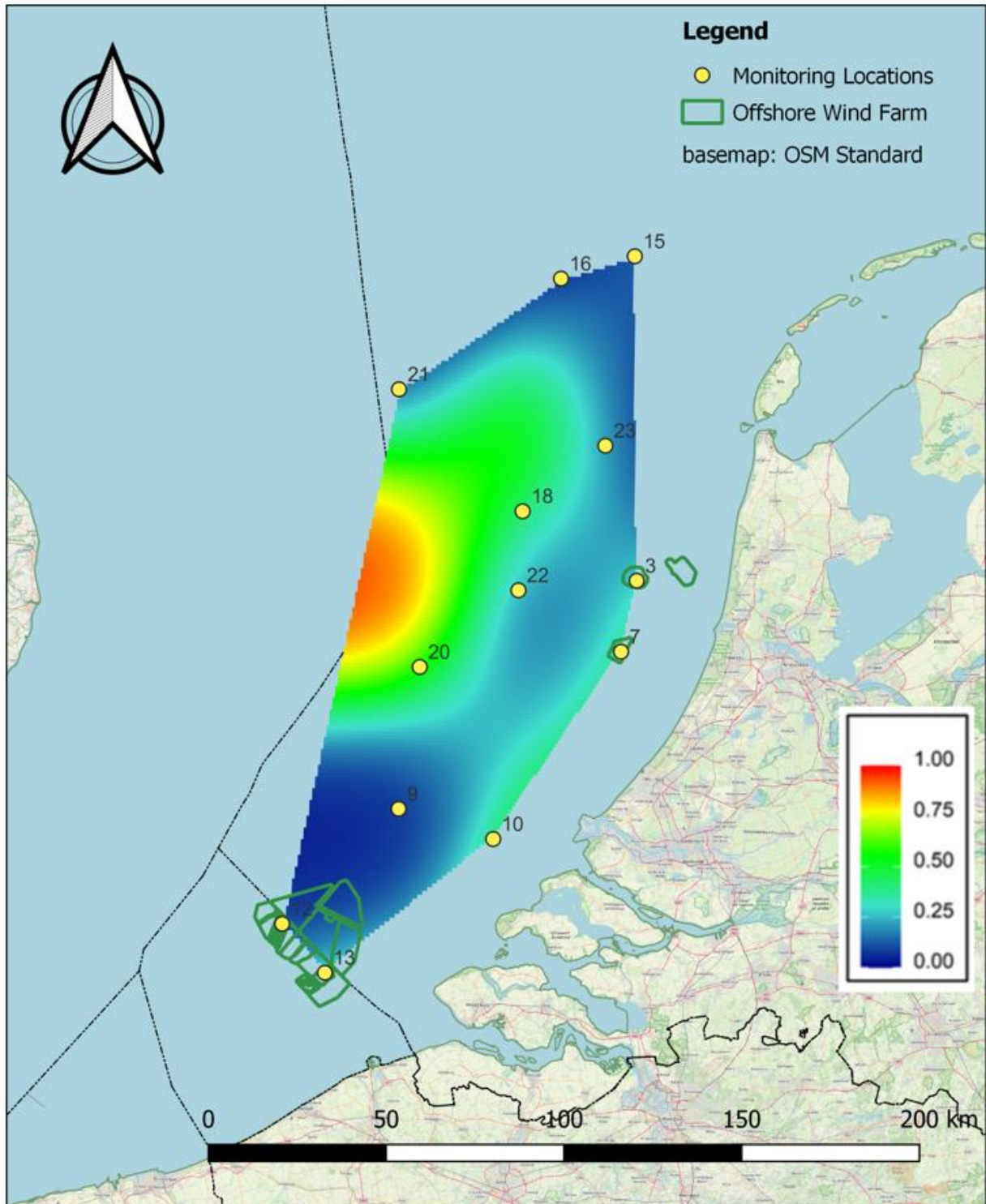


Figure 3-11. Predictor effect plot of the tensor smoother. Only the spatial tensor smoother effect varies, while the temporal effects are ignored (they average out to zero) and all other covariates are fixed at their mean values. The colour indicates the average predicted probability of presence per night.

3.4 Movement analysis

The resulting dataset consists of 2604 monitoring nights in which Nathusius' pipistrelle was recorded during 228 nights (8.8 % of the nights). In total 1059 minutes were recorded with Nathusius' pipistrelle bat activity.

Figure 3-6 shows the positive minutes with bat activity after sunset throughout the season for the different monitoring locations and corresponding distances from shore. Monitoring locations relatively close to the coast (<30 km) receive bats generally a few hours after dark and later in the night records are scarce. Further away the variation in timing increases. There are more records later in the night, but the number of records just after dark also increases, indicating the recorded individual was already present at these monitoring locations, or in its vicinity. Note also the frequent records during daylight hours (the night length increases from 566 min on night number 230 to 915 min at night number 321), in particular at the locations further away from the coast.

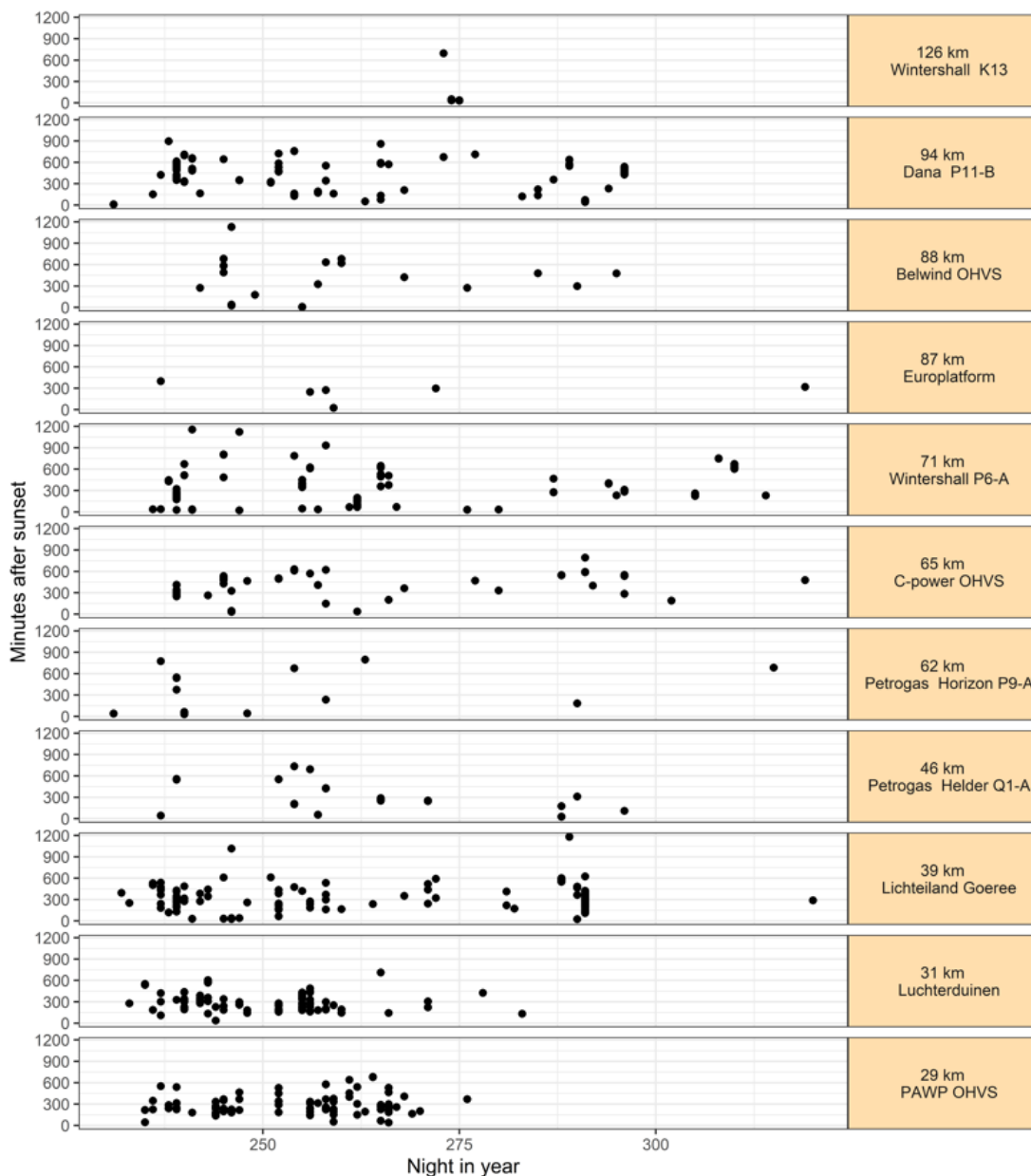


Figure 3-12. Minutes with bat activity after sunset at the different monitoring locations throughout the season. Note that monitoring locations Neptune platform K12-BP, Neptune platform L10A-AC and Gemini OHVS 2 Buitengaats are excluded in this analysis (See Figure 2-1 for a map of the monitoring locations) and that the distances from shore are assessed at a direction of 67.5 degrees (ENE).

Coefficient plots of the smoothers (Annex 4) show that Distance from shore is a significant predictor for the timing of occurrence offshore, whereas Night in year was found to be not important. The model had a reasonable fit. The mean absolute deviation (MAD) of the model was found to be 164.3 minutes. When regressing a linear line between observed and predicted response values, the slope of this line was found to be close to one (1.1). No violations of the model assumptions were found in the residual diagnostic plots.

In order to visualize the influence of the covariate Distance to Shore, we calculated the predicted values from the model. In the predictor effect plot only the term of interest varies, while the other covariate is fixed at its mean value (Fig. 3-13). The solid line represents the expected value of the predictions, and the red dashed lines indicate the 95% confidence interval.

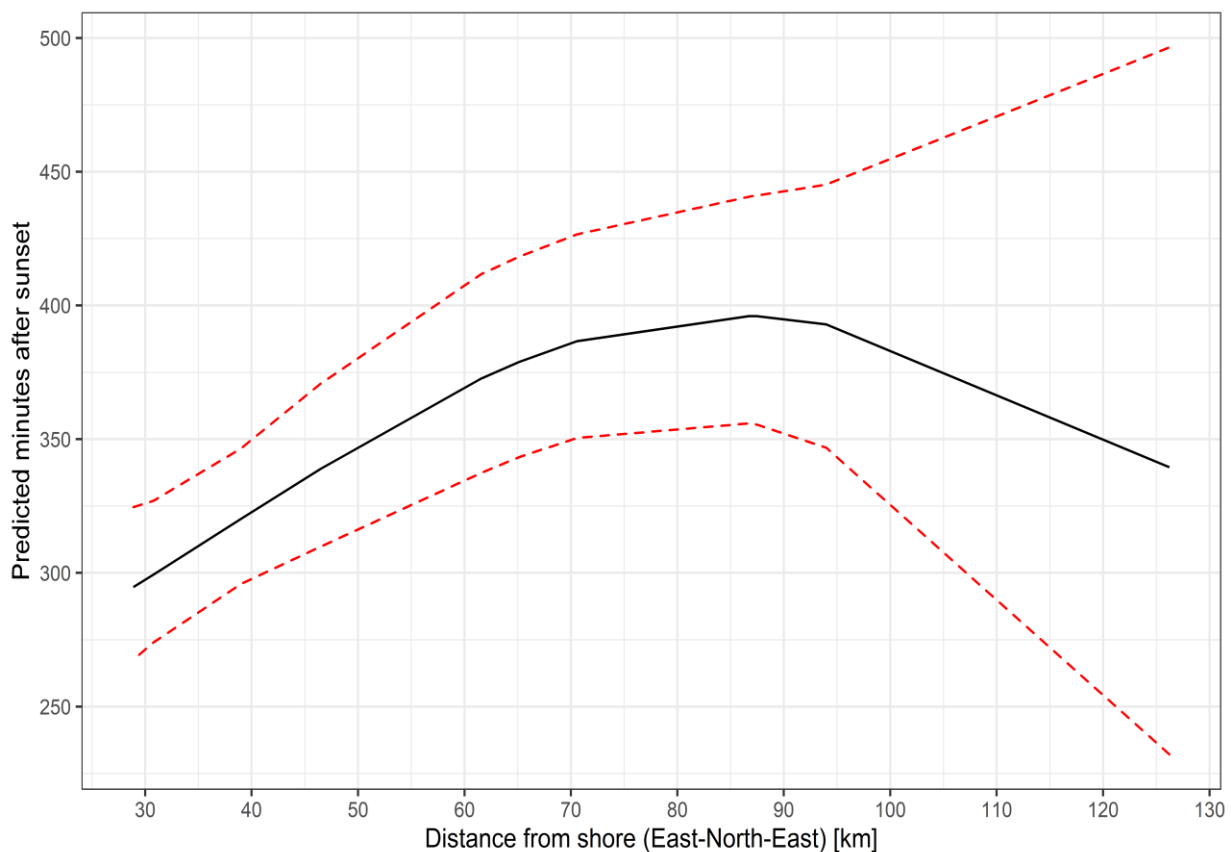


Figure 3-13. Predictor effect plot of the covariate Distance from shore (calculated from ENE to WSW).

The recorded bat activity varied between the locations (Figure 3-12). The first records occurred within an hour after sunset at each location, irrespective of its distance from the coast. The average recorded bat activity however occurs rather late at night; five hours after sunset at a distance of 30 km from shore and this increases linearly to a little more than 6 hours after sunset 60 km from shore, which corresponds to an average movement speed of 25.1 km/h. From 60 km onwards it starts slowing down due to an increasing proportion of occurrences early in the night. Beyond 85 km the proportion of occurrences early in the night is greater than the proportion late at night causing a decrease in the average time of occurrence.

4 Discussion

Our study reconfirms the general pattern of occurrence of bats at the southern North Sea. *Nathusius' pipistrelle* is the most commonly recorded species offshore, whereas other species seem to be scarce (Boshamer & Bekker 2008, Hüppop & Hill 2016, Lagerveld et al 2014, 2017, 2021, Petersen et al 2014, Walter et al 2007).

4.1 Occurrence in spring

During this study the first *Nathusius' pipistrelle* spring record occurred on 16 March 2020 and the last on 10 June 2019, but most individuals were recorded from mid-April until mid-May (see Paragraph 3.2 and Annex 2 for details). In the German Bight *Nathusius' pipistrelles* were observed between 20 April and 26 May (Hüppop & Hill 2016). Further east, at the Vistula Split in Poland, the first *Nathusius' pipistrelle* was recorded at the end of April, but migration peaked mid-May and lasted till the end of the month (Jarzembowski 2003). In Finland the timing of the migration differed between years, but on average it was 20 days later than in Northern Germany (Rydell et al 2014). The timing of spring migration at these locations, being closer to the breeding areas, is as expected; the migration took place later than we found for *Nathusius' pipistrelle*.

The recorded bat activity in spring was reduced in comparison to that in autumn. This corresponds with the findings of previous offshore studies at the southern North Sea (Hüppop & Hill 2016, Lagerveld et al 2017). On land lower bat activity in spring is also a widespread, but poorly documented phenomenon that occurs from Ireland (Russ et al 2003), via the Dutch coastal provinces (Lagerveld et al 2017) to continental Europe (Perks & Goodenough 2020). The lower intensity of spring migration we found is likely caused by a combination of factors:

1. Mortality before the return migration to the breeding areas.
2. Reduced availability of insects in spring. A radar study on bird and insect migration showed that nocturnal insect movements were almost non-existent in spring, but had a strong peak in summer and early autumn (Shi et al 2021). The virtual offshore absence of insects in spring might be an additional driver for migrating bats to minimize their time spent foraging above the North Sea, thus reducing the chance of being detected by our acoustic recorders.
3. As shown for long-distance migrant birds, spring migration is more rapid and takes place at higher altitudes, particularly with wind assistance of the prevailing southwesterly tail winds (Eastwood 1967, Lack 1963a). Assuming migratory bats behave like migrant birds, they may use less stopovers and fly above the detection range of our acoustic detectors, resulting in under-recording of acoustic activity in spring.

4.2 Spatio-temporal occurrence in autumn

In autumn the first individual was recorded 17 August 2020 and the last on 5 December 2019, with the majority passing through in September and October (see Paragraph 3.2 and Annex 2 for details). Our data show a seasonal pattern in offshore occurrence with a peak from early September to the end of September and a possible smaller second peak at the end of October. This seasonal pattern broadly confirms the results from our study on *Nathusius' pipistrelle* at three offshore wind farms within 25 km off the Dutch mainland coast from 2012 - 2016, showing a peak early September and a subsequent decline till the end of the studied period around mid-October (Lagerveld et al. 2021), and reflects the general timing of the species' migration from the breeding areas at higher latitudes to the wintering areas at lower latitudes (Hüppop & Hill 2016, Lagerveld et al 2014, Pētersons 2004, Rydell et al 2014). However, the apparent increase at the end of October may point at gender and/or age-related differences in timing and extent of migration, which has been found for several other bat species (e.g. Jonasson & Guglielmo 2016, Petit et al 2001). In Europe, female-biased migration has been shown for Common noctules by ring recoveries and isotope analysis. Females migrate longer distances

than males, probably maximizing their yearly energy intake, benefitting from high insect biomass at higher latitudes during the reproductive season, whereas males are more sedentary or local migrants (Lehnert et al 2018, Petit & Mayer 2000). *Nathusius' pipistrelles* migration strategy shows similarity to Common noctules' strategy. Our first peak coincides with the phenology of departure from the breeding areas and migration towards the wintering areas (e.g. Hüppop & Hill 2016, Petersen et al 2014), presumably mainly consisting of females and juveniles (Petersons 2004). The records later in the season probably consists predominantly of adult males (Jarzembowski 2003, Petersons 2004). During the reproductive season, adult males stay along the migration route of the females and try to attract passing females in order to mate with them (Jahelkova & Horacek 2011). After the mating season some males migrate to wintering areas at lower latitudes, while others are more or less sedentary and stay to winter in the same area (Petersons 2004, Sachanowicz et al 2019).

Nathusius' pipistrelles at the monitoring locations closest to the mainland (approximately 30 km from shore) were recorded on average 5 hours after sunset. Up to ca 60 km offshore the average time of occurrence shows a linear relationship with the distance from land, which corresponds to an average movement speed of 25.1 km/hr. This speed corresponds with the flight speed range found by Troxell et al (2019) of 24.8-27.3 km/hr and Bach et al (2022) of 16.2 – 28.4 km/hr.

Although the timing of occurrence shows on average a westward movement over sea up to 60 km from shore, the overall pattern of occurrence during the night shows much variation. At each monitoring location, irrespective of its distance from shore, bats have been recorded during the first hour after sunset. At monitoring locations relatively close to the coast (< 30 km) these records may include early arrivals from land. However, at locations further offshore bats must be involved who roosted at, or in the vicinity of, the monitoring location. Therefore, bat activity at sea does not only involve individuals which have departed the same night from the coast. In particular at locations further away from the coast bats occur which are on their way for more than one night. Interestingly, the timing of offshore occurrence did not change over the season, thus the time of departure does not depend on the night length.

