Additional analyses of bat migration across the North Sea

Integration of telemetry and passive acoustic monitoring – WOZEP research programme (2019-2023)

Authors: Sander Lagerveld, Julia Karagicheva & Martin Poot

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Summary

In this report, the available migration data of Nathusius' pipistrelles collected within the Wozep bat research programme 2016 - 2023 are re-examined, in light of the differences found between telemetry and bat detector studies. Wozep stands for Wind op zee ecologisch programma and is an integrated research programme aimed at reducing the knowledge gaps concerning the effects of offshore wind farms on the North Sea ecosystem. A key aim is to investigate spring and autumn migration patterns of Nathusius' pipistrelles in greater detail by integrating telemetry data with passive acoustic monitoring data. This represents a novel step in combining these complementary datasets, with the expectation that their synthesis will yield new insights relevant to applied research questions, particularly in the further development of strategies to mitigate the impacts of offshore wind farms on bats, as well as in guiding future field research priorities, for example by identifying where and how collision risks should be empirically quantified. Additionally, observations of migratory routes and flight behaviour extending beyond the original study area, previously limited to the northern part of North Holland, are incorporated into the analysis.

The aim of this report is to examine the obtained tracking and acoustic data in more detail to:

1. Investigate the similarities and differences amongst the spring tracking and acoustic data, and assess the important predictors (environmental conditions) for spring migratory movements
2. Determine the important predictors (environmental conditions as well as the individual characteristics) for autumn departure decisions and examine the general movement pattern of bats tagged along the Dutch coast (in Zuid-Holland, Noord-Holland and Friesland).

The key findings of the two analyses presented in this report are:

- Two distinct cohorts of spring migrating Nathusius' pipistrelles are identified, likely originating from respectively the United Kingdom and the European mainland, reflecting multiple migratory strategies explaining offshore occurrence.
- Acoustic monitoring detection is limited, primarily detecting bats during stopovers or under suboptimal conditions, while actively migrating individuals studied with telemetry, particularly at high altitudes or with strong tailwinds, likely remain undetected.
- Environmental factors strongly affect departure decisions: bats preferentially migrate with moderate tailwinds (in higher wind speeds than previously assumed) in clear skies and avoid crosswinds or rain.
- In autumn sex and age depended seasonal patterns are present and departures occur preliminary within two hours after sunset.
- Spring migration shifts from mainland-drifted individuals in March–April to predominantly UK-origin bats in May–June, a period critical for mitigation measures because of the high proportion of likely pregnant females in this cohort. Because these females have successfully overwintered and are approaching reproduction, their loss in spring is likely to have greater ecological consequences than the loss of females during autumn migration.
- Autumn (August-November): Migration probability peaked in late August, dropped during mating, and rose again from mid-October, suggesting mating limits migration in early autumn. These movement patterns along the coast indicate multiple overlapping strategies such as migration to hibernation sites, barrier movements, and mating-related movements. Overall, our findings indicate that the seasonal migration patterns in autumn are strongly modulated by reproductive behaviour, while their night-to-night departure decision is based on current atmospheric conditions.

These findings provide a basis for the following recommendations:

- Priority should be given to evaluating current autumn curtailment measures and developing complementary strategies for the spring migration period, providing rapid mitigation benefits. Curtailment practices should be reviewed and refined based on recent insights into bat migration, including wind speed thresholds and expert consultation. Given the lack of knowledge regarding

collisions offshore and impacts on bat populations, there is no alternative but to prioritise mitigation offshore. At the same time, the effectiveness of these measures cannot yet be substantiated.

- To better understand offshore occurrence potentially explained by different origin of migrating bats from respectively the UK and the European mainland, targeted spring tagging studies in northern France and Belgium. Complementary monitoring in the northern North Sea, combining both acoustic and tracking methods as proven to be successful in reconstructing spatial origin and migratory pathways, is also recommended to assess the extent and timing of bat activity in the more northern offshore regions, given an expanding MOTUS network with sufficient coastal and offshore coverage, not only in the Dutch EEZ.

Given the existing knowledge gaps, which hamper the substantiation of the current offshore bat mitigation protocol the following two recommendations are proposed:

- Collision risk assessment can build on operational thermal camera systems, supplemented by passive acoustic detectors under the BirdSafe and developing POWER projects.
- Research on potential attraction to offshore wind farms and lighting is also advised, with experimental studies under development in the POWER project.

1 Introduction

The EU aims to be climate neutral by 2050, meaning an economy with net-zero greenhouse gas emissions. The development of offshore wind farms (OWFs) plays an important role in the Dutch energy transition to comply with this European target. With the finalization of the Windfarm Hollandse Kust (noord) in 2023, a total of 4.7 GW has been realized. By the end of 2032, the Netherlands wants to achieve approximately 21 GW of installed offshore wind energy capacity, and the government is considering that offshore wind energy should be able to grow even further after that depending on future energy demand (Rijkswaterstaat Noordzeeloket).

Despite the environmental gain, there are concerns about the impact of OWFs on biodiversity and protected species like bats, which are found at sea during migration, and in some cases during foraging trips from the mainland (Ahlén et al. 2009, Brabant et al. 2021, Hüppop & Hill 2016, Lagerveld et al. 2014, 2021, 2023, 2024a, Lagerveld & Mostert 2023).

Wind op zee ecologisch programma (Wozep)
In 2016, the Ministry of Economic Affairs (now Ministerie van Economische Zaken en Klimaat, EZK) commissioned Rijkswaterstaat (RWS) to establish an integrated research programme aimed at reducing the knowledge gaps concerning the effects of offshore wind farms on the North Sea ecosystem. This led to the creation of the Wind op zee ecologisch programma (Wozep). Wozep ran from 2016 to 2023 and has now entered its second implementation phase (2024–2030), operating as an independent sub-programme under the Uitvoeringsbureau MONS.

The research results from Wozep are applied within the Kader Ecologie en Cumulatie (KEC). The KEC assesses the cumulative effects of proposed offshore wind farms, together with existing and planned ones, on species protected under nature conservation legislation. The thematic focus areas of Wozep are:
- Birds
- Bats
- Marine mammals and underwater sound
- Benthos, fish and electromagnetic fields
- Ecosystem effects
- Data and information management

The objectives of Wozep are to:
- Reduce the uncertainty surrounding assumptions and knowledge gaps in the KEC, Environmental Impact Assessment (MER) and 'Passende Beoordeling' (PB - 'Appropriate Assessment');
- Reduce uncertainty regarding assumptions and knowledge gaps related to long-term effects of large-scale offshore wind energy expansion (in preparation for future offshore wind deployment roadmaps);
- Develop knowledge to support the design of effective mitigation measures.

Knowledge gaps bats and offshore wind farms
Regarding bats, significant knowledge gaps remain across all three objectives. For instance, little is known about the number of bats migrating across the North Sea, what proportion these represent of the total populations, and wat the actual population size is of the relevant species. This lack of information hampers the ability to predict long-term effects. Also given the lack of knowledge regarding collisions offshore, there is no alternative but to prioritise mitigation offshore. At the same time, the effectiveness of these measures cannot yet be substantiated. Therefore, for bats, the emphasis logically lies on the third objective, developing, implementing, and improving mitigation measures, to minimise potential short-term risks and impacts as effectively as possible. Research into collision risk remains outside the scope of this report, the analyses presented here focus on offshore and coastal bat migration, providing essential ecological context for the evidence-informed impact assessments and the further development of mitigation measures.

1.1 Background

1.1.1 Main species of interest

Several species of bat have been recorded at the North Sea, including Nathusius' pipistrelle *Pipistrellus nathusii*, Common pipistrelle *Pipistrellus pipistrellus*, Common noctule *Nyctalus noctula*, Leisler's bat *Nyctalus leislreri*, Particoloured bat *Vespertilio murinus*, Northern bat *Eptesicus nilssonii* and Serotine bat *Eptesicus serotinus* (Boshamer & Bekker 2008, Brabant et al. 2021, Hüppop & Hill 2016, Lagerveld et al. 2014, 2021, 2023, Lagerveld & Mostert 2023). As 81% of the observed bats in the German Bight (Hüppop & Hill 2016), 76% of the stranded individuals at offshore platforms (Boshamer & Bekker 2008) and 92% of the acoustic recordings in the Dutch Southern North Sea refer to Nathusius' pipistrelle (Lagerveld et al 2023), this species is regarded as the priority species when it comes to the impact of offshore wind developments in the Netherlands.

The breeding areas of Nathusius pipistrelle are located in central and eastern Europe, in particular around the Baltic Sea. Populations in central Europe are sedentary or migrate over short distances (Sachanowicz et al. 2019), while eastern European populations perform long-distance migrations (Hutterer et al. 2005). After the breeding season (May-July), females and their offspring migrate predominantly to their wintering areas in southern and western Europe, including the Netherlands, Belgium, France and the United Kingdom (Mitchell-Jones et al. 1999, Russ et al. 2001). To date, the longest known distance covered during migration is from Russia to France, a distance of 2486 km (Vasenkov et al. 2022). During the autumn migration (August – October) mating takes place along the way where adult males defend territories and advertise to attract passing females (Jahelkova & Horacek 2011). Some males also migrate to wintering areas at lower latitudes, while others stay and winter in the same area (Pētersons 2004, Sachanowicz et al. 2019).

1.1.2 Bats and wind farms onshore

Wind farms on land are known to cause mortality amongst bats due to collisions (Johnson et al. 2003, Bach & Rahmel 2004, Kunz et al. 2007, Arnett et al. 2008, Rydell et al. 2010, Cryan et al. 2014, Thaxter et al. 2017) and possibly barotrauma (Grodsky et al. 2011, Rollins et al. 2012, Lawson et al. 2020), affecting both migratory and local populations (Lehnert et al. 2014). It is estimated that in Germany about 250,000 bats are 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). In temperate regions most fatalities concern migratory species and occur during late summer and autumn (Rydell et al. 2010, Voigt et al. 2015, Frick et al. 2017, Rodrigues 2018). The location of wind farms is an important determinant of the mortality rate (Rydell et al. 2010).

1.1.3 Mitigation measures onshore to prevent bat collisions

Next to a well-chosen location to minimize impacts, the number of fatalities can be reduced by operational measures. Effective mitigation has been achieved by limiting the production time of wind turbines by switching them off during periods when bats are most active (Adams et al. 2021, Arnett et al. 2011, Peste et al. 2015). A wide range of mitigation measures has been developed and implemented at onshore wind farms to reduce the risk of bat collisions with turbine blades. These measures can be broadly categorised into spatial-planning, operational and technological approaches.

- Spatial planning and micro-siting:
  Early-stage mitigation involves site selection and turbine placement based on known bat habitats, roosts, and flight paths. Avoiding siting turbines near forest edges, water bodies, or linear landscape features known to guide bat movement can significantly reduce collision risk.
- Curtailment:
  An effective and widely applied mitigation measure onshore is the temporary curtailment of turbine operation during periods of high bat activity. Curtailment thresholds are typically based on combinations of wind speed, temperature, time of night, and season, as most acoustic bat activity is recorded in the first hours after sunset in higher temperatures and low-wind conditions (Hayes 2017, Klop et al. 2023).
    - Fixed curtailment strategies involve predefined cut-in wind speeds (e.g., increasing from 3–4 m/s to 6–7 m/s), reducing rotor activity when bats are likely to fly.