Beyond 85 km from shore the proportion of occurrences early in the night becomes greater than the proportion late at night causing a decrease in the average time of occurrence, indicating that the recorded bats do not cross the North Sea in one night. Interestingly, Bach et al (2022) found travel distances of radio tracked *Nathusius' pipistrelles* between 103 – 131 km per night. Flight mechanical theory however predicts that bats can fly longer distances (Hedenström 2009) which would allow them to cross the North Sea in one night.

Furthermore, given the afore mentioned range in flight speed (16.2 to 28.4 km/hr), we expected the first bats to arrive at the locations closest to shore within two hours after sunset if they start migrating offshore directly after departure from their roost sites in the coastal zone. The delayed arrival on the offshore locations can be caused by bats departing from roosting sites further inland, or by bats from coastal sites foraging a prolonged period above land prior to their North Sea crossing.

Our model predicted an offshore distribution of *Nathusius' pipistrelle* with higher probabilities of bat presence further away offshore off the North Holland coast. The increase from east to west can be explained by individuals detected during consecutive nights as they interrupt their migratory flight to roost during daylight hours at sea. Thus resulting in an overall higher probability of presence per night further away from the coast. This pattern of occurrence is only present off the North Holland coast and seems to be absent further north and further south. This may be explained by spatial differences in the number of individuals migrating over the southern North Sea.

Bats prefer to migrate over land and avoid major ecological barriers as the sea as much as possible (Ahlén et al 2009). This habitat preference can lead to a concentration of migrating bats along the coast (Frey et al 2012), similar to migratory birds (Alerstam 1993, Berthold 1990). In the Netherlands many *Nathusius pipistrelles* are observed during migration along the Afsluitdijk (Lagerveld et al., 2017); a 32 km dam connecting the provinces Noord-Holland and Friesland which are separated by the large fresh water lake IJsselmeer. Continuing from the Afsluitdijk bats encounter the Dutch North Sea coast, where they either continue offshore, or change direction and follow the coast in a SSW direction. It seems plausible that more bats cross the North Sea in the wake of the Afsluitdijk, resulting in a higher probability of bat presence off the coast of North Holland, in comparison to other coastal areas. In addition, the orientation of the North Sea

coastline changes from a NNE-SSW orientation at higher latitudes to a more NE-SW orientation in the southern part of the Netherlands and ENE – WSW in Belgium. The latter corresponds to the likely main migration direction. Therefore further south bats could be more inclined to follow the coastline instead of crossing the North Sea to reach the United Kingdom, resulting in a lower probability of offshore presence in the southern part of our study area.

Finally, we found a significant difference in the occurrence of Nathusius' pipistrelle between 2020 and the previous years. Although 2017-2020 is a short period to draw firm conclusions, a decline cannot be ruled out. Unfortunately, there is a lack of data on systematically monitored Nathusius' pipistrelle to verify or falsify a decline.

4.3 Environmental predictors

In order to understand the offshore occurrence of Nathusius' pipistrelle in more detail, we investigated the relationship of a suite of environmental variables and the probability of presence of Nathusius' pipistrelle (see Table 2-4). Apart from spatio-temporal parameters described in the previous section, the following environmental parameters are important predictors for the probability of presence offshore: tailwind, crosswind, and lunar phase.

Acoustic monitoring from 2012-2016 at three offshore wind farms close to the Dutch coast revealed that wind direction had a marked influence on the probability of bat presence at sea (Lagerveld et al. 2021). The offshore occurrence in autumn peaked with a wind direction from ENE. This corresponds with the direction of the migration paths of virtually all ringing recoveries in Great Britain (National Nathusius' Pipistrelle Project 2022). We used this presumed optimal wind direction to calculate the tailwind and crosswind component of the wind vector.

The tail wind component predicts the highest probability of presence of Nathusius' pipistrelle with a wind speed of 2 m/s from the ENE. A further increase in wind speed does not coincide with higher probability of presence, but even leads to an apparent decrease. In low to moderate headwind conditions the probability of presence is still positive, and the same applies to low to moderate crosswinds, in particular during crosswinds from land. In other words, bats do also migrate over the North Sea with low to moderate headwinds and crosswinds, but they prefer to do so with tailwind. Tailwind has been found as important factor for bat migration in both the Dutch and the Belgian North Sea (Brabant et al 2021, Lagerveld et al 2021), and off the eastern coast of the United States (Hatch et al 2013). Low to moderate wind speeds are thought to be the preferred conditions for bats to migrate (Ahlén et al 2009, Brabant et al 2021, Hüppop & Hill 2016, Lagerveld et al 2014, 2021), but the decrease in activity with higher wind speeds from the ENE may be an artefact. Migrating bats, theoretically, adapt their flight altitude to optimize the use of tail winds (Hedenström 2009). If they fly higher to take advantage of the stronger tailwinds at higher altitudes, they can fly above the detection range of the acoustic equipment (> 45 m above sea level), resulting in under-recording of acoustic activity during these conditions. That migratory bats actually do fly at high altitudes over sea during strong tailwind conditions has been shown by Hatch et al. (2013) who photographed multiple bats at heights of over 200 m off the US east coast with tailwinds up to 10 m/s.

Increasing crosswinds (from either SSE or NNW) decreased the probability of presence, indicating that moderate or high crosswinds are avoided. Note that the probability of presence peaks at a wind speed of 1 m/s from the SSE, indicating that crosswinds from land are preferred over crosswinds from sea. It may therefore also be possible that wind drift caused by crosswinds from land does play a role in the offshore occurrence of bats, as suggested by Hüppop & Hill (2016) who recorded bats in the German Bight mainly during southerly winds.

Predation risk and insect availability are postulated as important factors shaping activity patterns in response to moon illumination, as insectivorous bats are both predator and prey (Lang et al., 2006; Kronfeld-Schor et al., 2013). Predators of Nathusius' pipistrelle and other insectivorous bats include several species of owls, diurnal raptors, gulls and crows (Speakman, 1991; Sieradzki & Mikkola, 2020). Although bats constitute only a small proportion of the diet of aerial predators in Europe (Speakman, 1991; Sieradzki & Mikkola, 2020), bats reduce predation risk by their choice of foraging areas (Baxter et al., 2006) and by their timing of roost departures (Lima & O'Keefe, 2013). Predation risk is likely to increase with higher moon illumination, since bats become more visible. However, most insectivorous bats from temperate areas do not seem to avoid moonlit nights (Lima & O'Keefe, 2013). In Europe, so far only Daubenton's bat *Myotis daubentonii* was found

to reduce its activity significantly during higher phases of the moon (Ciechanowski et al., 2007). This study also found an almost significant negative relationship between Nathusius' pipistrelles activity and moon illumination (Ciechanowski et al., 2007). Consequently we cannot exclude the possibility that predation risk may be a factor affecting migratory movements and thus the offshore occurrence of Nathusius' pipistrelle.

Another important factor for the occurrence of bats, prey availability, can also show a relationship with the lunar phase (Kronfeld-Schor et al., 2013). The diet of Nathusius' pipistrelle mainly consists of Chironomidae (Diptera) (Beck, 1995), of which some species are known to adjust their emergence to specific phases during the lunar cycle (Danthanarayana, 1976). In autumn, insects from coastal areas may disperse over sea, when this coincides with easterly winds. Insect migration activity may also be associated with the lunar phase (Danthanarayana, 1976). In particular during late summer/early autumn many insects migrate over sea (Drake & Gatehouse, 1995; Chapman et al., 2004; Drake & Reynolds, 2012). They are likely attracted to illuminated offshore platforms, thereby facilitating bats to forage in the vicinity of these platforms during their migratory flight over sea (e.g. Ahlén et al., 2009; Šuba et al., 2012). Thus, the observed relationship between the lunar phase and offshore bat occurrence may be caused by reduced migratory bat activity during higher phases of the moon to avoid predation, or by bats making use of increased insect availability over sea, or by a combination of both factors.

Temperature could not be included in our model due to a strong correlation with night in year. Although the latter, i.e. seasonal timing, is considered the most important driver for obligate migrants (Hedenström 2009), temperature is stated as most important environmental factor influencing the phenology of migration (Pettit & O'Keefe 2017). Lagerveld et al (2021) found temperature to be of minor importance ($p=0.09$) for Nathusius' pipistrelles occurrence at three offshore wind farms off the Dutch mainland coast. In the time period concerned the majority (89%) of their observations occurred during nights with average temperatures $>15^{\circ}\text{C}$. Brabant et al (2021) found also a positive relationship between temperature and offshore occurrence off the Belgian coast. Temperature can have an indirect effect on bat migration as cue for prey availability at sea (e.g. Drake & Gatehouse 1995). This increase in offshore insect availability can be caused by either insect migration or offshore drift of insects that are more active during higher temperatures (Drake & Reynolds 2012).

Of the suite of environmental variables we used to predict the probability of presence of Nathusius' pipistrelle (see Table 2-4), atmospheric pressure and cloud cover were found not to be important, whereas a change in atmospheric pressure and rain possibly had a minor influence on the offshore presence. In contrast, previous studies found cloud cover (Cryan & Brown 2007), atmospheric pressure (Brabant et al 2019, Cryan & Brown 2007, Hüppop & Hill 2016, Lagerveld et al 2014, Smith & McWilliams 2016) and rain (Hüppop & Hill 2016, Pettit & O'Keefe 2017) as important predictors for the offshore occurrence of bats.

4.4 Limitations of our study

Although we collected acoustic data on echolocation signals of bats with a high temporal resolution, our analysis was based on absence-presence of bat activity per night to overcome limitations that are characteristic for current acoustic detection methods. These methods cannot translate echolocation signals to the number of animals, nor can they distinguish between individuals. In other words, a sequence of calls in a certain time frame can originate from one individual in the detection range or from multiple individuals passing through the detection range. Since the detection range of acoustic recorders is limited and our recorders were deployed at a height of ca 15 m, our results are only valid up to ca 45 m above sea level. Lagerveld et al (2021) provide a more detailed description of these limitations.

5 Conclusions

This study reconfirms that *Nathusius' pipistrelle* is the most common bat species at the southern North Sea. Due to a lack of data in spring we limited the analysis to its occurrence in autumn. Our analysis revealed that its occurrence offshore continues till later in the year than previously thought. This prolonged migration period may be caused by adult males that start migrating when females have left after the mating season.

Furthermore, the results from our study show that offshore bat occurrence varies considerably during the night, in particular at locations further away from the coast, rendering it difficult to predict specific periods throughout the night in which bats can or cannot be expected. An important contributor to the extensive variation consist of bats which travel over sea during consecutive nights and roost at offshore constructions during the day. The average timing of occurrence shows a linear relationship with the distance to the coast between 30 and 60 km from shore, corresponding to an average movement speed of 25.1 km/h.

Our study predicts an offshore distribution of *Nathusius' pipistrelle* with higher probabilities of bat presence per night further away offshore off the North Holland coast. This east-west gradient is caused by individuals who are detected multiple nights when they continue their migration after a roost at sea during the day. The increased probability of occurrence off the coast of North Holland in comparison to that further north and south may reflect real differences in bat abundance.

The effect of wind speed and wind direction should always be considered together. Our analysis shows that most bat activity is to be expected with a light tailwind (from ENE), although higher wind speeds may result in animals flying at altitudes above the detection range of our bat detectors. In addition, the offshore occurrence of bats can also be expected with light to moderate crosswinds, in particular from land, as well as with light to moderate headwinds.

Bat presence is decreased between full moon and last quarter, and increased just before new moon. The observed relationship between the lunar phase and offshore bat occurrence may be caused by reduced migratory bat activity during higher phases of the moon to avoid predation, or by bats making use of increased insect availability over sea, or by a combination of both factors.

Finally, we found a significant difference in the occurrence of *Nathusius' pipistrelle* between 2020 and the previous years. Although 2017-2020 is a short period to draw firm conclusions, a decline cannot be ruled out.

6 Recommendations

To reduce the potential impact of offshore wind farms on bats, mitigation measures which are based on the probability of the presence, should take the following factors into account:

1. Seasonal occurrence: autumn migration takes place between late August and late October.
2. Daily temporal occurrence: bats occur throughout the entire night, in particular at locations further away from the coast. Occasionally, bat activity occurs during daylight hours, in particular during the first hours after sunrise at locations further away from the coast.
3. Wind: most migration can be expected during tailwind conditions. but the decrease in activity with higher wind speeds might be an artefact. High flying individuals during stronger tailwind conditions should be considered. Offshore migration also occurs with light to moderate crosswinds, in particular from land, as well as headwinds. Note that the wind speeds mentioned in this report refer to wind speeds measured at an altitude of 10 m above sea level, and that wind speed increases with height. Mitigation measures therefore should not be based on wind speeds measured at nacelle level when using information from this report.
4. Lunar phase: reduced bat migration activity between full moon and last quarter, and a strong increase just before new moon.
5. Spatial distribution: spatial differences seem to be present in the offshore occurrence of bats; the highest densities are likely present west off the coast of North Holland.

Continuation of the acoustic monitoring, using the same monitoring network, could be used to monitor the long-term trend of bat migration intensity over the southern North Sea.

It is urgently needed to obtain more information on flight heights in spring and autumn. Unfortunately *Nathusius' pipistrelle* cannot be equipped with a GPS tag. Measuring flight heights may be done with bat detectors at various heights. However, an offshore wind turbine seems not to be a good option due to the inherent disturbances (fatality risk, attraction to lights and limited detection range of the bat detector in the rotor zone). An offshore mast without illumination would be the preferred option.

Due to the low numbers of acoustic detections in spring it may be more effective to study spring migration using telemetry. Telemetry data (both in spring and autumn) may also result in information on sex and age specific differences in the migration ecology. Furthermore it may provide information on the attraction by offshore wind farms, as well as the flight behaviour within a wind farm.

7 Acknowledgements

We would like to thank Dana Petroleum (Joris Fris, David Meereboer, John Muermans, Ton Könst, Frans Schijff, Ab Toet, Michael van der Velden), Eneco (Systke van den Akker, Nienke Ladage, Marin van Regteren, Johnny Sinke, Renzo Schildmeijer, Ron Schenkeveld), Gemini (Luuk Folkerts, Peter Huiberts, Doden Thorsten), Neptune Energy (Alexander Hiemstra, Jelle van Kooten, Fokko Leeman, Michel Verkerke, Fred Volders), Royal Belgian Institute of Natural Sciences (Robin Brabant), Petrogas (Kees Brusselmans, Bert de Graaf, Vedran Micetic, Bart Smits, Gert Stam, Cor Vlaar, John Wuijster), Venco (Gerald Koster, Koertjan Sieders), Wintershall (Vincent Beens, Sander Bruinsma, Gert-Jan Cazemir, Toon Koopman, Mario Kuiper, Ricardo Wijthoef) for providing logistical support and facilitating the monitoring at respectively gas production platform P11-B, Princess Amalia Wind Farm (PAWP) & Luchterduinen, Gemini Buitengaats, gas production platforms L10AC & K12-B, Lichteiland Goeree & Europlatform, Belwind & C-Power, gas production platforms P9 Horizon & Q1 Helder, and gas production platforms P6-A & K13A. Last but not least, we like to acknowledge the valuable input of our reviewers from Wageningen Marine Research and Rijkswaterstaat: Martin Baptist, Tammo Bult, Dagmar van Nieuwpoort and Maarten Platteeuw.

8 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

References

- Adams, E.M., Gulka, J. & Williams, K.A. (2021). A review of the effectiveness of operational curtailment for reducing bat fatalities at terrestrial wind farms in North America. *PLoS ONE*, 16, e0256382.
- Ahlén, I., Baagøe, H.J. & Bach, L. (2009). Behavior of Scandinavian Bats during Migration and Foraging at Sea. *J. Mammal.*, 90, 1318–1323. <https://doi.org/10.1644/09-mamm-s-223r.1>
- Alerstam, T. (1993). *Bird Migration*. First paperback edition. Cambridge University Press, Cambridge, UK,
- Arnett, E.B., Brown, W.K., Erickson, W.P., Fiedler, J.K., Hamilton, B.L., Henry, T.H., Jain, A., Johnson, G.D., Kerns, J., Koford, R.R. et al. (2008). Patterns of Bat Fatalities at Wind Energy Facilities in North America. *J. Wildl. Manag.*, 72, 61–78.
- Arnett, E.B., Hein, C.D., Schirmacher, M.R., Huso, M.M.P. & Szewczak, J.M. (2013). Evaluating the Effectiveness of an Ultrasonic Acoustic Deterrent for Reducing Bat Fatalities at Wind Turbines. *PLoS ONE*, 8, e65794.
- Bach, L. & Rahmel, U. (2004). Summary of wind turbine impacts on bats—Assessment of a conflict. *Bremer Beiträge Nat. Nat.*, 7, 245–252.
- Bach, P., Voigt, C. C., Götsche, M., Bach, L., Brust, V., Hill, R., Hüppop, O., Lagerveld, S., Schmaljohann, H., & Seebens-Hoyer, A. (2022). Offshore and coastline migration of radio-tagged *Nathusius' pipistrelles*. *Conservation Science and Practice*, 4, e12783. <https://doi.org/10.1111/csp2.12783>
- Baerwald, E.F., Edworthy Rydell, J., Holder, M. & Barclay, R.M.R. (2009). A Large-Scale Mitigation Experiment to Reduce Bat Fatalities at Wind Energy Facilities. *J. Wildl. Manag.*, 73, 1077–1081.
- Barataud, M. (2016). Acoustic ecology of European bats. Species, identification, study of their habitats and foraging behaviour. Biotope, Mèze; Muséum nationale d'Histoire naturelle (Inventaires et biodiversité series), Paris, France.
- Berthold, P. (1990). *Vogelzug: Eine Einführung und kurze aktuelle Gesamtübersicht*. Wissenschaftliche Buchgesellschaft, Darmstadt, Germany.
- Boshamer, J.P.C. & Bekker, J.P. (2008). *Nathusius' pipistrelles (Pipistrellus nathusii)* and other species of bats on offshore platforms in the Dutch sector of the North Sea. *Lutra*, 51, 17–36.
- Brabant, R., Laurent, Y., Mutteti, J., Jonge Poerink, B. & Degraer, S., (2019). al The influence of meteorological conditions on the presence of *Nathusius' pipistrelle (Pipistrellus nathusii)* at sea. In Degraer, S., Brabant, R., Rumes, B & Vigin, L. (Eds). *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: Marking a Decade of Monitoring, Research and Innovation*. (pp.117-124). Royal Belgian Institute of Natural Sciences.
- Brabant, R., Laurent, Y., Jonge Poerink, B., Degraer, S. (2021). The Relation between Migratory Activity of *Pipistrellus* Bats at Sea and Weather Conditions Offers Possibilities to Reduce Offshore Wind Farm Effects. *Animals.*, 11(12), 3457. <https://doi.org/10.3390/ani11123457>.
- Ciechanowski, M., Zajac, T., Biłas, A. & Dunajski, R. (2007). Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology*, 85, 1249–1263.
- Cryan, P.M., Brown, A.C., (2007). Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. *Biol. Conserv.*, 139, 1-11. doi:10.1016/j.biocon.2007.05.019.