    - Shut down on demand (SDOD) systems use real-time acoustic monitoring via bat detectors to trigger turbine shutdowns when bat activity exceeds a set threshold. This approach allows for targeted mitigation with minimal energy loss.
    - Smart curtailment based on predictive modelling:
      Recent advances involve adaptive curtailment systems that combine acoustic monitoring with meteorological and ecological data to predict bat activity. Statistical or machine learning algorithms can forecast high-risk periods, enabling more efficient turbine management.
- Deterrent technologies:
  Acoustic deterrents emitting ultrasonic noise at frequencies that disrupt bat echolocation have been tested with varying success. These systems aim to discourage bats from approaching turbines without altering turbine operation, although long-term effictivenessremains under evaluation.

Collectively, these approaches have made onshore wind farms increasingly capable of balancing energy production with bat conservation objectives. The combination of curtailment systems, acoustic deterrents, and ecological planning now represents the state of the art in onshore mitigation practice.

1.1.4 Bats and mitigation measures offshore

There are no reliable estimates on bat fatalities offshore as observational studies to assess the fatality risk as well as flight behaviour in OWFs have not been conducted so far. In contrast to terrestrial systems, mitigation measures for bats at offshore wind farms are still at an exploratory stage due to limited empirical knowledge of bat behaviour and occurrence over open water. Offshore mitigation measures must also contend with harsh environmental conditions, restricted access, and low but uncertain bat activity levels.

- Strategic spatial planning:
  At the planning level, offshore mitigation may include locational avoidance of areas known to coincide with bat migration corridors or coastal departure zones. Such strategies rely on improving the understanding of offshore bat movements.
- Curtailment:
    - Fixed curtailment strategy is implemented in the Netherlands. Based on the precautionary principle, mitigation measures have been issued for the Dutch offshore wind farms to protect bats during the autumn migration period (Boonman 2018, Staatscourant 2016, 2022, Boonman & Japink 2022).
    - Shut down on demand (SDOD) systems: Experimental research is exploring the feasibility in the offshore environment (operation in one of the Dutch offshore windfarms, after deploying it in a semi-coastal site, pers. com. DTbat). In principle, such systems could enable automated shutdowns offshore, but high levels of environmental noise and technical maintenance constraints currently limit their practicability, besides many unknowns about the effectivity of the measure offshore because of the lack of knowledge on collisions and the behaviour of bats near offshore wind turbines.
- Deterrent systems:
  These systems have not been tested offshore.

In summary, while the mitigation toolkit for offshore environments conceptually mirrors that of onshore systems, its implementation remains constrained by ecological, technical, and logistical uncertainties. The adaptation of proven onshore techniques, particularly curtailment strategies, depends on substantial advances in offshore research, both on general ecology of migration and behaviour of bats at sea, as well as on collision.

1.2 Wozep bat research programme 2016 – 2023

The Wozep bat research programme includes various (sub)projects, all of which are aimed to fill important knowledge gaps and eventually answer the overall research question: what is the relevance of the (presumed) mortality due to offshore wind farms for bats, in particular for Nathusius' pipistrelle population(s) crossing the southern North Sea. To be able to answer that question, information is needed on the

population size of the relevant (sub)populations migrating over sea, behavioural research at a larger scale (i.e. their occurrence in space and time over sea) and behavioural research at the scale of the offshore wind turbine (i.e. the fatality risk during an encounter with an offshore wind turbine).

Within the programme, two methods have been used to study bat behaviour at a larger scale: 1) telemetry with the MOTUS Wildlife Tracking System at the Dutch coastal provinces in autumn (Lagerveld et al 2024b), and at the east coast of the UK in spring (Lagerveld et al 2024a), and 2) passive acoustic monitoring with a network of 14 acoustic detectors at the Dutch North Sea (Lagerveld et al 2023).

1.2.1 Telemetry with the MOTUS Wildlife Tracking System

A network of MOTUS receivers was built gradually from 2017 onwards. Starting in Noord Holland, the network increased every year and resulting in a dense network in northern Noord-Holland. Outside that area the network extends along the coast from Westkapelle to Ameland in the Netherlands and from Landguard to Caister-at-Sea in the UK.

During five consecutive years (2018 – 2022) a total of 566 bats were tagged in autumn, including 409 in Noord-Holland, 99 in Zuid-Holland and 58 in Friesland. Due to the high receiver coverage in the northwestern parts of Noord-Holland only this area was considered suitable to investigate the number of departures over sea. It was found that a relatively small percentage (6 - 10%) of bats departed over sea directly from this area, whereas most bats (69%) were heading in a southerly direction. An additional 7% headed north and 14% east. Some individuals were observed departing over sea further south along the coast. Therefore, the overall percentage of 6-10% of bats -tagged in the study area- departing over sea must be regarded as a conservative estimate. Not all the individuals departing over sea involved bats heading towards the UK, as overseas movements parallel to the coast and subsequent continuation along the Dutch coast were also observed. Nevertheless, the coastal route along the Dutch coast seemed to be preferred over the route over sea. So far, the movements of bats tagged in Zuid-Holland and Friesland have not been examined. Likewise, all movements along the Dutch coast have not been analysed in relation to season, environmental conditions, sex and age.

In 2020 Wozep initiated bat tagging in spring at the east coast of the UK, which was continued in 2021 and 2022 by Kepwich Ecological Services, Norfolk and Norwich Bat Group and Wageningen Marine Research. The 2020 and 2021 data revealed that bat migratory movements are highly influenced by barrier effects, sex-biased timing of migration and the adaptive use of winds (Lagerveld et al 2024a). Because the sea is in principle a hostile environment for bats, they aim to avoid flying over sea. This results in concentrated migratory movements along the coast, and crossings over sea are shortened by deviating from the general migration directions. Males depart from the UK later in the season compared to females. Departures over sea coincide with moderate tailwinds, enabling bats to more than double their airspeed, reaching ground speeds of up to 16.8 m/s (60.5 km/h). The results of this study furthermore suggest that bats select altitudes with favourable wind conditions and that they seek altitudes of several hundred meters, possibly extending up to 2,500 m. Low-altitude migration occurs when wind conditions are less favourable.

1.2.2 Passive acoustic monitoring offshore with bat detectors

Passive acoustic monitoring took place from 2015 – 2020 (cf. Lagerveld et al. 2017a, 2021, 2023). The acoustic monitoring revealed that most migratory movements in autumn occur from mid-August until late October and most bats in the Dutch North Sea occur off the coast of the province of Noord-Holland (Lagerveld et al. 2023). North Sea crossings during the autumn migration frequently last longer than one night; the day is spent roosting at an offshore structure. The strongest migration occurs during nights with tailwinds from east-northeast (ENE), but bats are also recorded offshore with low to moderate headwinds or crosswinds. Bat presence decreased between the full moon and the last quarter and increased just before the new moon. In spring bats are recorded from mid-March until mid-June (Lagerveld et al 2017a). The offshore acoustic occurrence in spring has not been analysed yet in relation to (potential) environmental predictors.

In some cases, both monitoring methods produce seemingly contradictory insights into bat migration ecology. These include in particular differences in seasonal and nocturnal timing of occurrence, and differences in observed wind speeds (Lagerveld et al 2023)(Lagerveld et al 2024a).

1.3 Aim of this report

In this report, the available migration data of Nathusius' pipistrelles collected within the Wozep bat research programme 2016 - 2023 are re-examined, in light of the differences found between telemetry and bat detector studies. A key aim is to investigate spring and autumn migration patterns in greater detail by integrating telemetry data with passive acoustic monitoring data. This represents a novel step in combining these complementary datasets, with the expectation that their synthesis will yield new insights relevant to applied research questions, particularly in the further development of strategies to mitigate the impacts of offshore wind farms on bats and improve impact assessments. Additionally, observations of migratory routes and flight behaviour extending beyond the original study area, previously limited to the northern part of North Holland, are incorporated into the analysis.

The aim of this report is to examine the obtained tracking and acoustic data in more detail to:

1. Investigate the similarities and differences between the spring tracking and acoustic data and assess the important predictors (environmental conditions) for spring migratory movements.
2. Determine the important predictors (environmental conditions as well as the individual characteristics) for autumn departure decisions and examine the general movement pattern of bats tagged along the Dutch coast (In Zuid-Holland, Noord-Holland and Friesland).

While the implementation of the mitigation toolkit for offshore environments remains strongly constrained by ecological, technical, and logistical uncertainties, the present report aims to contribute to the advancement of the necessary knowledge to support impact assessments and future developments and advances in mitigation measures. In addition to addressing the identified research questions, the report seeks to formulate a set of evidence-based recommendations relevant to research, policy and management. These recommendations will focus on:

- the implications and applicability of the findings for impact assessments, and the planning and spatial design of offshore wind farms, and
- potential measures to enhance the protection of bats during migration across marine environments, particularly in relation to the currently applied operational fixed curtailment strategy in the Netherlands, solely restricted to autumn.

Furthermore, the report seeks to identify priorities for future research, encompassing both fundamental studies on the ecology and behaviour of bats during offshore migration and empirical investigations into actual collision risks at sea. By integrating scientific insights with applied policy considerations, the study aims to contribute to a more ecologically informed and sustainable development of the offshore wind energy sector with respect to bat conservation.

1.4 Report structure and methodological approach

This applied ecological report comprises two main chapters, each presented as a draft version of a scientific paper prepared in the format intended for submission to a peer-reviewed journal. Accordingly, both chapters adhere to a standard scientific structure, including an abstract, introduction, methods, results, and discussion section, accompanied by a reference list and supplementary appendices containing supporting data and materials.

Each paper describes the study design, data collection procedures, analytical methods, and statistical techniques employed to address the research questions. Owing to the applied nature of this report, particular emphasis is placed on the ecological relevance and practical implementation of the chosen methods.

Following the two main chapters, a general discussion synthesises the findings across both studies, integrating them within the broader context of applied bat research and conservation in relation to the offshore wind energy.

The report concludes with a section on policy implications and recommendations, which translates the scientific outcomes into actionable guidance for mitigation strategies and directions for future research.

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2 Directional variation and method-specific detection patterns in offshore bat migration: implications for wind farm mitigation

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2.1 Abstract

1. Curtailment of wind farms effectively reduces collision mortality in bats. Implementing this measure in offshore wind farms requires knowledge on the spatiotemporal occurrence and environmental predictors of migration over sea. In bats, such information can be obtained through acoustic monitoring and individual tracking. However, these techniques provide seemingly contradictory insights into migration patterns.
2. We used a Bayesian capture–recapture state-space model to investigate how environmental predictors influence spring departure decisions of Nathusius' pipistrelle *Pipistrellus nathusii* migrating over the North Sea. The model was applied to both acoustic and tracking data, enabling comparable analyses across methods and incorporating uncertainty in migration dates of tracked bats. Additionally, we examined nightly offshore bat occurrence to further explore differences in movement patterns detected by the two techniques.

3. Wind conditions at 200 m above sea level were identified as key driver of Nathusius' pipistrelle spring migration. In May–June, most bats migrated from the United Kingdom under westerly and northwesterly tailwinds. Tracked individuals flew in stronger supportive winds (median windspeed 7.0 m/s) than acoustically recorded bats (median windspeed 6.6 m/s), which were also detected under crosswinds and headwinds. In March–April, acoustic detections occurred mainly during strong southerly winds (median windspeed 8.5 m/s), suggesting that early-season migrants largely consisted of individuals migrating over the European mainland and drifted northwards onto the North Sea by strong crosswinds.
4. Acoustic detectors primarily recorded bats that landed on offshore platforms, likely because they were unable to cross the North Sea in a single flight due to less favorable wind conditions, or because they departed from more inland locations. In contrast, tracking data mainly represented bats that successfully crossed the North Sea in a non-stop flight under moderate supportive tailwinds.
5. *Synthesis and applications*: Combining observation techniques improves our understanding of bat migration patterns. Additionally, acoustic monitoring can capture migration from different geographic origins. Current mitigation measures for offshore wind farms at the North Sea rely solely on acoustic data, likely overlooking the part of the population that crosses over sea with optimal wind support. Acoustic and tracking data are therefore complementary rather than contradictory, and both methods should be used together when developing mitigation measures.