-
- Cryan, P.M., Gorresen, P.M., Hein, C.D., Schirmacher, M.R., Diehl, R.H., Huso, M.M., Hayman, D.T., Fricker, P.D., Bonaccorso, F.J., Johnson, D.H., et al. (2014). Behavior of bats at wind turbines. *Proc. Natl. Acad. Sci. USA*, 111, 15126–15131.
- Dowle, M., & Srinivasan, A. (2021). *Data.table*: Extension of 'data.frame'. Retrieved from <https://CRAN.R-project.org/package=data.table>.
- Drake, V.A. & Gatehouse, A.G. (1995). *Insect Migration: Tracking Resources through Space and Time*; Cambridge University Press: Cambridge, UK.
- Drake, V. & Reynolds, D. (2012). *Radar Entomology: Observing Insect Flight and Migration*; Cabi: Wallingford, UK.
- Dunn, P. K. & Smyth, G.K. (1996). Randomized Quantile Residuals. *Journal of Computational and Graphical Statistics*, 5(3), 236–244. Retrieved from <https://www.jstor.org/stable/1390802>.
- Eastwood, D., (1967). *Radar ornithology*, Menthuen, New York.
- Frey, K., Bach, L., Bach, P. & Brunken, H. (2012). Fledermauszug entlang der südlichen Nordseeküste. *Naturschutz und Biologische Vielfalt*, 128, 185-204.
- Friendly, M. Fox, J., & Chalmers, P. (2021). *Matlib*: Matrix functions for teaching and learning linear algebra and multivariate statistics. Retrieved from <https://CRAN.R-project.org/package=matlib>.
- Gilmour, L.R.V., Holderied, M.W., Pickering, S.P.C. & Jones, G. (2020). Comparing acoustic and radar deterrence methods as mitigation measures to reduce human-bat impacts and conservation conflicts. *PLoS ONE*, 15, e0228668.
- Gräler, B., Pebesma, E. & Heuvelink, G. (2016). Spatio-temporal interpolation using *gstat*. *The R Journal*, 8, 204–218. Retrieved from <https://journal.r-project.org/archive/2016/RJ-2016-014/index.html>.
- Grodsky, S.M., Behr, M.J., Gendler, A., Drake, D., Dieterle, B.D., Rudd, R.J., Walrath, N.L. (2011). Investigating the causes of death for wind turbine-associated bat fatalities. *J. Mammal.*, 92, 917–925.
- Grolemund, G. & Wickham, H. (2011). Dates and times made easy with *lubridate*. *Journal of Statistical Software*, 40(3), 1–25. Retrieved from <https://www.jstatsoft.org/v40/i03/>.
- Hayes, M.A. (2013). Bats killed in large numbers at United States wind energy facilities. *Bioscience*, 63, 975–979.
- Hatch, S.K., Connelly, E.E., Divoll, T.J., Stenhouse, I.J. & Williams, K.A., (2013). Offshore Observations of Eastern Red Bats (*Lasiurus borealis*) in the Mid-Atlantic United States Using Multiple Survey Methods. *PLoS ONE*, 8, e83803. <https://doi.org/10.1371/journal.pone.0083803>.
- Hedenström, A. (2009). Optimal migration strategies in bats. *J. Mammal.*, 90, 1298–1309, doi:10.1644/09-MAMM-S-075R2.1.
- Hintzen, N., Bastardie, F. & Beare, D. (2017). *Vmstools*: For analysing fisheries VMS (vessel monitoring system) data. Retrieved from <https://CRAN.R-project.org/package=vmstools>.
- Hüppop, O. & Hilgerloh, G. (2012). Flight call rates of migrating thrushes: effects of wind conditions, humidity and time of day at an illuminated offshore platform. *Journal of Avian Biology*, 43, 85-90.
- Hüppop, O. & Hill, R. (2016). Migration phenology and behaviour of bats at a research platform in the south-eastern North Sea. *Lutra*, 59, 5–22.

-
- Jahelkova, H. & Horacek, L. (2011). Mating system of a migratory bat, *Nathusius' pipistrelle* (*Pipistrellus nathusii*): Different male strategies. *Acta Chiropterologica*, 16, 139–147.
- Jarzembowski, T. (2003). Migration of the *Nathusius' pipistrelle* *Pipistrellus nathusii* (Vespertilionidae) along the Vistula Split. *Acta Theriologica*, 48, 301–308.
- Jonasson, K.A. & Guglielmo, C.G. (2016). Sex differences in spring migration timing and body composition of silver-haired bats *Lasionycteris noctivagans*. *Journal of Mammalogy*, 97(6): 1535–1542, <https://doi.org/10.1093/jmammal/gyw119>.
- Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E.D., Dayan, T. & Helfrich-Forster, C. (2013). Chronobiology by moonlight. *Proc Biol Sci.*, 280(1765), 20123088. <https://doi.org/10.1098/rspb.2012.3088>
- Kunz, T.H., Arnett, E.B., Erickson, W.P., Johnson, G.D., Larkin, R.P., Strickland, M.D., Thresher, R.W., Tuttle, M.D. (2007). Ecological impacts of wind energy development on bats: Questions, hypotheses, and research needs. *Front. Ecol. Environ.*, 5, 315–324.
- Lack, D. (1963a). Migration across the southern North Sea studied by radar part 5. Movements in August, winter and spring, and conclusion. *Ibis*, 105, 461–492.
- Lack, D. (1963b). Migration across the southern North Sea studied by radar part 4: Autumn. *Ibis*, 105, 1–54.
- Lagerveld, S., Jonge Poerink, B., Haselager, R., Verdaat, H. (2014). Bats in Dutch offshore wind farms in autumn 2012. *Lutra*, 57, 61–69.
- Lagerveld, S., Gerla, D., van der Wal J.T., de Vries P., Brabant R., Stienen E., Deneudt K., Manshanden J. & Scholl, M. (2017). Spatial and temporal occurrence of bats in the southern North Sea area. Wageningen Marine Research (University & Research centre), Wageningen Marine Research report C090/17.
- Lagerveld, S., Jonge Poerink, B. & Geelhoed, S.C.V. (2021). Offshore Occurrence of a Migratory Bat, *Pipistrellus nathusii*, Depends on Seasonality and Weather Conditions. *Animals*, 11, 3442. <https://doi.org/10.3390/ani11123442>.
- Lang, A.B., Kalko, E.K.V., Romer, H., Bockholdt, C., Dechmann, D. (2006). Activity levels of bats and katydid in relation to the lunar cycle. *Oecologia* 146, 659–666.
- Lawson, M., Jenne, D., Thresher, R., Houck, D., Wimsatt, J. & Straw, B. (2020). An investigation into the potential for wind turbines to cause barotrauma in bats. *PLoS ONE*, 15, e0242485.
- Lazaridis, E. (2014). Lunar: Lunar phase & distance, seasons and other environmental factors. Retrieved from <http://statistics.lazaridis.eu>.
- Lehnert, L.S., Kramer-Schadt, S., Teige, T., Hoffmeister, U., Popa-Lisseanu, A., Bontadina, F., Ciechanowski, M., Dechmann, D.K.N., Kravchenko, K., Presetnik, P., Starrach, M., Straube, M., Zoephel, U. & Voigt, C.C., (2018). Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration. *Proc. R. Soc.*, B.2852018217420182174 <http://doi.org/10.1098/rspb.2018.2174>.
- Lenth, R.V. (2022). Emmeans: Estimated marginal means, aka least-squares means. Retrieved from <https://CRAN.R-project.org/package=emmeans>.
- Lima, S.L. & O'Keefe, J.M. (2013). Do predators influence the behaviour of bats? *Biol Rev.*, 88, 626–644. <https://doi.org/10.1111/brv.12021>
- National *Nathusius' Pipistrelle* Project (2022). Available online: <https://www.bats.org.uk/our-work/national-bat-monitoring-programme/surveys/national-nathusius-pipistrelle-survey> (accessed on 29 March 2022).

-
- Pebesma, E.J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, 30, 683–691.
- Pebesma, E. (2018). Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal*, 10(1), 439–446. doi:10.32614/RJ-2018-009.
- Perks, S.J. & Goodenough, A.E. (2020). Abiotic and spatiotemporal factors affect activity of European bat species and have implications for detectability for acoustic surveys. *Wildlife Biology* 2020(2). <https://doi.org/10.2981/wlb.00659>.
- Petersen, A., Jensen, J.K., Jenkins, P., Bloch, D. & Ingimarsson, F., (2014). A review of the occurrence of bats (*Chiroptera*) on islands in the North East Atlantic and on North Sea installations. *Acta Chiropterologica*, 16, 169–195.
- Petersons, G.,(2004). Seasonal migrations of north-eastern populations of Nathusius' bat *Pipistrellus nathusii* (*Chiroptera*). *Myotis*, 41-42, 29-56.
- Petit, E., Balloux, F. & Goudet, J., (2001). Sex-based dispersal in a migratory bat: a characterization using sex-specific demographic parameters. *Evolution*, 55(3), 635-640. <https://doi.org/10.1111/j.0014-3820.2001.tb00797.x> .
- Petit, E. & Mayer, F., (2000). A population genetic analysis of migration: the case of the noctule bat (*Nyctalus noctula*). *Mol. Ecol.* 9, 683-690. doi:10.1046/j.1365-294x.2000.00896.x.
- Pettit, J.L. & O'Keefe, J.M., (2017). Day of year, temperature, wind, and precipitation predict timing of bat migration. *Journal of Mammalogy*, 98 (5), 1236-1248. <https://doi.org/10.1093/jmammal/gyx054>.
- R Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>.
- Rollins, K.M., Meyerholz, D.K., Johnson, G.D., Capparella, A.P. & Loew, S.S. (2012). A forensic investigation into the etiology of bat mortality at a wind farm: Barotrauma or traumatic injury? *Vet. Pathol.*, 49, 362–371.
- RStudio Team. (2020). *RStudio: Integrated development environment* for r. Boston, MA: RStudio, PBC. Retrieved from <http://www.rstudio.com/>.
- Russ, J. M., Briffa, M. & Montgomery, W.I. (2003). Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. *J. Zool.*, 259, 289–299.
- Rydell, J., Bach, L., Dubourg-Savage, M.J., Green, M., Rodrigues, L. & Hedenström, A. (2010). Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterologica*, 12, 261–274.
- Rydell, J., Bach, L., Bach, P., Diaz, L. G., Furmankiewicz, J., Hagner-Wahlsten, N., Kyheröinen, E-M., Lilley, T., Masing, M., Max Mayer, M., Pétersons, G., Šuba, J., Vasko, V., Vintulis, V. & Hedenström, A. (2014). Phenology of migratory bat activity across the Baltic Sea and the south-eastern North Sea. *Acta Chiropterologica*, 16(1), 139-147.
- Sachanowicz, K.; Ciechanowski, M.; Tryjanowski, P.; Kosicki, J.Z., (2019) Wintering range of *Pipistrellus nathusii* (*Chiroptera*) in Central Europe: has the species extended to the north-east using urban heat islands? *Mammalia*, 83, 260–271. <http://doi.org/10.1515/mammalia-2018-0014>
- Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., ... Crowley, J. (2021). GGally: Extension to 'ggplot2'. Retrieved from <https://CRAN.R-project.org/package=GGally>.

-
- Shi, X., Schmid, B., Tschanz, P., Segelbacher, G. & Liechti, F. (2021). Seasonal Trends in Movement Patterns of Birds and Insects Aloft Simultaneously Recorded by Radar. *Remote Sens.*, 13, 1839. <https://doi.org/10.3390/rs13091839>.
- Sieradzki, A. & Mikkola, H. (2020). A Review of European Owls as Predators of Bats. <https://doi.org/10.5772/intechopen.90330>.
- Signorell, A. et al., (2021). DescTools: Tools for descriptive statistics. Retrieved from <https://cran.r-project.org/package=DescTools>.
- Smith, A.D. & McWilliams, S.R. (2016). Bat Activity during Autumn Relates to Atmospheric Conditions: Implications for Coastal Wind Energy Development. *J. Mammal.*, 97, 1565–1577.
- Speakman, J.R. (1991). The impact of predation by birds on bat populations in the British Isles. *Mammal Review*, 21, 123–142.
- Thieurmel, B. & Elmarhraoui, A. (2019). Suncalc: Compute sun position, sunlight phases, moon position and lunar phase. Retrieved from <https://CRAN.R-project.org/package=suncalc>.
- Tierney, L. (2018). *Codetools: Code analysis tools for r*. Retrieved from <https://CRAN.R-project.org/package=codetools>.
- Troxell, S.A., Holderied, M.W., Pétersons, G. & Voigt, C.C. (2019). Nathusius' bats optimize long-distance migration by flying at maximum range speed. *J. Exp. Biol*, 222(4), jeb176396. <https://doi.org/10.1242/jeb.176396>.
- Voigt, C.C., Lehnert, L.S., Pétersons, G., Adorf, F. & Bach, L. (2015). Wildlife and renewable energy: German politics cross migratory bats. *Eur. J. Wildl. Res.*, 61, 213–219.
- Walter, G., Matthes, H. & Joost, M. (2007). Fledermauszug über Nord- und Ostsee — Ergebnisse aus Offshore Untersuchungen und deren Einordnung in das bisher bekannte Bild zum Zuggeschehen. *Nyctalus*, 12, 221–223.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York. Retrieved from <https://ggplot2.tidyverse.org>.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., ... Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43), 1686. doi:10.21105/joss.01686.
- Wood, S.N. (2017). *Generalized additive models: An introduction with r* (2nd ed.). Chapman, Hall/CRC.
- Wright, K. (2021). Corrgram: Plot a correlogram. Retrieved from <https://CRAN.R-project.org/package=corrgram>.

Justification

Report C031/22A
Project Number: 4315100117

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved: Dr. ir. T.P. Bult
Director

B/a Dr. C.J. Wiebinga

Signature: 

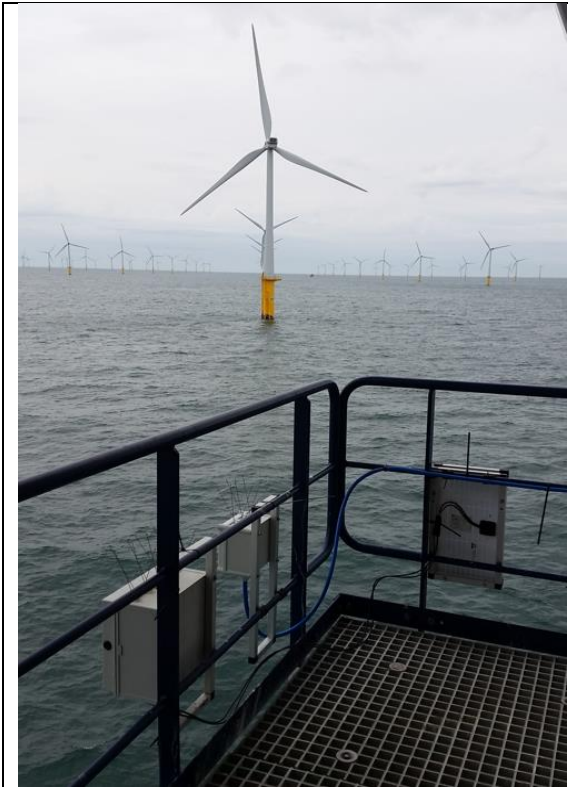
Date: 20 July 2023

Approved: Dr. ir. M.J. Baptist
Senior Researcher

Signature: 