Keywords

Acoustic monitoring, Bat migration, Bayesian capture-recapture state-space models, Collision mortality, Curtailment, Motus wildlife tracking system, Nathusius' pipistrelle, Offshore wind farms

2.2 Introduction

Worldwide offshore wind farms are expanding rapidly, raising concerns about their potential impact on a suit of species groups. Even non-marine species such as bats can collide with wind turbines during their migration over sea (Ahlén et al., 2009; Cryan and Brown, 2007; Hüppop et al., 2019; Lagerveld et al., 2021, 2014). Significant reductions of the number of bat fatalities have been achieved by the curtailment of wind farms on land, which involves a reduction of the operational time of wind turbines during periods with increased bat activity (Adams et al., 2021; Baerwald et al., 2009; Voigt et al., 2022; Whitby et al., 2024). Accurately predicting bat migration peaks over sea would therefore be of considerable help to develop effective curtailment strategies for offshore wind farms.

A principal area for offshore wind developments is the North Sea, where Nathusius' pipistrelle *Pipistrellus nathusii* is the most frequently recorded migratory bat (Brabant et al., 2021; Hüppop and Hill, 2016; Lagerveld et al., 2014). The species is particularly vulnerable to collisions with wind turbines (EUROBATS,

2015; Kruszynski et al., 2022) and recent genetic research suggests a population decline (Van Schaik et al., 2025), highlighting the need for conservation measures.

Understanding migration patterns of bats, however, remains challenging due to their elusive and nocturnal lifestyle. To date, most detailed knowledge has come from acoustic monitoring and tracking studies. Acoustic monitoring involves the detection and analysis of bat echolocation calls, and when stationary acoustic detectors are deployed, it enables long-term monitoring of migratory bat activity patterns (Hüppop and Hill, 2016; Ijäs et al., 2017; Johnson et al., 2011; Lagerveld et al., 2021, 2023b; Rydell et al., 2014). Tracking studies on the other hand, provide the most detailed insights into bat migration ecology, including departure and routing decisions (Bach et al., 2022; Dechmann et al., 2017; Hurme et al., 2025; Lagerveld et al., 2024; McGuire et al., 2012; True et al., 2023), and flight behavior during long-distance endurance migratory flights (Lagerveld et al., 2024; O'Mara et al., 2019). For small bat species, such as Nathusius' pipistrelle, movements over larger distances can currently only be tracked using the Motus Wildlife Tracking System (Mitchell et al., 2025; Taylor et al., 2017), as alternative systems like the Sigfox IoT network (Wild et al., 2023) use tags that are currently too heavy for these small-sized animals.

In some cases, different monitoring methods yield seemingly contradictory insights into the patterns of migration. These discrepancies likely stem from methodological differences in both detection and analysis. For example, tracking data suggest that migration from the east coast of the UK to the European mainland takes place from early May until mid-June (Lagerveld et al., 2024), while acoustic monitoring has shown that bats occur at the southern North Sea from late-March until early June (Lagerveld et al., 2023a). Acoustic data also indicate that sea crossings often span more than one night due to diurnal stopovers at offshore platforms (Lagerveld et al., 2023b), whereas tracking data shows that migratory bats are able to cross the North Sea in a single three to five hour non-stop flight (Lagerveld et al., 2024).

Furthermore, acoustic detections of migratory bats are generally recorded during low wind speeds (Brabant et al., 2021; Cryan and Brown, 2007; Johnson et al., 2011; Lagerveld et al., 2021, 2014; Sjollema et al., 2014), while tracking data and visual observations show that departures more often coincide with moderate or strong winds (Hatch et al., 2013; Lagerveld et al., 2024). Additionally, differences in estimated wind parameters associated with bat departure decisions may arise from methodological limitations inherent to each monitoring technique. For instance, acoustic detectors have a very limited detection range, typically between 25 – 100 m, depending on the species, type of detector and environmental conditions (Adams et al., 2012; Barataud, 2020) -and thus- primarily record low-flying individuals at close range. In contrast, Motus receivers can detect animals flying at altitudes of several kilometers and at distances of 5 - 15 kilometers (Mitchell et al., 2025; Taylor et al., 2017). However, their capacity to detect low-flying individuals is much more restricted, typically limited to a range of about 2 kilometers (Taylor et al., 2017). Acoustic data

thus represents bat activity at low-altitude, potentially underestimating the prevalence of bats migrating at higher altitudes, possibly under different wind conditions. Conversely, low-flying bats may be underrepresented in Motus data.
These discrepancies highlight the need to combine information from data collected with both techniques to better understand the observed offshore occurrence of migratory bats in space and time. Analyzing the two datasets in a comparable way is not only important for the development of curtailment measures to reduce bat fatalities in offshore wind farms, but also for a more comprehensive understanding of bat migration in general.

Between 2018 and 2021, we conducted continuous acoustic monitoring at 13 offshore platforms in the southern North Sea. From 2021 to 2023, we tracked 27 Nathusius' pipistrelles from the east coast of the UK to the European mainland using the Motus Wildlife Tracking System. With the collected data, we adapted Bayesian capture-recapture models in a state-space formulation (Auger-Méthé et al., 2021; Gimenez et al., 2007; Royle, 2008) to estimate probabilities of bat migratory departures. The flexibility of this type of model allowed its use for both acoustic and tracking data, enabling analysis within a similar analytical framework. Capture-recapture state-space models are also robust to small sample sizes and can account for uncertainty in departure timing. This was particularly useful in the analysis of tracking data that comprised crossings of a limited number of individuals.