Date: 20 July 2023

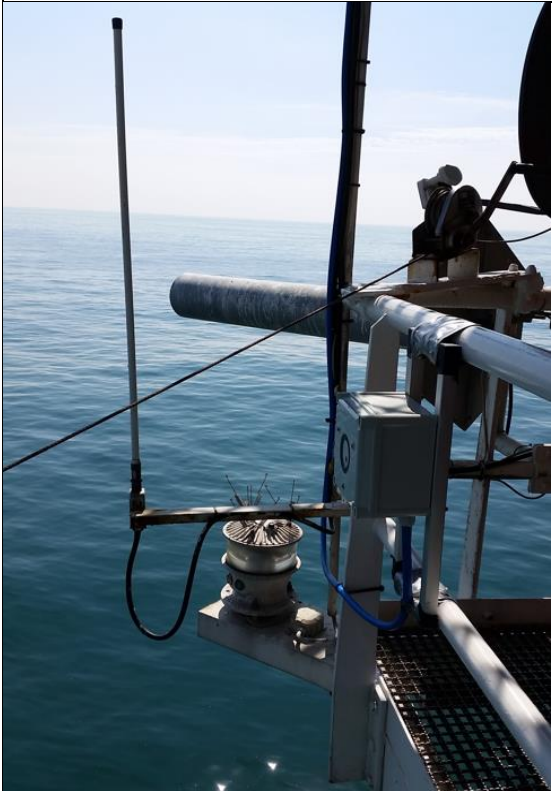
Annex 1: monitoring locations



Belwind OHVS



C-Power OHVS



Europlatform



Gemini OHVS



Wintershall K13



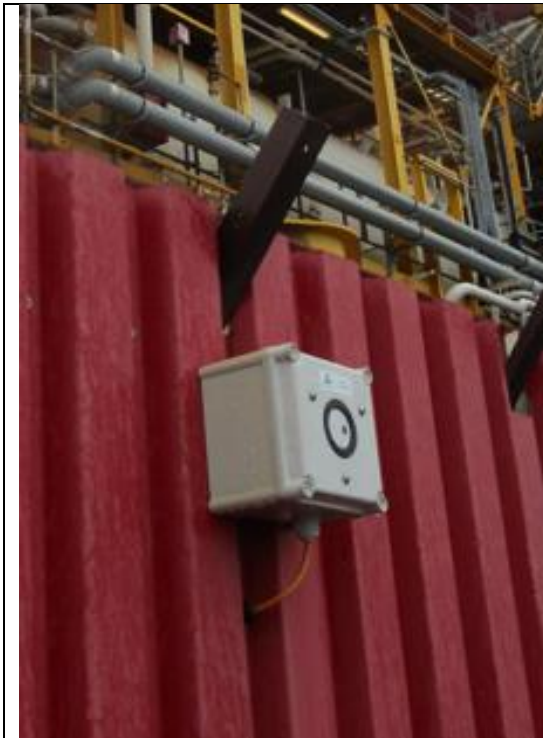
Lichteiland Goeree



Luchterduinen OHVS



PAWP OHVS

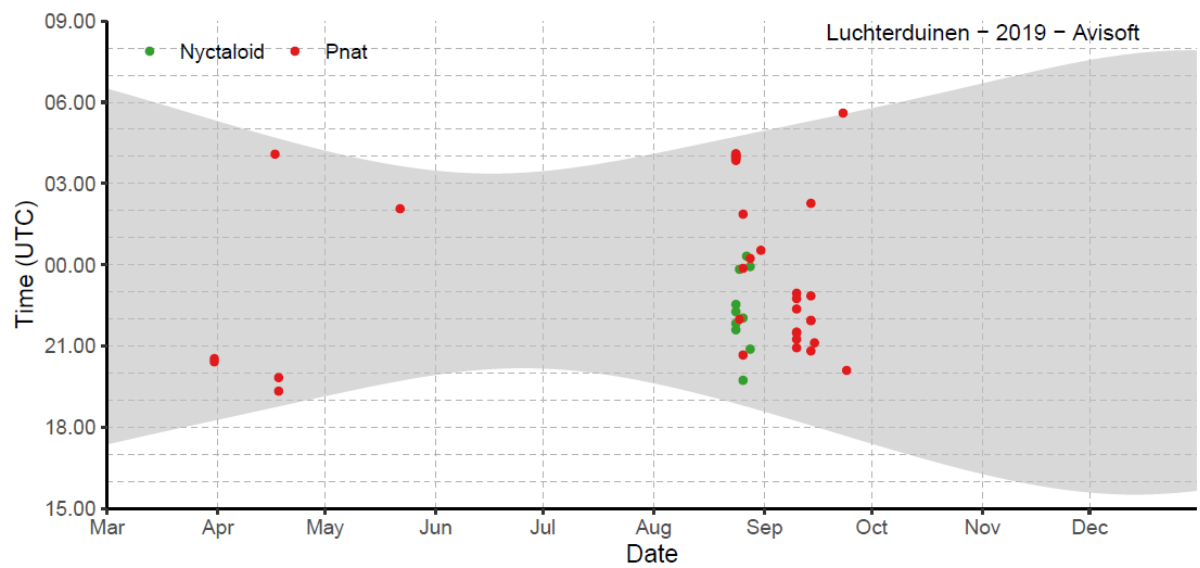
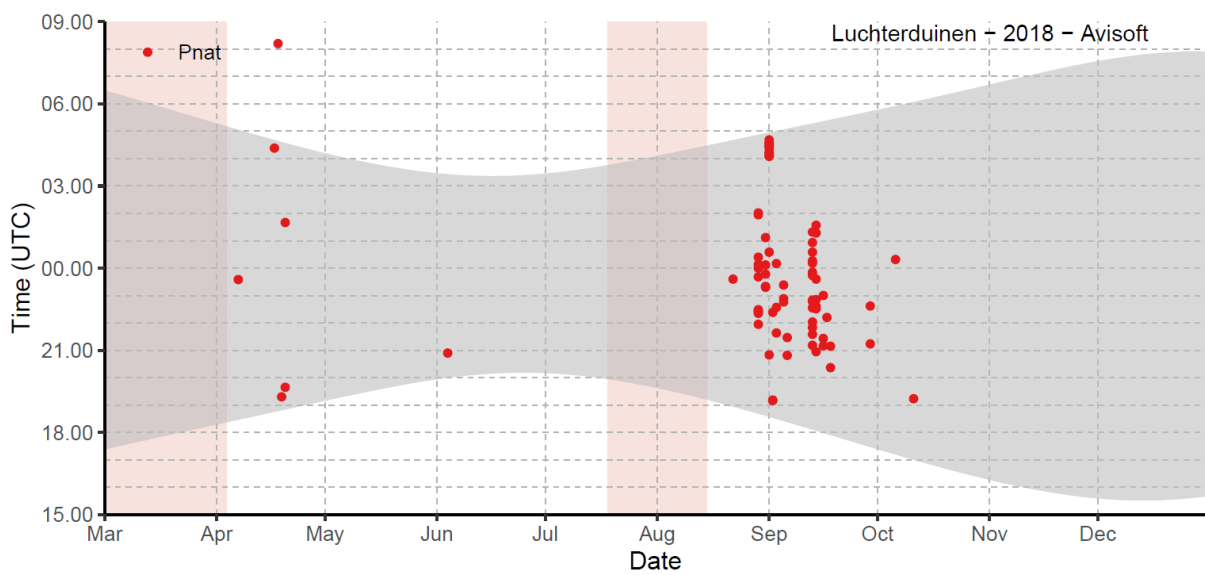
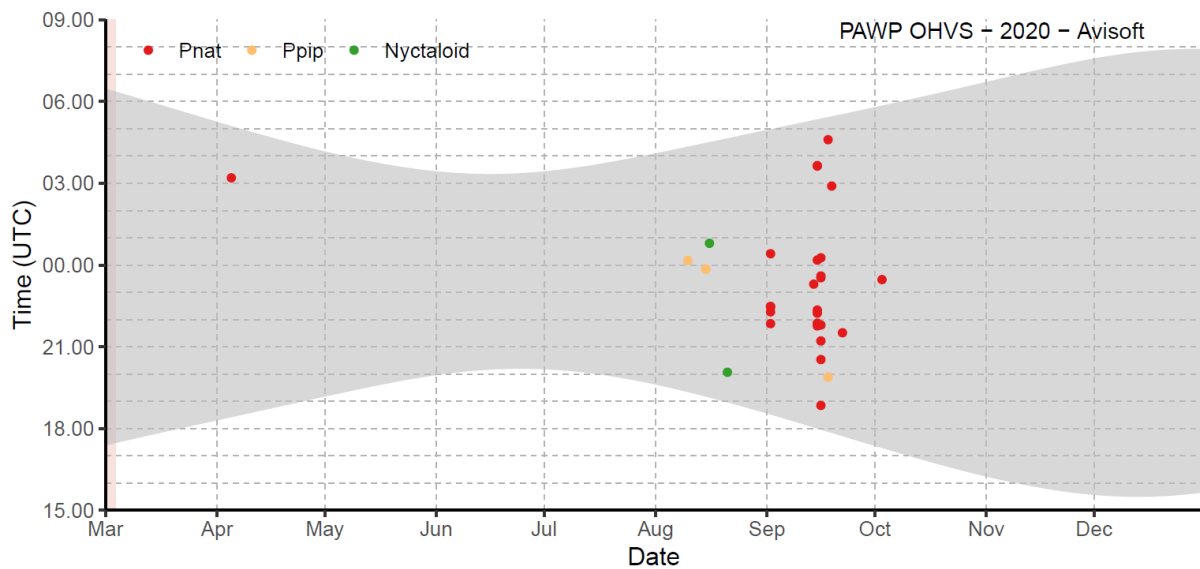


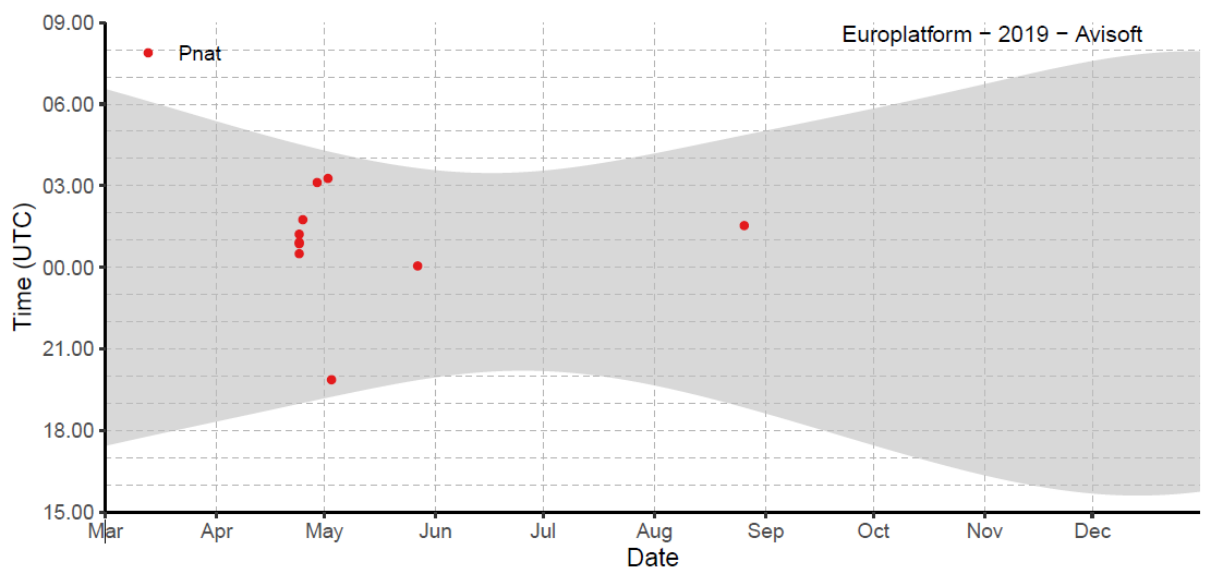
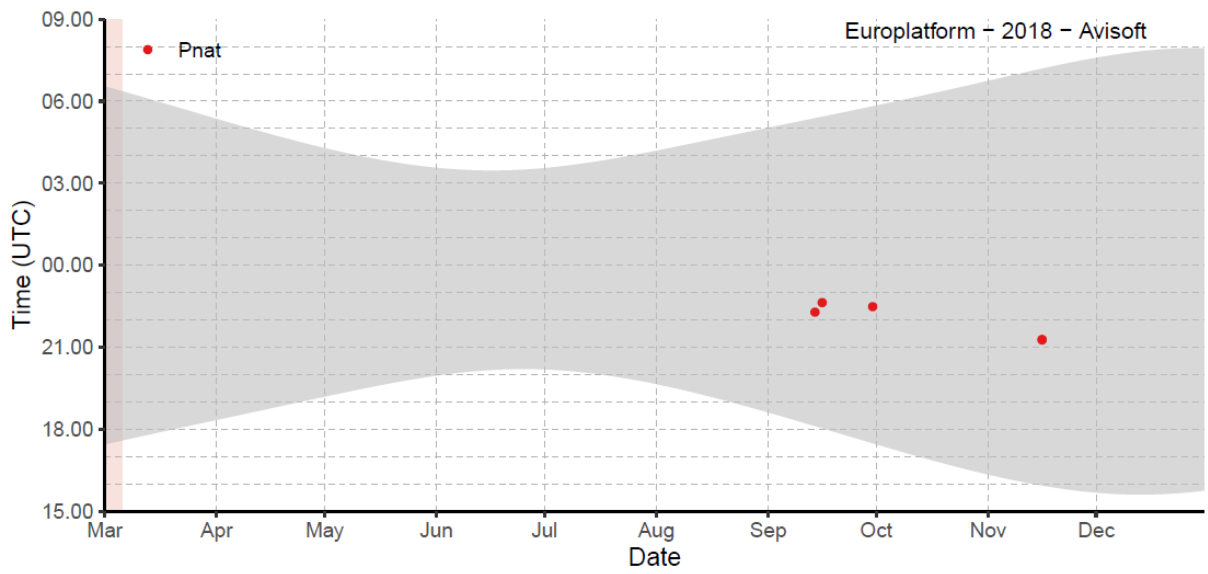
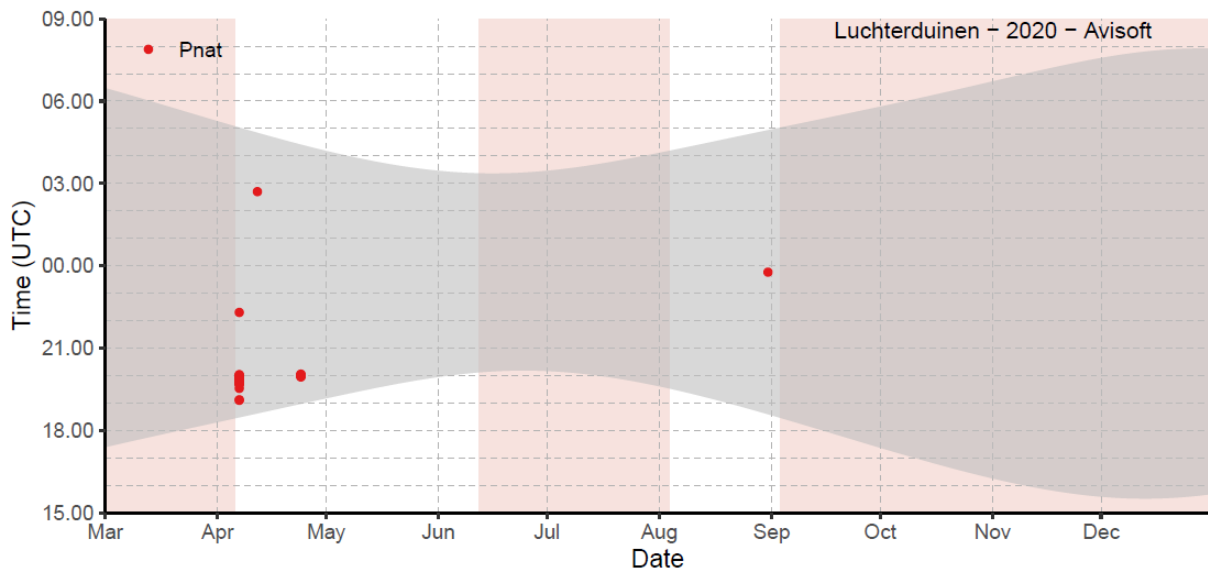
Petrogas Q1-A (Helder)

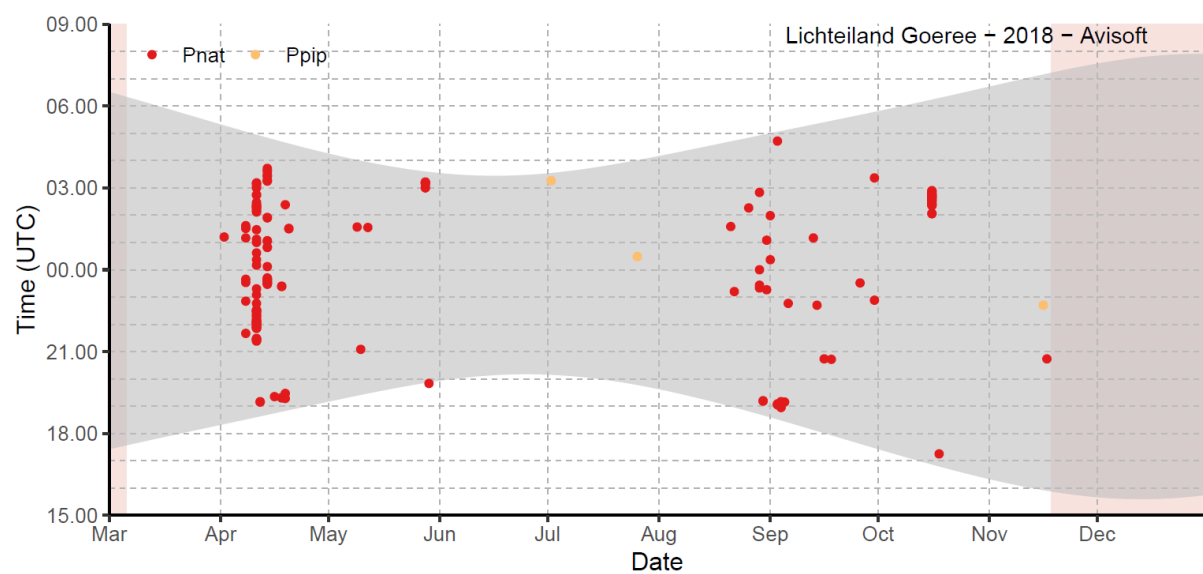
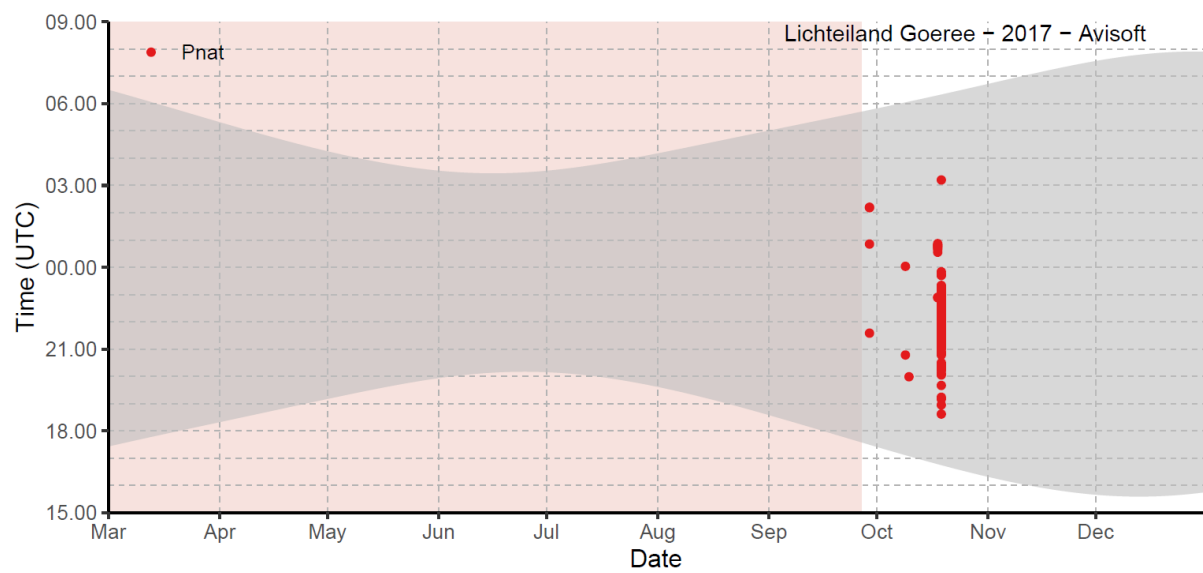
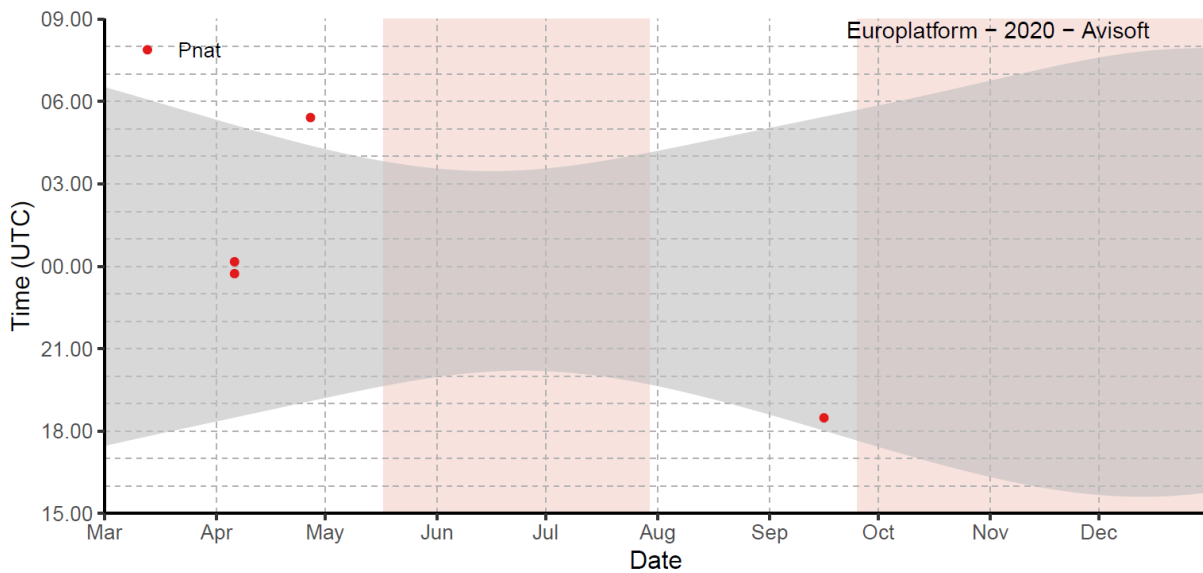