By bringing the acoustic and tracking data to the same structure and applying similar -yet separate- analysis, we preserved the distinct characteristics of each monitoring method while enabling direct comparison of outcomes. This approach minimizes methodological biases and enabled us to: 1) examine the species' spring occurrence throughout the season and the night, 2) identify environmental conditions serving as migratory cues, 3) compare patterns observed across monitoring methods to explain both differences and consistencies in detected occurrence, and 4) recommend mitigation strategies for offshore wind farms.

2.3 MATERIAL & METHODS

2.3.1 Tagging & tracking bats

Bat trapping and tagging were carried out at three sites: Minsmere (52.247° N, 1.619° E), Benacre National Nature Reserve (52.387° N, 1.707° E), and the Landguard Bird Observatory (51.938° N, 1.320° E), over three consecutive years (Figure 1). Fieldwork comprised 14 trapping sessions between 29 March and 15 May 2021 at Minsmere; 10 sessions between 5 April and 10 May 2022 (two at Landguard and eight at Minsmere); and 12 sessions between 29 March and 11 May 2023 (three at Benacre and nine at Minsmere). Trapping sessions lasted an average of 4.5 hours and were conducted under Natural England project licenses 2021-55582-SCI and 2022-63237-SCI.

We used 0.26 g NTQB2-1 radio-transmitters (LOTEK Wireless, Canada) with burst intervals between 6.7 and 7.3 s and an expected lifespan of 51–61 days. Each transmitter broadcasted a uniquely coded signal at 150.1 MHz, allowing the identification of individual animals. To follow the movements of tagged bats, we used the Motus Wildlife Tracking System (Mitchell et al., 2025; Taylor et al., 2017). In the study area about 125 Motus receiver stations were operational from 2021 – 2023 (Figure 1).

In total, 122 bats were tagged, comprising 18 males and 104 females. The number of individuals tagged differed across years, with 20 in 2021, 24 in 2022, and 78 in 2023. Tagging also varied seasonally, with 2 bats tagged in March, 25 in April, and 95 in May. One individual was predated and two tags were found detached. The remaining 119 bats were all detected in the UK and 27 individuals were subsequently recorded on the European mainland.

Details on trapping and tagging, processing of raw monitoring data, date of last detection in the UK and arrival on the mainland of each individual can be found in supplementary file 1.

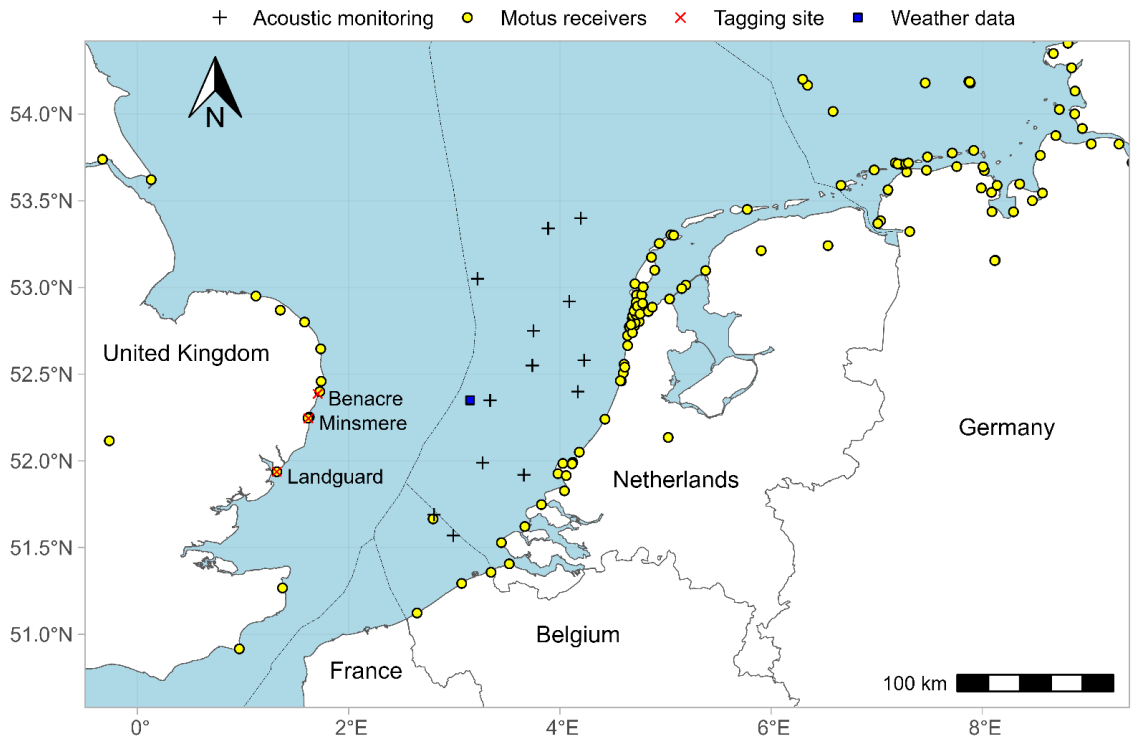

Figure 1: Southern North Sea and bordering countries, including bat tagging sites, offshore acoustic monitoring locations, Motus receiver network and weather data location

2.3.2 Acoustic monitoring

We performed continuous acoustic monitoring at 13 offshore platforms in the southern North Sea (figure 1), using an UltraSoundGate 116Hnbm system with an electret ultrasound microphone FG-DT50 (Avisoft Bioacoustics, Germany), installed at an average height of 21 m above sea level. Monitoring was conducted from March until June during four consecutive years (2018-2021). The effective monitoring effort included 4309 nights in total, respectively 1037, 1517, 914 and 841 per year. After retrieving and processing the raw monitoring data we removed the other bat species from the dataset (2.7% of the recordings), using R version 4.5.1 (R Core Team, 2025) and R studio (R-Studio Team, 2025). The dataset included 2777 Nathusius' pipistrelle recordings of which 152 (5.5%) contained feeding buzzes/intense exploration calls (cf Barataud, 2020). To visualize the monitoring results, we made date-time plots using the R-package ggplot2 (Wickham, 2016) in combination with gghourglass (de Vries, 2025), in which the recorded bat activity is shown throughout the season and the night. Details on software settings, installation of the equipment, monitoring locations, monitoring periods and the processing of raw monitoring data can be found in supplementary file 2.