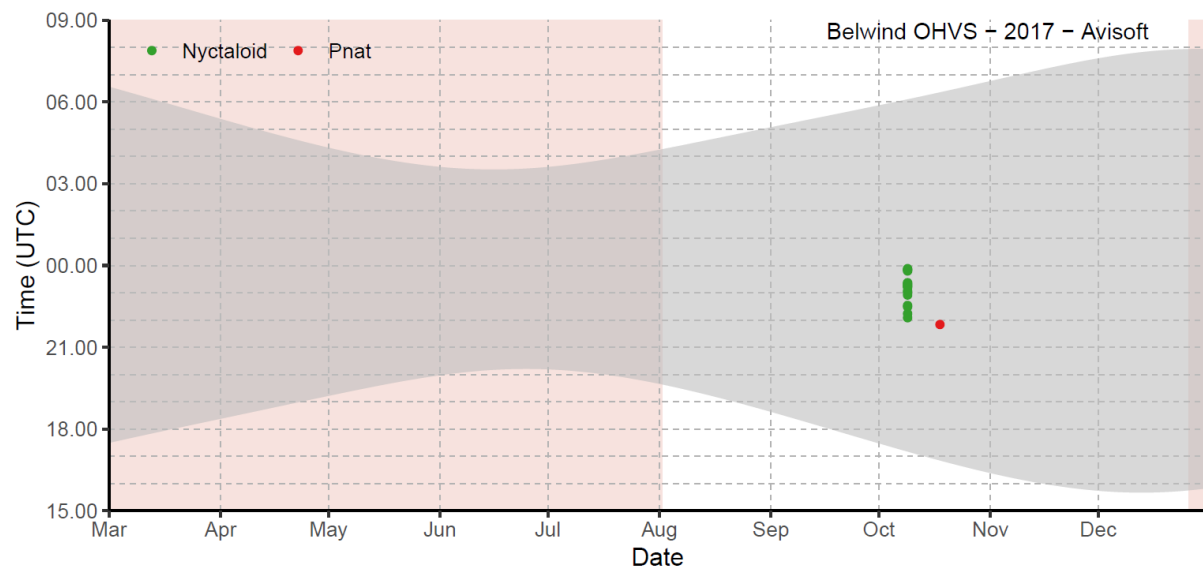
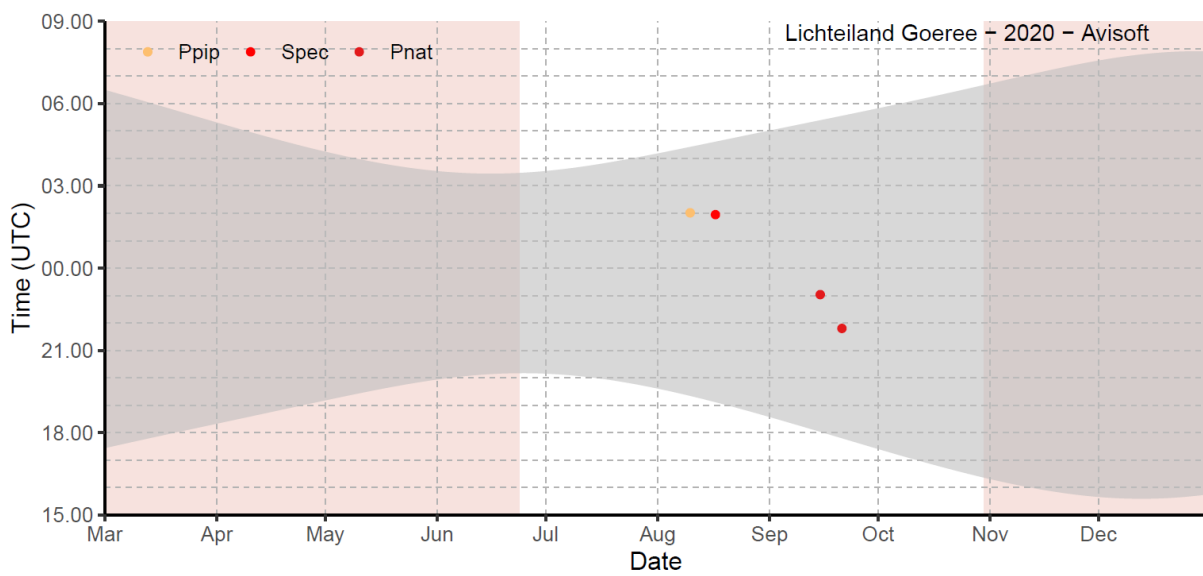
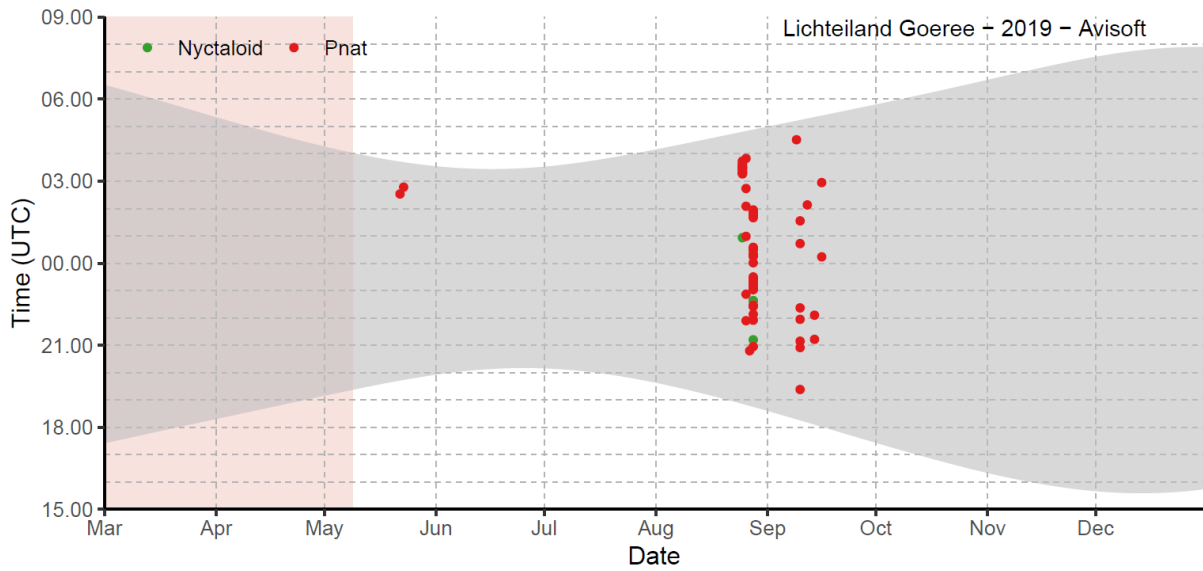
Petrogas P9-A (Horizon)

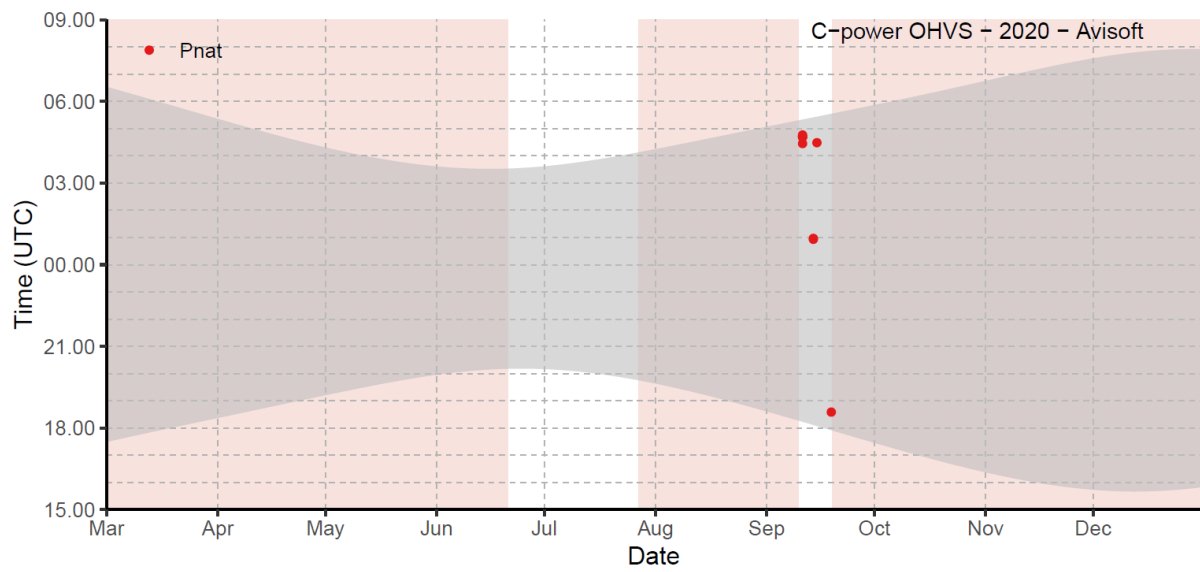
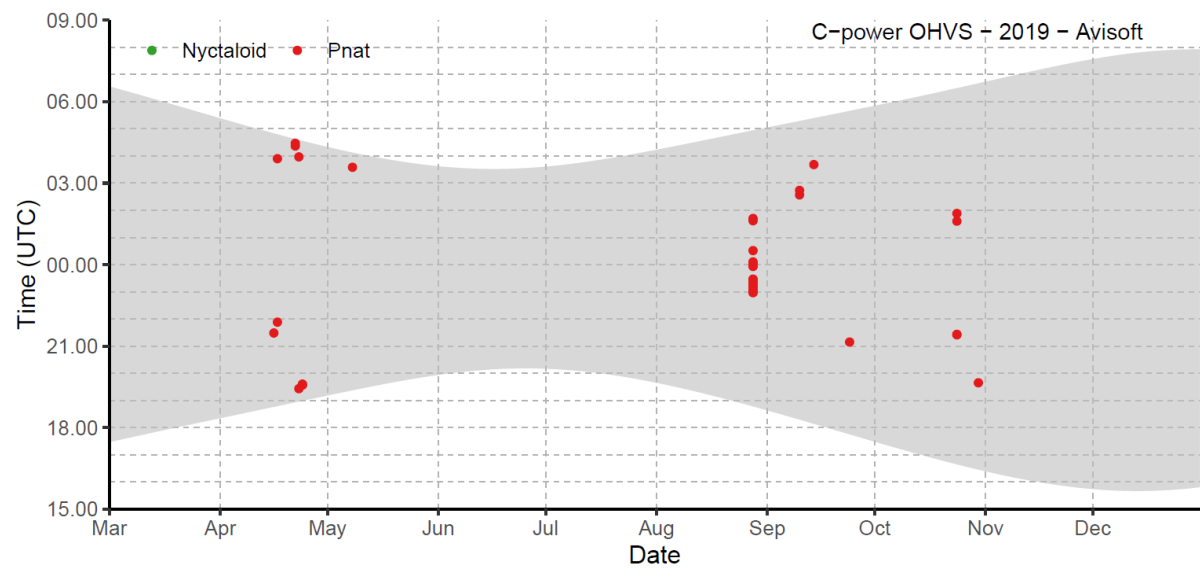
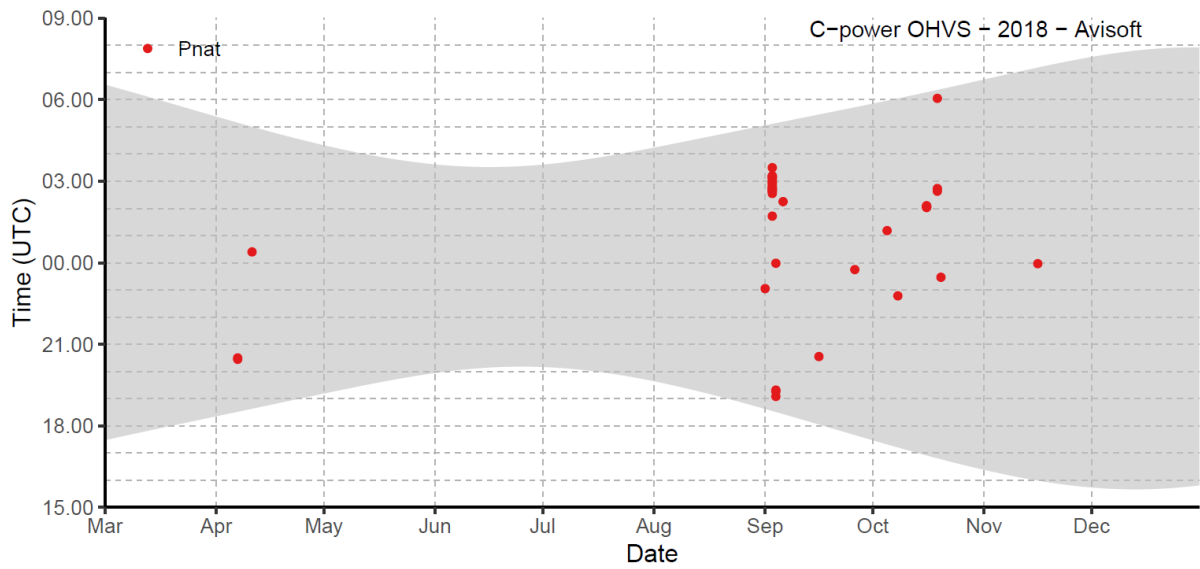
Photos of the monitoring locations Dana P11-B, Neptune L10, Neptune K12 and Wintershall P6-A are not available.

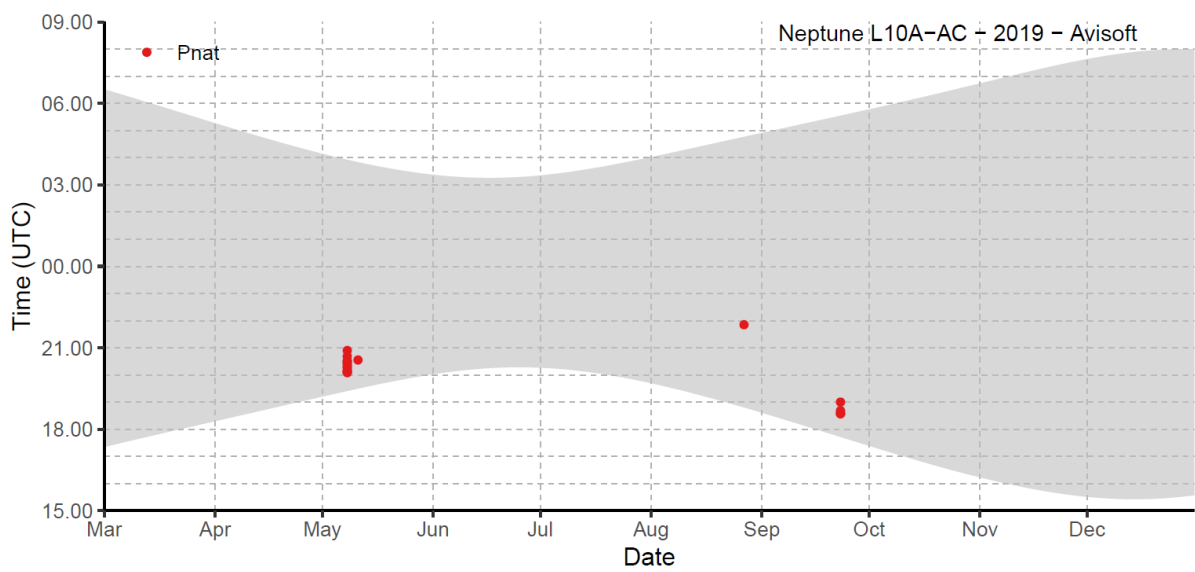
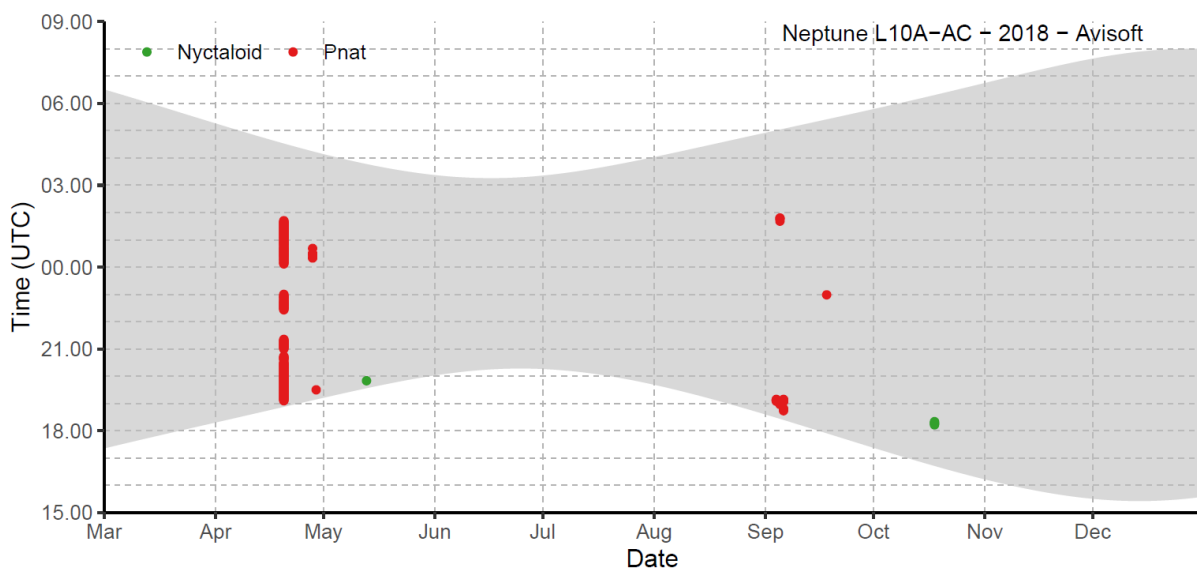
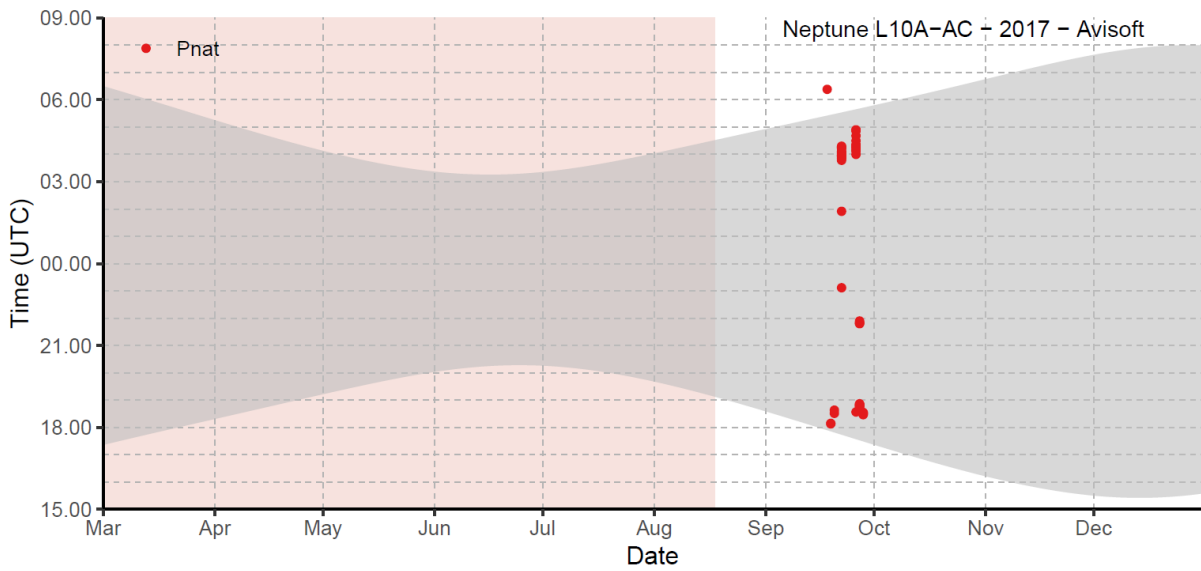


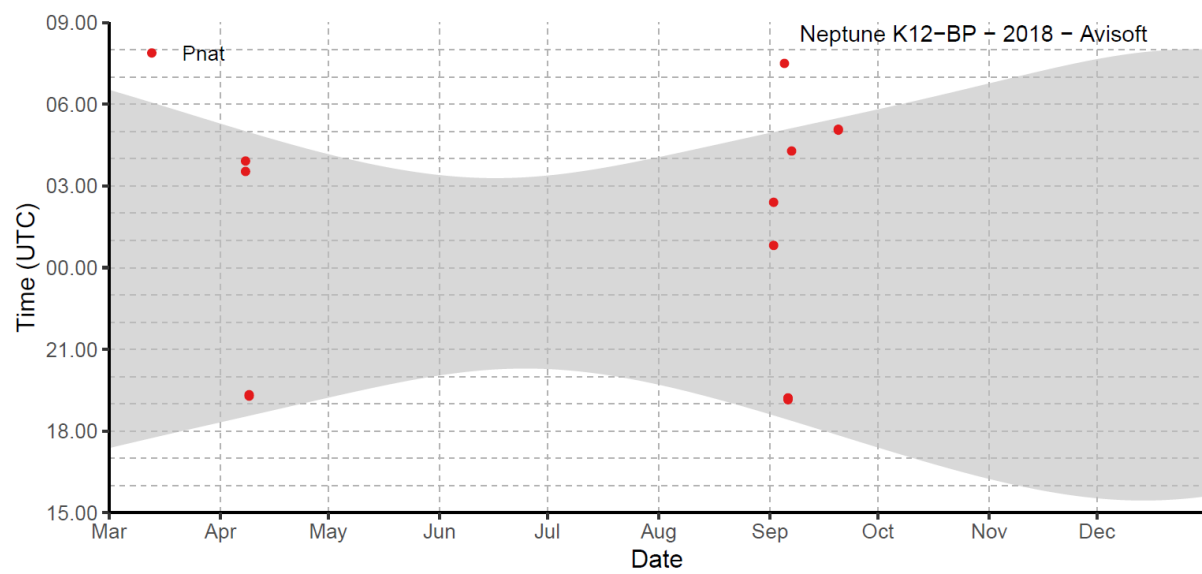
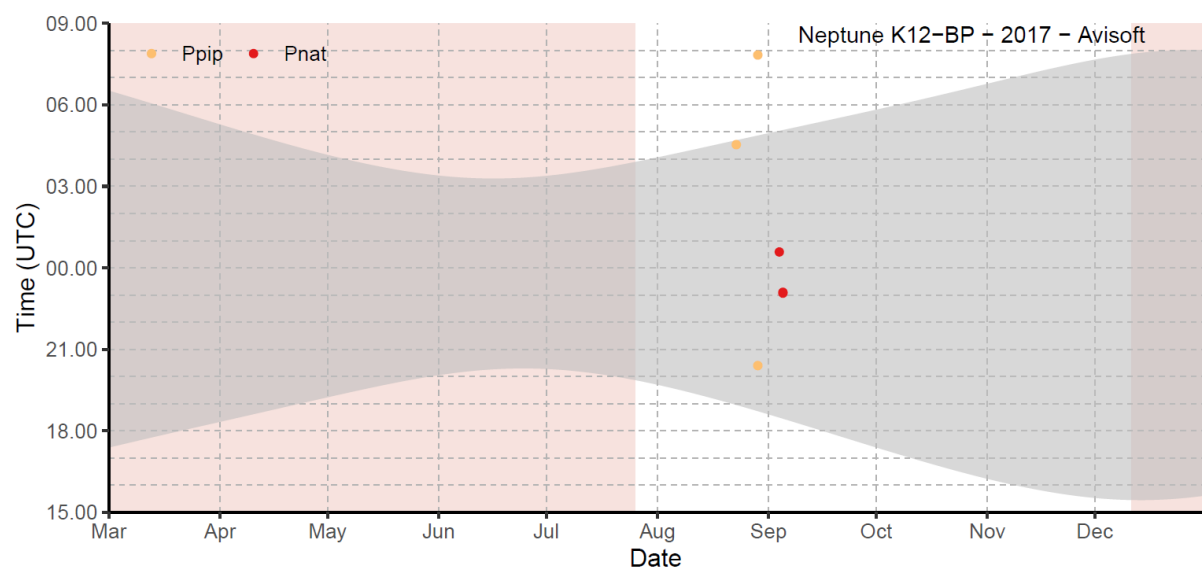
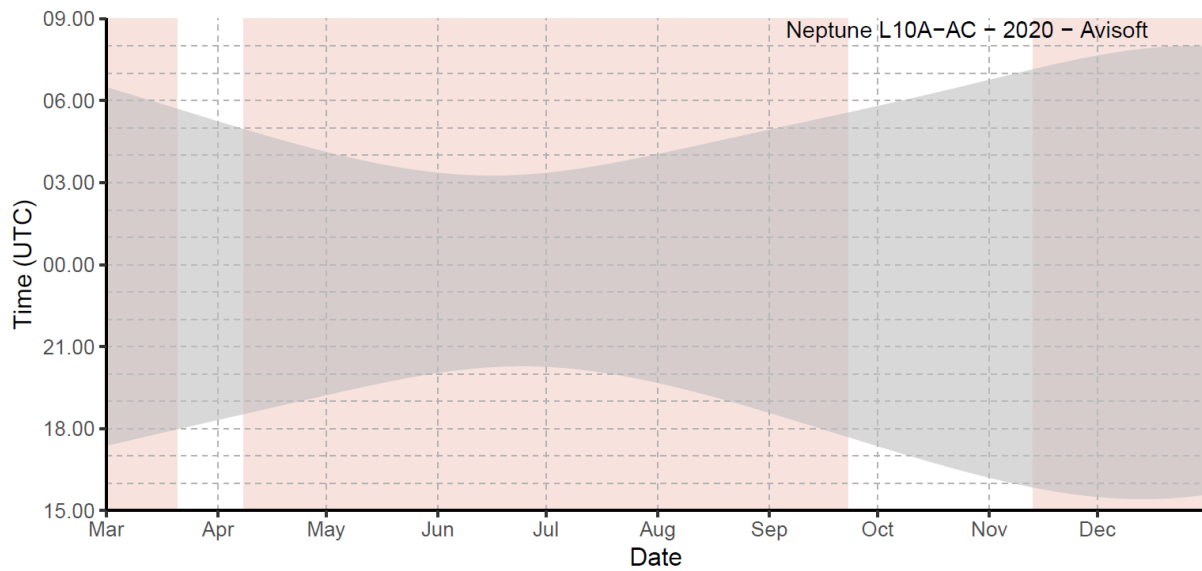


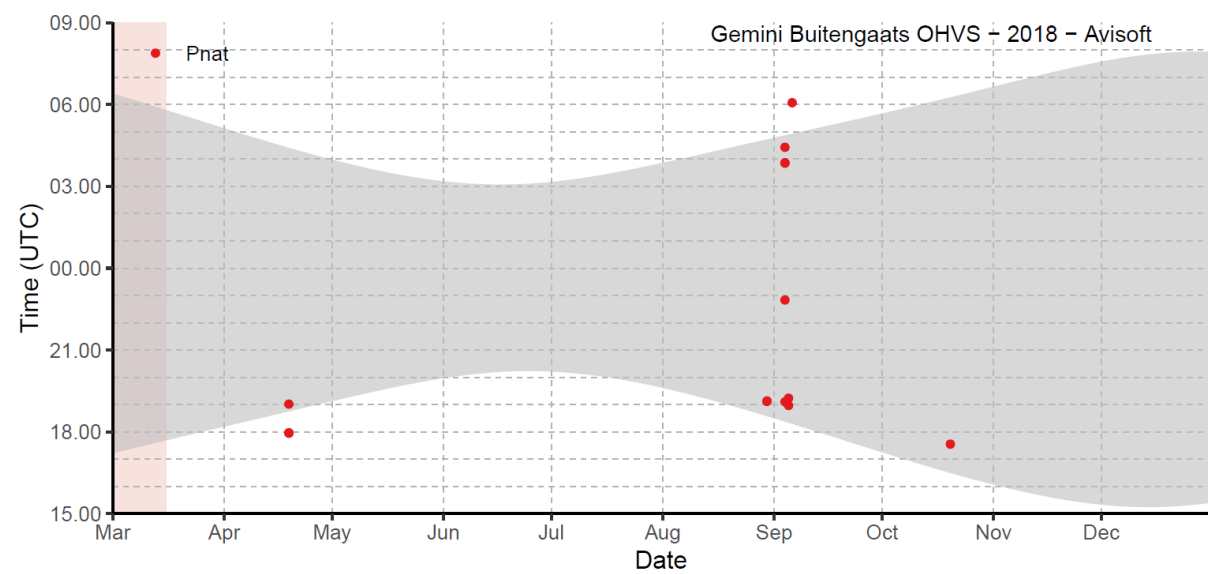
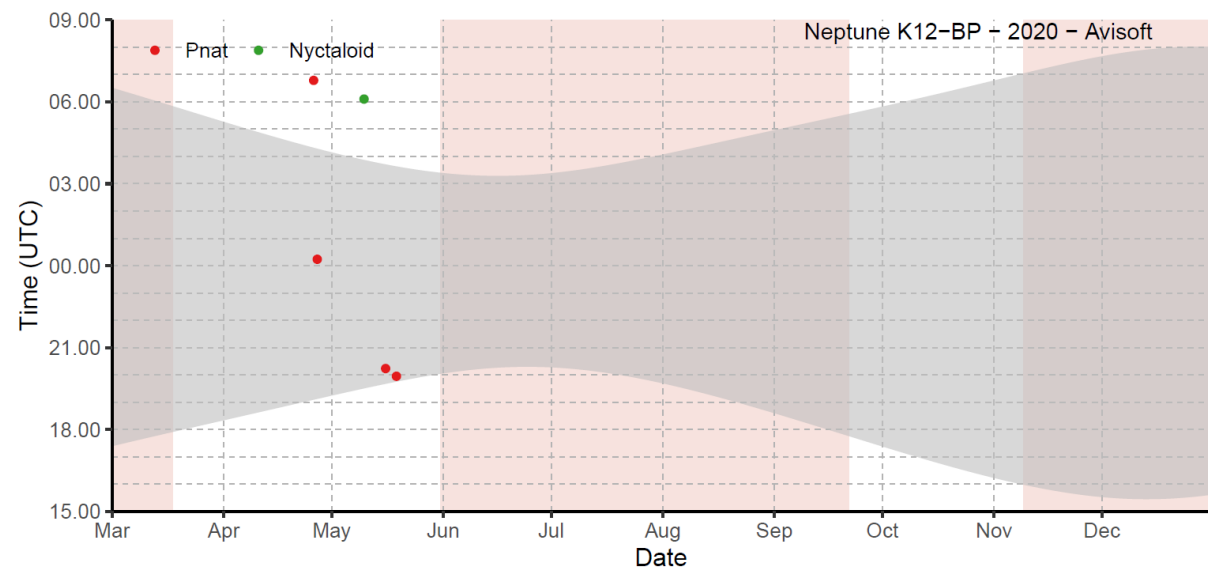
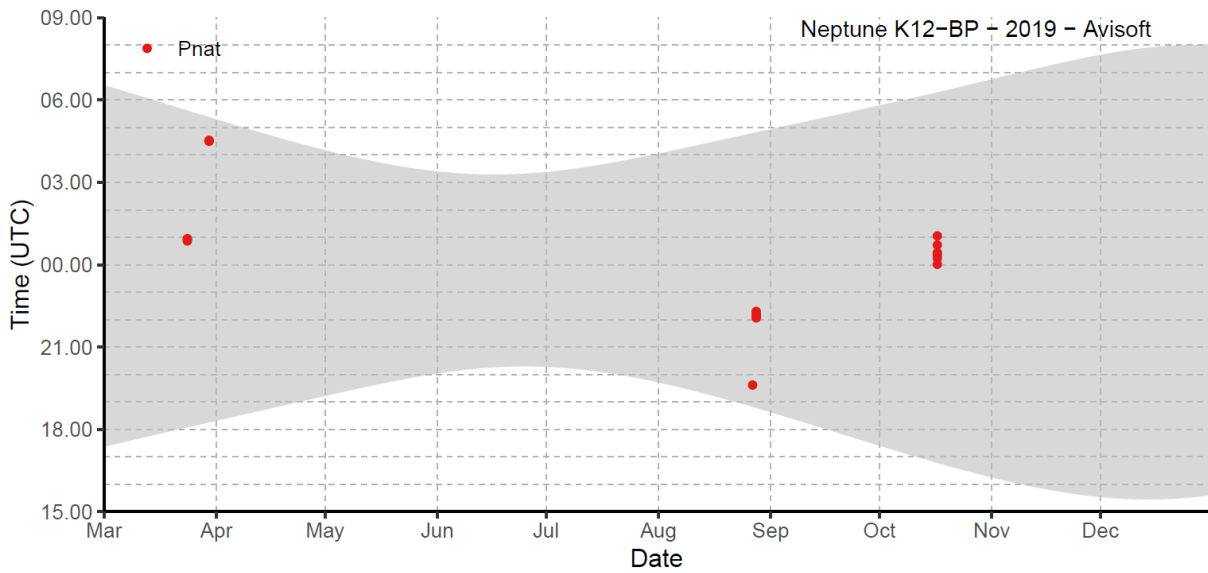


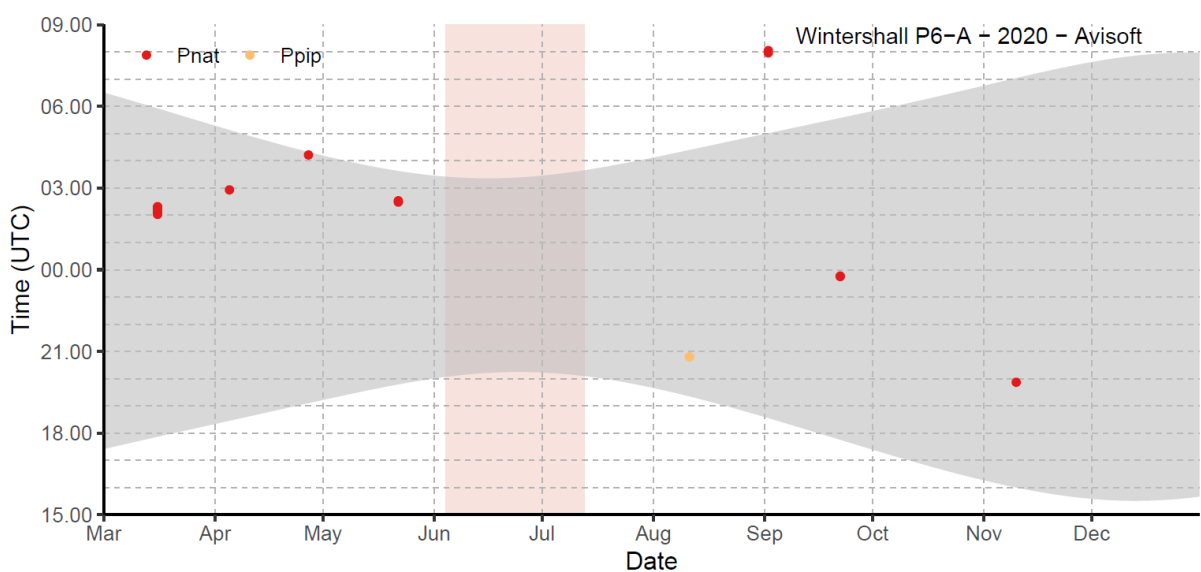
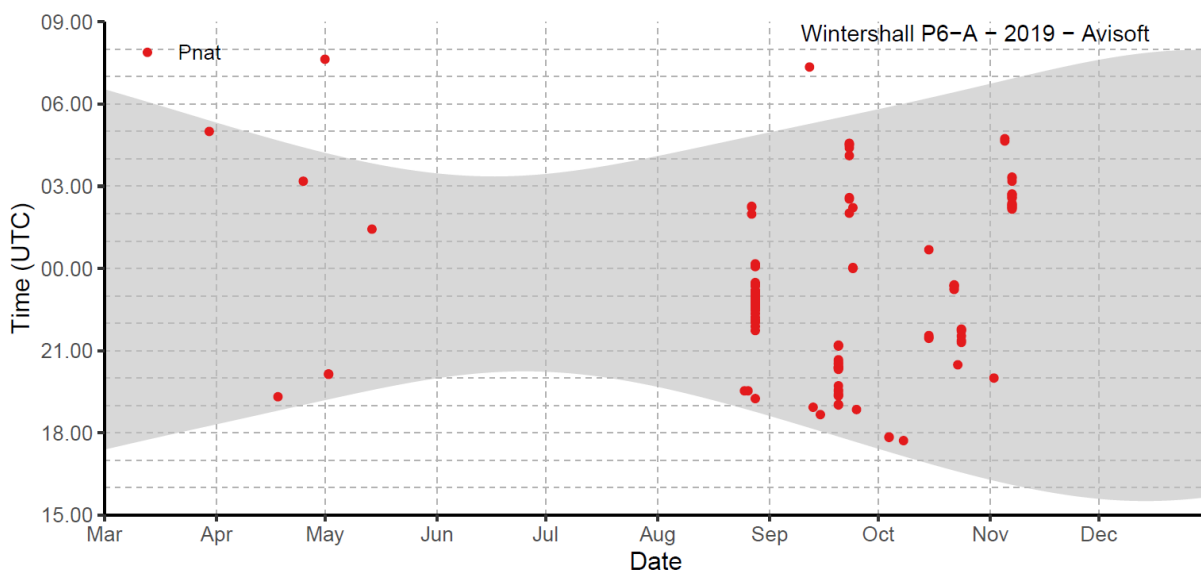
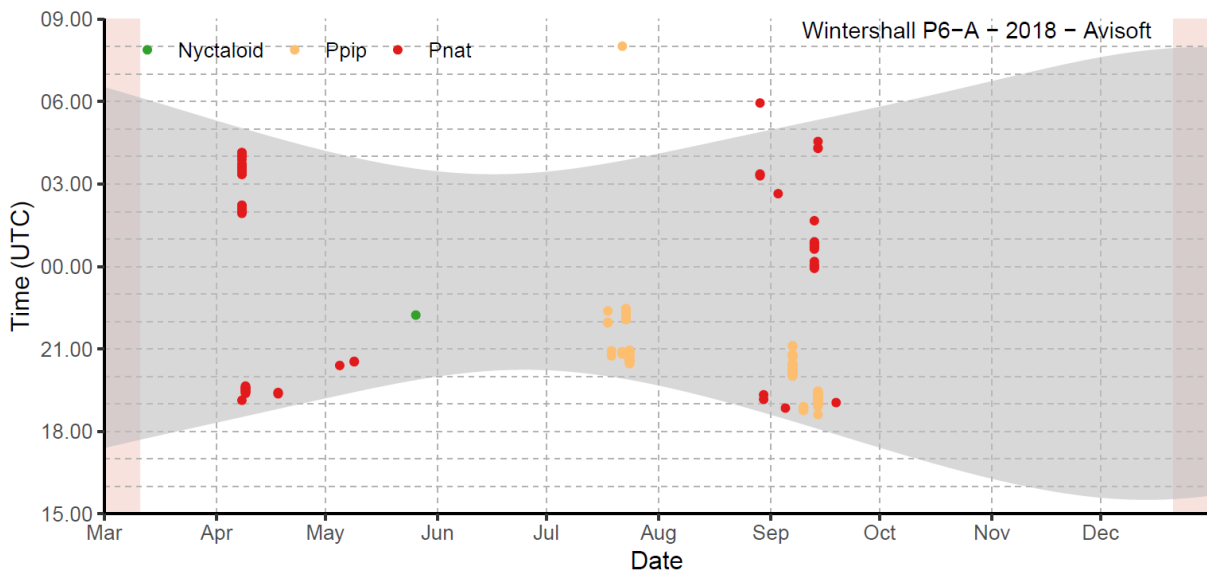