In the acoustic dataset, we assumed that the recorded bat activity at a particular moment refers to one individual bat as multiple bats simultaneously present at an offshore location in the southern North Sea has been documented only once (Lagerveld et al., 2014), and is therefore considered rare. Using an interval of two hours without bat activity to separate individuals resulted in 172 distinguished individual bats. We checked the sensitivity of this assumption by using alternative timeframes of 30 min, 60 min, four hours and one night. This resulted in an increase of 17 and 11 bats, and a decrease of 5 and 17 bats respectively. Thus, applying alternative timeframes resulted in a slight difference in the distinguished number of individuals (max 10 %). For each individual, we determined the first and last recorded occurrence and calculated the total duration it was detected at the offshore platform.

2.3.3 Weather data and lunar phase

All weather data were downloaded (2 July 2025) from the Climate Data Store of Copernicus (Hersbach et al., 2018), using the appropriate application user interface (https://cds.climate.copernicus.eu/how-to-api). Data were downloaded as a spatial raster (0.25x0.25°) with an hourly interval. For the analyses, data were selected from the raster cell located at 52.35° N 3.15° E (figure 1), which lies in the southern North Sea approximately halfway between Southwold in the UK (52.33° N 1.68° E) and Zandvoort in the Netherlands (52.37° N 4.53° E).

Several weather parameters were used in the analysis, including temperature at 2 m [K], total precipitation [m/h], eastward (U) and northward (V) wind speed components [m/s]. Wind speeds (U- and V-components) were provided for specific air pressure layers, which were converted to altitude layers using the barometric

equation (NASA, 1976). To match the relatively large geographical scale of this study we used wind data at 200 m above sea level, as winds above the surface layer (up to 100-150 m) more closely represent regional airflow patterns (Garratt, 1992).

We calculated the atmospheric pressure change by subtracting the atmospheric pressure on a particular day with the atmospheric pressure from the previous day, and derived the temperature in degrees Celsius by subtracting 273,15 from the temperature in Kelvin. To reflect weather conditions at departure we took the mean value of each parameter in the time-intervals between sunset and two hours after sunset. The lunar phase [radians] was obtained using the R-package *suncalc* (Thieurmel, 2022).

2.3.4 Analysis

We compared seasonal and nightly bat occurrence of the tracked bats and the acoustically detected individuals. Subsequently, we analyzed departure decisions in relation to environmental conditions. For the second analysis we modelled the probability of bat migratory departures for both acoustic and tracking data within a similar analytical framework. ChatGPT was used to assist in drafting and debugging parts of the statistical analysis code (R/JAGS). No AI-based tools were used to generate results or interpret outputs. All code and outputs were critically reviewed, tested, and validated by the authors.

2.3.4.1 Seasonal and nocturnal bat occurrence

The single night crossings from the tracking dataset with known departure time from the east coast of the UK and the arrival time at the Dutch coast (n=8) were used to examine the departure times relative to sunset, arrival times relative to sunrise, and the overall duration of the crossing. We compared the timing of occurrence in the night of the tracked bats with the acoustically recorded bats. In addition, we investigated whether acoustic bat presence in the night depends on seasonality and the spatial distribution. For this, we applied a generalized additive model (GAM) in the R-package mgcv (Wood, 2017), with time after sunset (when the bat was recorded for the first time) as the response variable. Night in year was entered as a low-rank thin-plate smoother to capture the seasonal-temporal pattern and latitude and longitude were included in a tensor product smoother to assess spatial differences. We made residual diagnostic plots and variograms to check for violations of the model assumptions.

2.3.4.2 Environmental predictors

From the tracking dataset, we selected the individuals detected on the European mainland, thereby confirming migration from the UK over the North Sea (n=27). The night of the crossing over the North Sea was known for 10 individuals (of which the actual departure and arrival time were recorded for eight bats). The departure night was unknown for the remaining 17 individuals. To account for uncertainty in migration

dates, we used a state-space modelling approach (Auger-Méthé et al., 2021; Baldwin et al., 2018). We estimated the probability of migratory departure across nights in a capture-recapture model in state-space formulation (Gimenez et al., 2007; Royle, 2008), structurally analogous to the nest survival models described in (Kéry and Schaub, 2011). In our model, migratory state was introduced as a matrix of individual 'encounter histories' throughout the migration period. The model estimated the probability that an individual transitions from a "non-migratory" state on night *t-1* to a "migratory" state on night *t*. This transition probability was modelled as a logistic function of environmental predictors. The 'encounter history' of each individual started with the date, when the individual was tagged. For each night, the state was classified as 1 (not yet departed, i.e. between the moment of tagging and the last detection in the UK), 0 (known to have departed from the UK), or NA (state is unknown, particularly, on the nights between the last registration in the UK and the first registration in continental Europe). This model setup allowed estimation of latent probability of migration (otherwise, transition from state 1 to state 0) for the nights with unobserved state. To treat the acoustic dataset in the same modeling setup as the tracking data, we created encounter histories for each individual bat. During data exploration, we observed that acoustically recorded bats in May and June often coincided with westerly winds, cf. the pattern found in bats tracked from the UK (Lagerveld et al., 2024), while in March-April detections were mainly associated with southerly winds. We therefore assigned the individual bats to either the March-April or May-June period, based on the date of detection. For bats from the March-April period, encounter histories started from the night before the first ever bat was recorded at sea (15th of March), or one day before the acoustic detector became operational later in the season. For individuals from the May-June period, encounter histories started on the 29th of April or one day before the detector was turned on. A total of 20 individual bats were excluded from the analysis because their pattern of occurrence across consecutive day and night periods indicated that they were potentially the same individuals detected before and after their diurnal stopover (cf Lagerveld et al., 2023b). These bats were detected around sunset (from one hour before to two hours after sunset) following detections during the previous night within three hours of sunrise. The estimated departure of the remaining bats recorded around sunset was allocated to the previous night, all other bats were allocated to the night in which they were recorded.