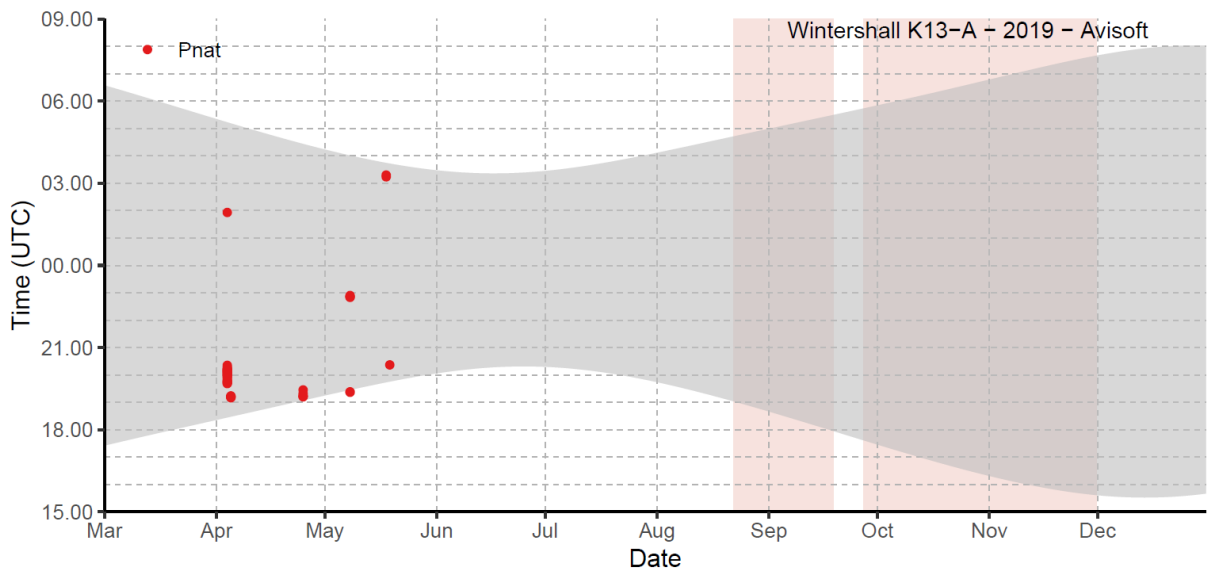
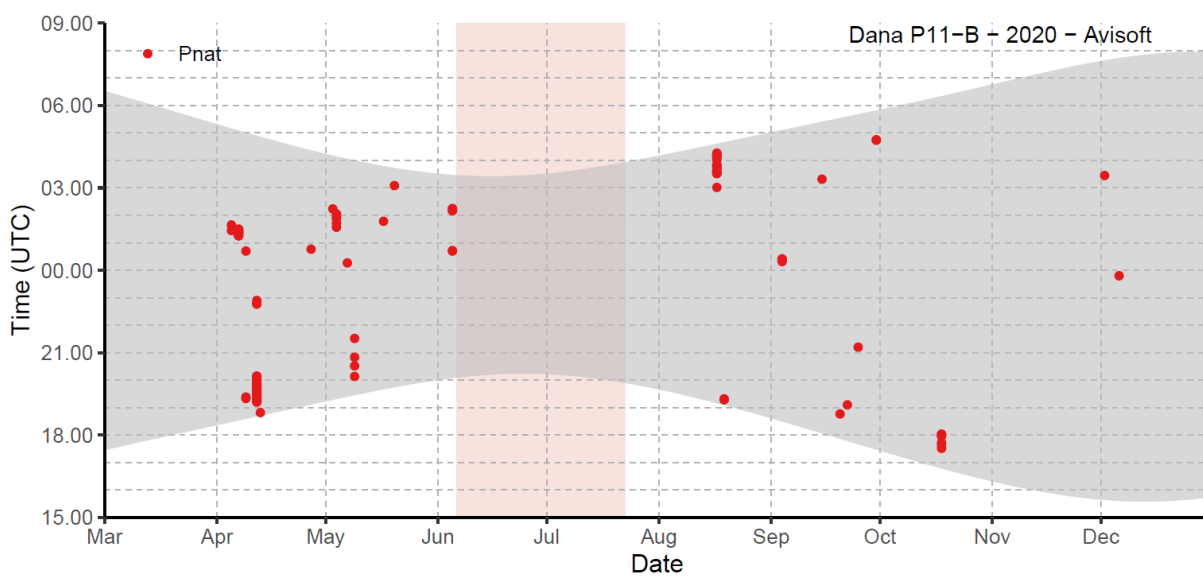
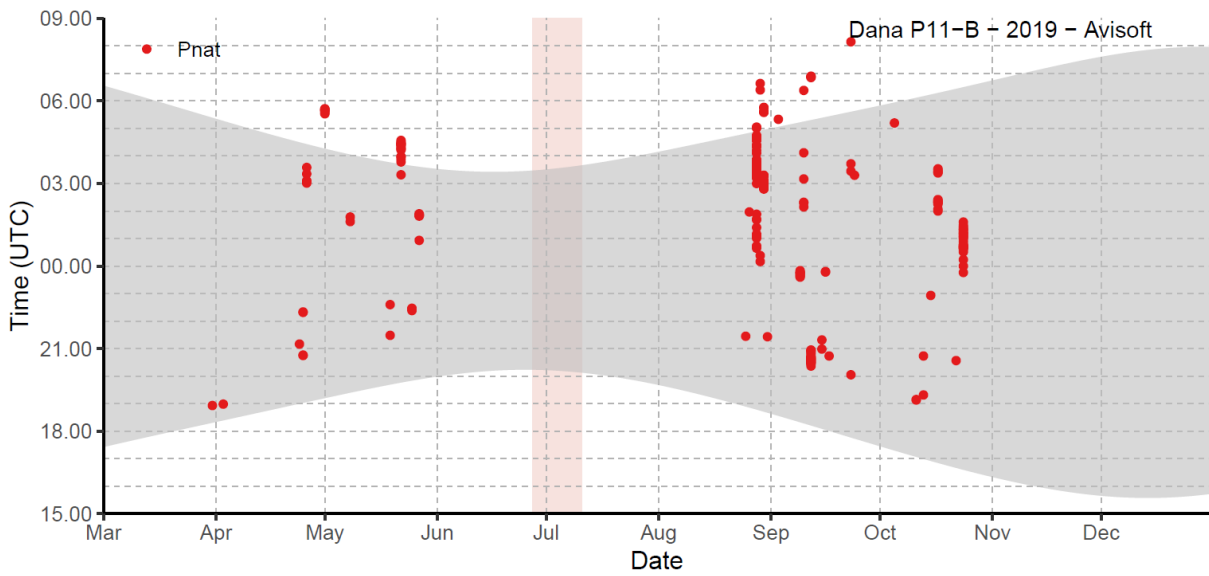


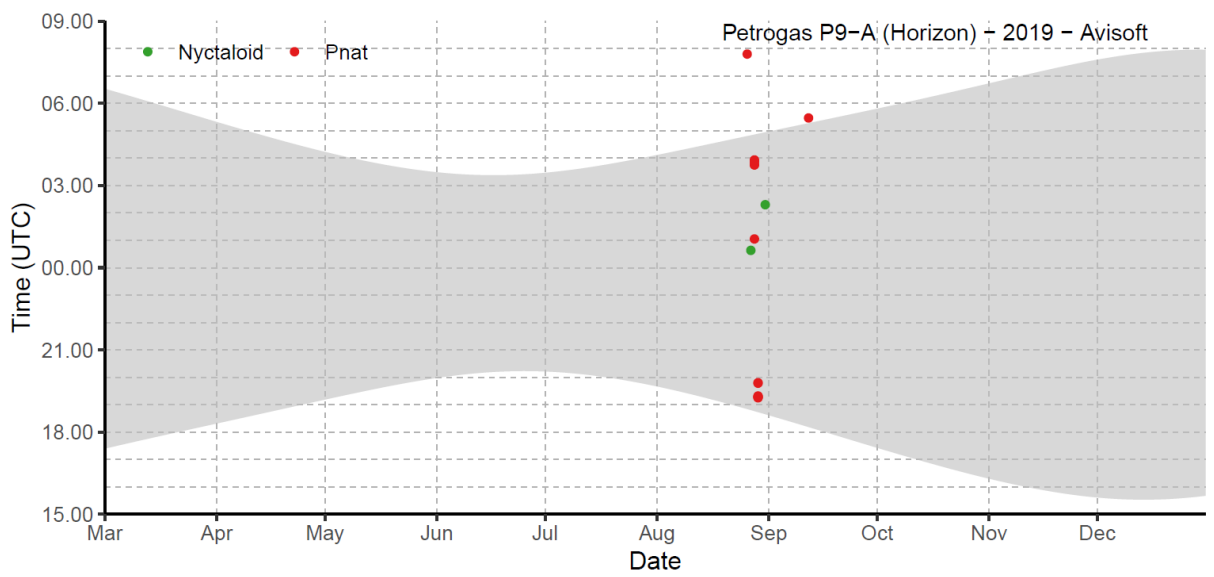
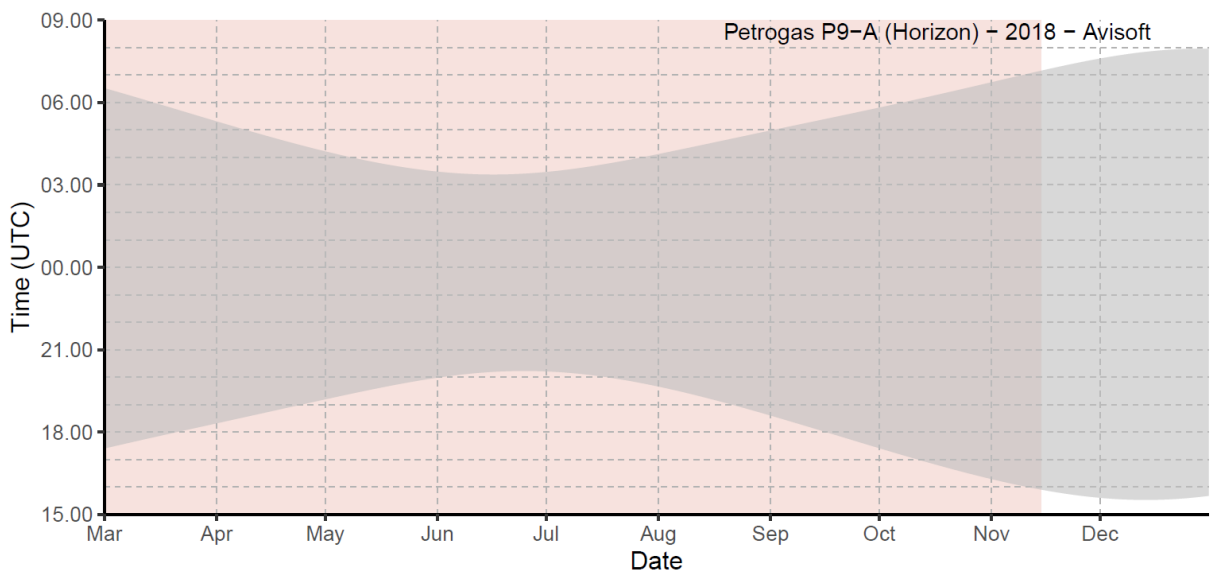
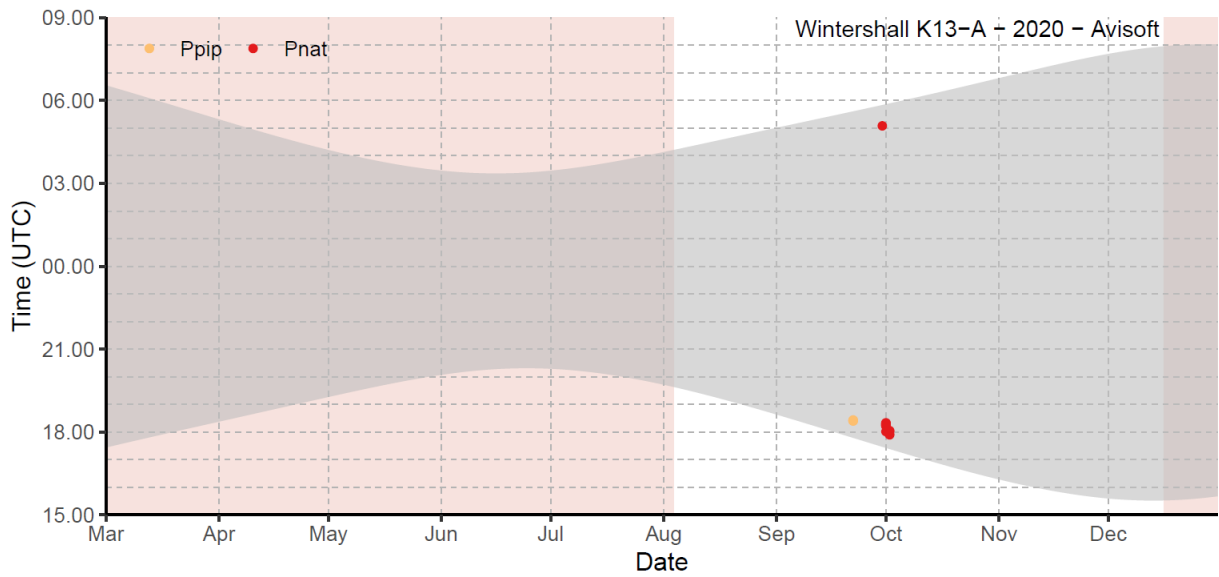


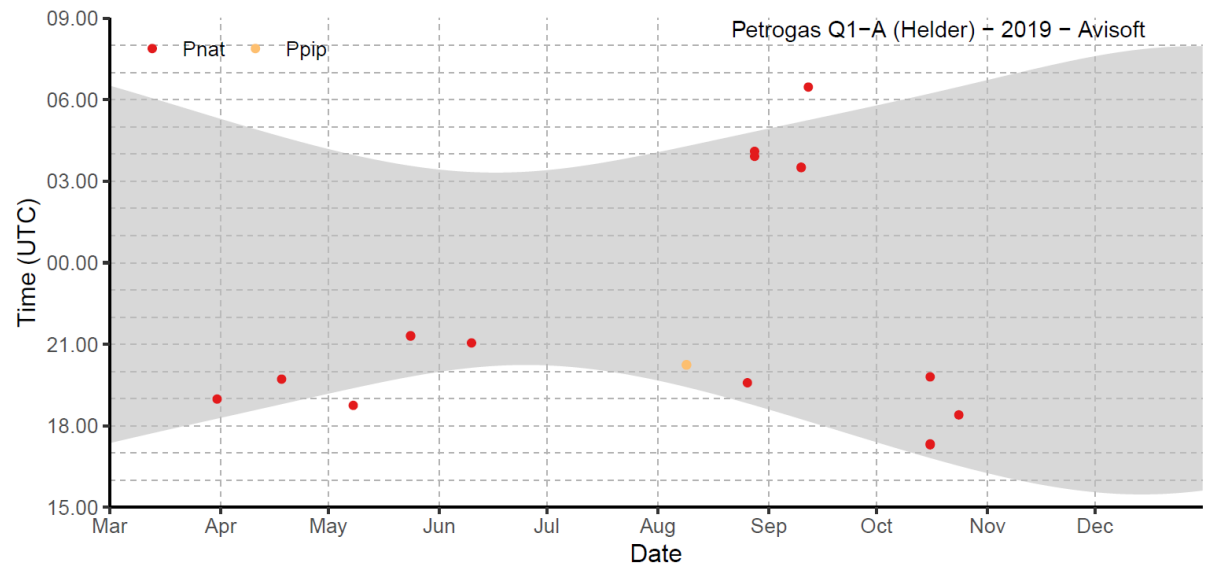
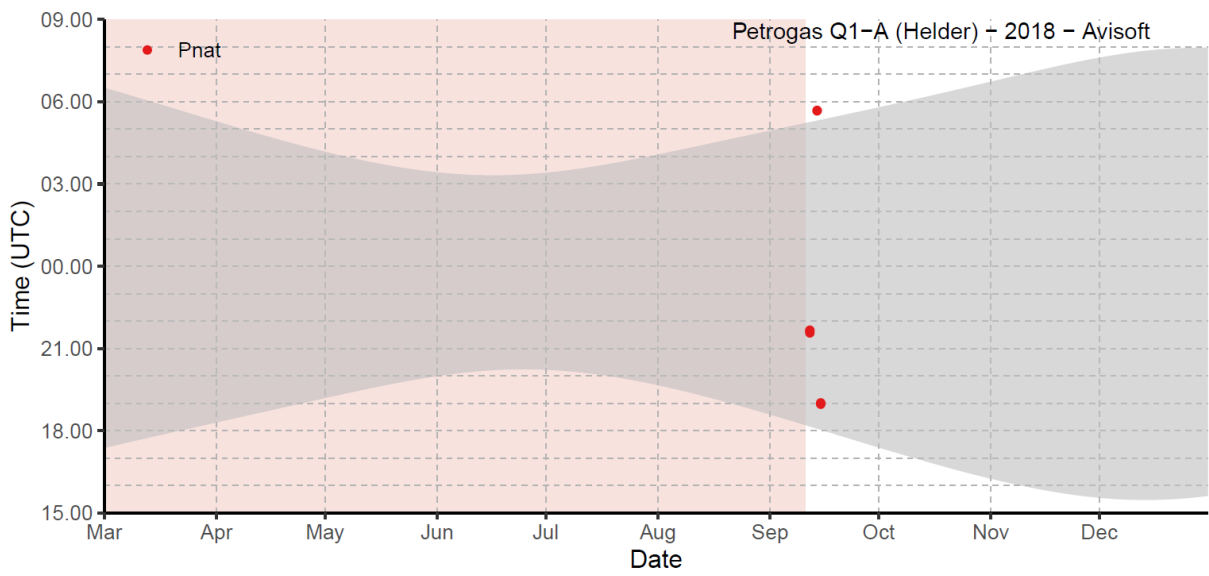
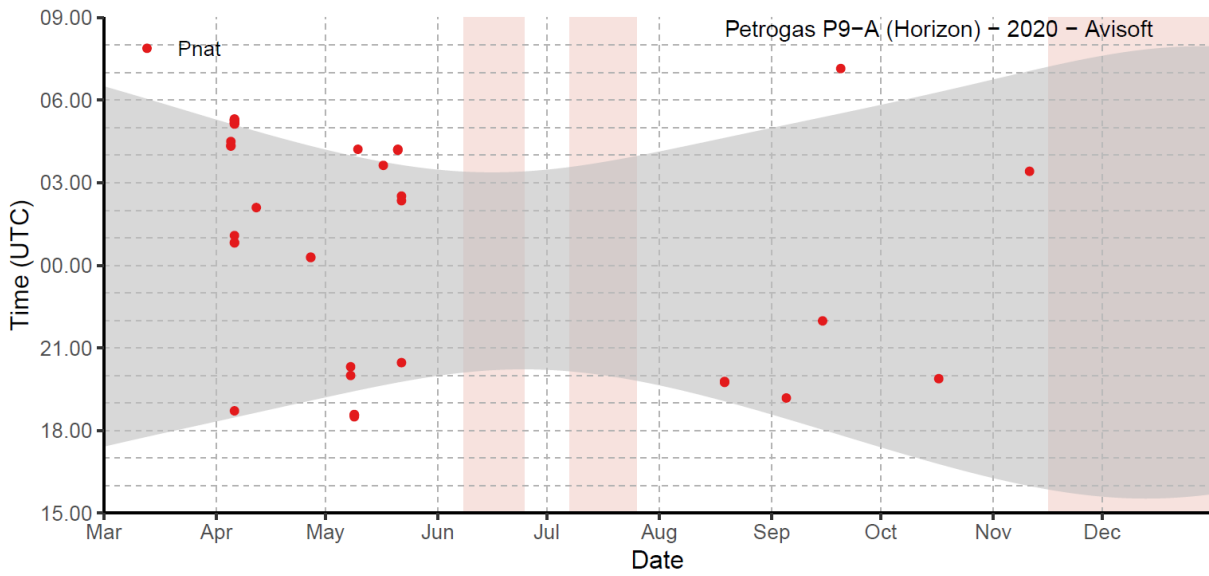












Annex 3: output spatiotemporal analysis

Table C-1. Coefficient summary table of the categorical and linear covariates. The interpretation is as follows: Consider a covariate x ; if x increases by a single unit, and all other covariates do not change, than the odds of detecting a bat call is multiplied by $\exp(\beta)$. The exponent of the 95% confidence interval (see columns " $\exp(q0.025)$ " and " $\exp(q0.975)$ ") is also given in this table.

term	β	Se	$\exp(\beta)$	$\exp(q0.025)$	$\exp(q0.975)$	p-value
(Intercept)	-3.3772	0.3990	0.0341	0.0156	0.0746	<2.22e-16***
Year 2018	-0.012581	0.291677	0.987498	0.557520	1.749088	0.965596
Year 2019	-0.344998	0.301178	0.708222	0.392470	1.278005	0.252005
Year 2020	-1.309882	0.336650	0.269852	0.139498	0.522015	9.9861e-05***
Rain	-0.8432	0.5030	0.4303	0.1606	1.1532	0.093644
Atmospheric pressure	0.0058	0.0144	1.0058	0.9778	1.0347	0.685948

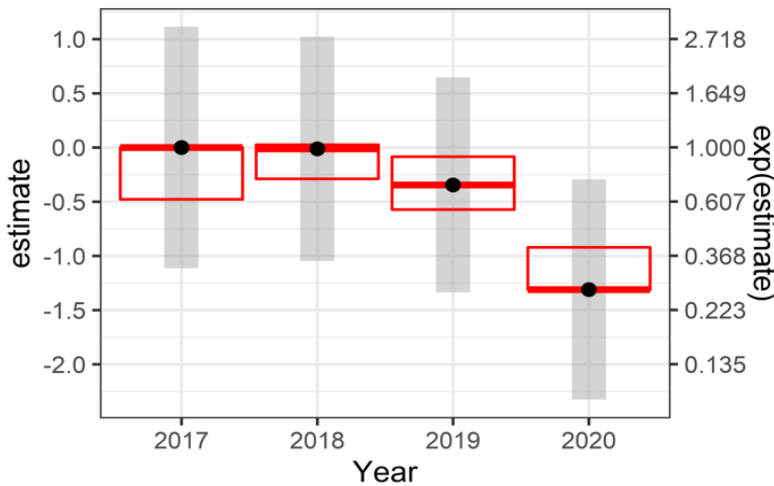


Figure C-1. Coefficient estimate plot of the year categories. The plots were made on the linear scale; the y-axis values on the right side show the exponent of the original y-axis values on the left. The black points indicate the correction factor of the intercept (2017 is the reference value, and thus has a value of zero), the grey shades indicate the 95% confidence intervals of the means, and the red crossbars indicate the confidence intervals for the Tukey tests for pairwise differences. If the red crossbars of two categories do not overlap with each other, differences can be regarded statistically significant. The qualitative interpretation is as follows: higher values of $f(x)$ indicate higher expected probability of detection, lower values indicate lower probability. The quantitative interpretation is as follows: suppose the year changes from year a to year b and all other covariates do not change, then the odds of a bat call detection will be multiplied by $\frac{\exp(f(\text{year}=b))}{\exp(f(\text{year}=a))}$.

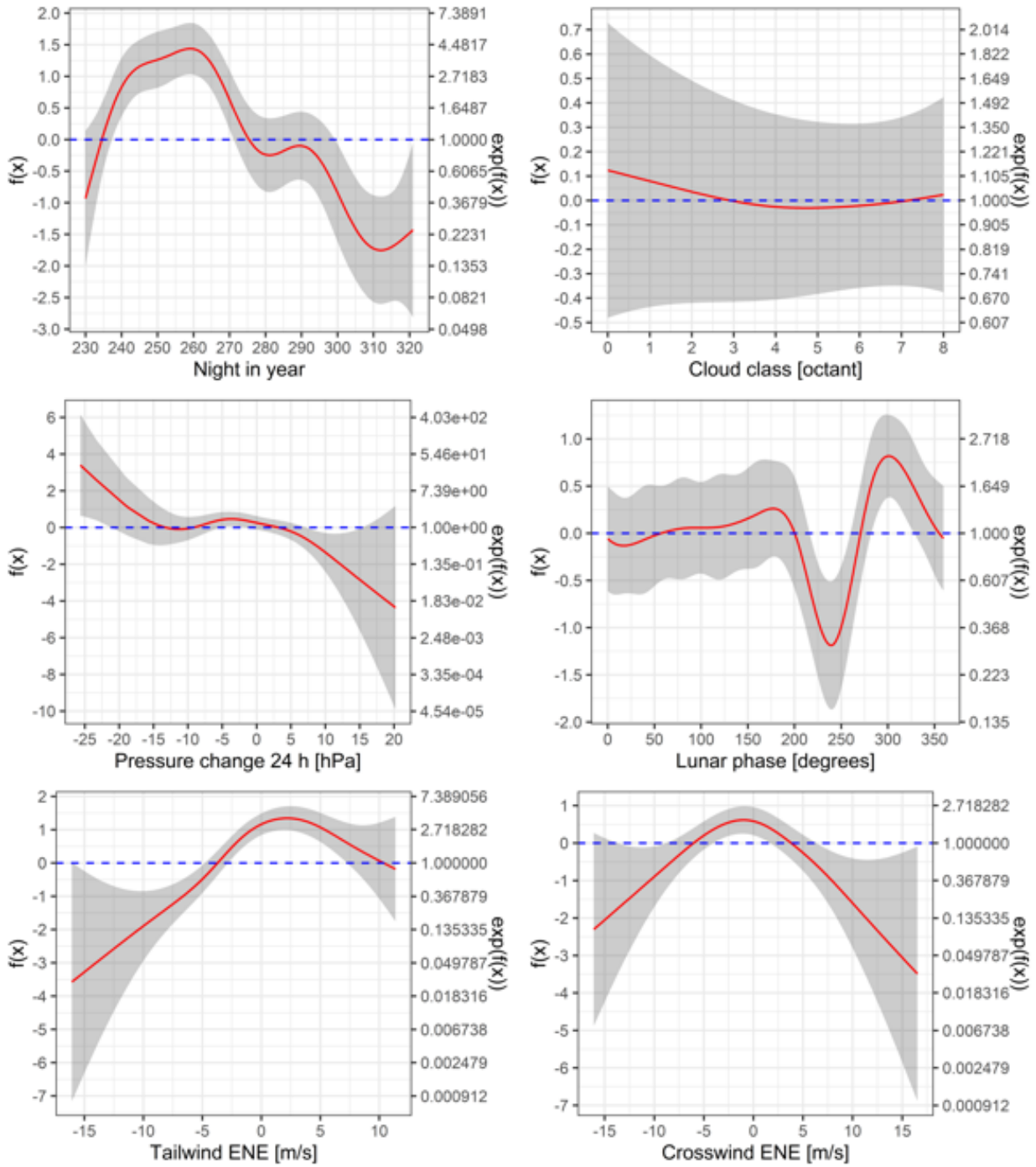


Figure C-2. Coefficient plots of the regular smoothers. The plots were made on the linear scale; the y-axis values on the right side show the exponent of the original y-axis values on the left. The solid red lines represents the relation between a covariate value (x -axis) and the effect of the covariate value (y -axis). The ribbon (shaded band) gives the 95% confidence interval. The qualitative interpretation is as follows: higher values of $f(x)$ indicate higher expected probability of detection, lower values indicate lower probability. The quantitative interpretation is as follows: suppose the covariate x changes from value a to value b and all other covariates do not change, then the odds of a bat call detection will be multiplied by $\frac{\exp(f(x=b))}{\exp(f(x=a))}$.

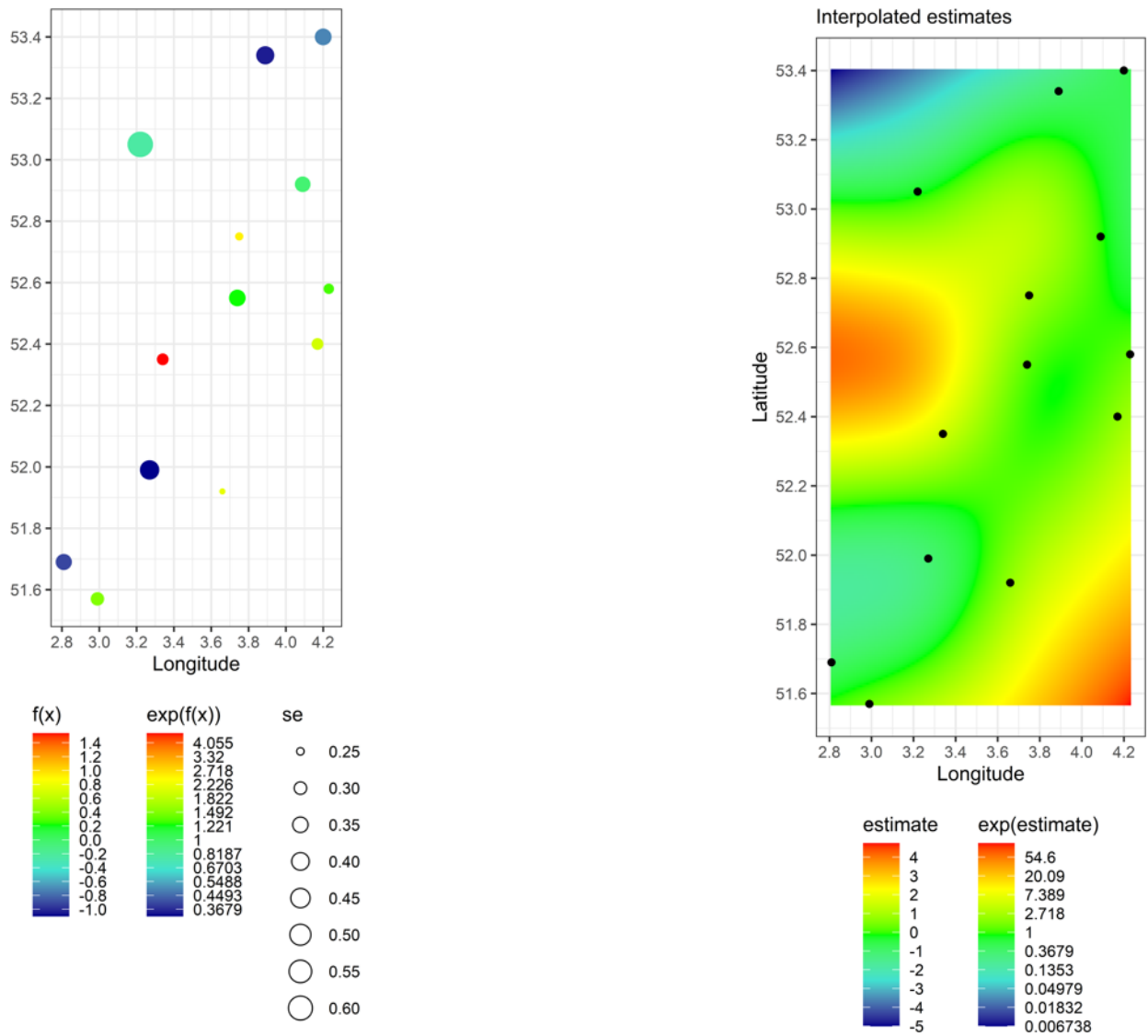


Figure C-3. Plot of the longitude-latitude tensor smoother. The plot on the left gives the mean estimate (indicated by colour) and standard error (indicated by the sizes of the points) at the actual monitoring locations. The plot on the right gives the interpolated mean estimates, where the black points indicate the actual monitoring locations. The qualitative interpretation is as follows: higher values of $f(x)$ indicate higher expected probability of detection, lower values indicate lower probability. The quantitative interpretation is as follows: suppose the spatial coordinates change from coordinates a to coordinates b and all other covariates do not change, then the odds of a bat call detection will be multiplied by $\frac{\exp(f(\text{coordinate}=b))}{\exp(f(\text{coordinate}=a))}$. Note that the estimates outside the boundaries of the monitoring locations are extrapolated, and thus not reliable.

Annex 4: output movement analysis

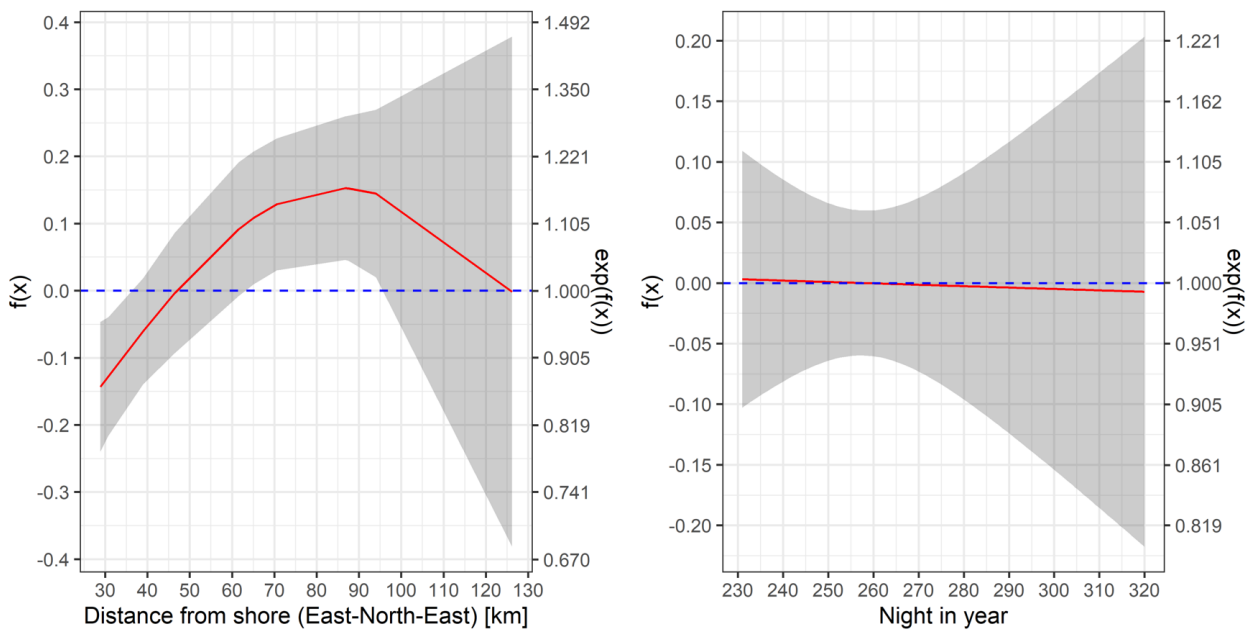


Figure D-1. Coefficient plots of the smoothers Distance from shore (ENE) and Night in year. The plots are made on the linear scale; the y-axis values on the right side show the exponent of the original y-axis values on the left. The solid red lines represents the relation between a covariate value (x-axis) and the effect of the covariate value (y-axis). The ribbon (shaded band) gives the 95% confidence interval. The qualitative interpretation is as follows: higher values of $f(x)$ indicate higher expected probability of detection, lower values indicate lower probability. The quantitative interpretation is as follows: suppose the covariate x changes from value a to value b and all other covariates do not change, then the odds of a bat call detection will be multiplied by $\frac{\exp(f(x=b))}{\exp(f(x=a))}$.

Wageningen Marine Research
T +31 (0)317 48 7000
E: marine-research@wur.nl
www.wur.eu/marine-research

Visitors' address

- Ankerpark 27, 1781 AG Den Helder
- Korringaweg 7, 4401 NT Yerseke
- Haringkade 1, 1976 CP IJmuiden

With knowledge, independent scientific research and advice, **Wageningen Marine Research** substantially contributes to more sustainable and more careful management, use and protection of natural riches in marine, coastal and freshwater areas.



Wageningen Marine Research is part of Wageningen University & Research. Wageningen University & Research is the collaboration between Wageningen University and the Wageningen Research Foundation and its mission is: 'To explore the potential for improving the quality of life'