The initial fully-parameterized acoustic model included night number (linear and quadratic), windspeed (linear and quadratic), harmonic terms representing wind direction (cos θ, sin θ, cos 2θ, sin 2θ). Assuming that preferred windspeeds and migration periods (March-April or May-June) may differ, depending on the wind direction, we included interactions between each harmonic term and windspeed as well as period. Because temperature was correlated with night number, we used the residuals of temperature (on date) as linear covariate in the model. Atmospheric pressure change and cloud cover were also included as linear covariates, while precipitation was modeled as a binary covariate. The effect of lunar phase was represented

by two sets of harmonic covariates, sine and cosine of the lunar phase (sinθ, cosθ) and their second-order harmonics (sin2θ, cos2θ).

The initial fully-parameterized tracking model included night number (linear and quadratic), windspeed (linear and quadratic), harmonic terms representing wind direction (cos θ, sin θ, cos 2θ, sin 2θ) and interactions between each harmonic term and windspeed. We did not test additional covariates in the tracking model to avoid overparameterization. In both models individual-level random intercepts were included to account for repeated observations within the encounter histories of the same bats. The standard deviation of the individual random effects was assigned a weakly informative half-Cauchy prior with scale 3. We simplified the models by sequentially removing covariates with the weakest support, based on whether the 95% posterior credible interval of their beta parameters overlapped zero and on the corresponding evidence ratio (ER). Convergence was confirmed for all parameters (Rhat < 1.01). The effects of the statistically significant covariates were visualized using R-package ggplot2 (Wickham, 2016).

2.4 RESULTS

2.4.1 Seasonal and nocturnal occurrence

The night of the crossing was known for 10 tracked bats, of which the actual departure time from the UK coast and subsequent arrival time on the Dutch coast was recorded for eight individuals. These bats departed about one hour after sunset and arrived approximately three hours before sunrise at the European mainland. The sea crossing took three to five hours to cover a median distance of 172 km at a median minimal groundspeed of 43 km/h (table 1 and figure 2).

The earliest migrant amongst the acoustically recorded bats was observed 15 March 2020 (night number 75) and the last 12 June 2021 (night number 163). Migration peaked in April (night number 91-120) and May (night number 121-150), with 50% and 39% of the individuals (n=172) respectively. Bats were recorded at all monitoring locations, though not every year. Figure 2 shows the overall bat occurrence throughout the season and the night.

Bats were generally acoustically recorded in the night and sometimes during daylight hours. Most bats were recorded around sunset and sunrise: 37% within one hour before until two hours after sunset, 31% within three hours before sunrise and 9% were recorded during daylight hours, up to 7 hours after sunrise. The remaining 23% were recorded between two hours after sunset and three hours before sunrise (a time interval of three to seven hours, depending on the night number). When bats were recorded within one hour before until two hours after sunset (n=64), in 28% of the cases (n=18) bats were recorded the previous

night three hours before sunrise (n=11, out of 46), or after sunrise (n=7, out of 15). The arrival time after sunset did not depend on the night number (p=0.450), nor the spatial location (p=0.173).

Most individuals (79%) were recorded less than 15 min: 103 bats (60%) less than 1 min, 16 bats (9%) between 1 – 5 min and 17 bats (10%) between 5-15 min. Longer observed individuals included 23 bats (13%) between 15-60 min, 6 bats (4%) between 1-2 hour, 3 bats (2%) between 2-4 hour and 4 (2%) bats were recorded more than 4 hours.

Detailed information on the yearly acoustic bat presence, occurrence throughout the season and the night, as well as the annual recorded bat activity for each monitoring location can be found in supplementary file 3.

Table 1: Departures and arrivals of single night crossings over the southern North Sea

Deploy-ment	**Departure**			**Arrival**			**Crossing**		
	Date/ Time [UTC]	Lat Long	Time after sunset [min]	Date/ Time [UTC]	Location	Time before sunrise [min]	Duration [min]	Min. distance [km]	Min. ground-speed [km/h]
31861	2-5-2021 20:00	N 52.25 E 1.62	40	2-5-2021 23:57	N 52.51 E 4.60	250	237	205	52
31904	17-5-2021 20:41	N 52.25 E 1.62	56	17-5-2021 23:59	N 51.62 E 3.67	230	198	157	48
31898	25-5-2021 21:52	N 52.65 E 1.74	114	26-5-2021 01:27	N 51.98 E 4.12	129	215	178	50
35902	6-5-2022 20:08	N 52.25 E 1.62	41	7-5-2022 01:09	N 52.24 E 4.43	173	301	191	38
39007	11-5-2022 21:10	N 52.25 E 1.62	95	12-5-2022 00:00	N 51.92 E 4.06	236	170	170	60
43046	14-5-2023 21:25	N 52.65 E 1.74	104	15-5-2023 02:24	N 51.75 E 3.83	87	298	174	35
44994	14-5-2023 20:43	N 52.25 E 1.62	62	15-5-2023 01:36	N 51.99 E 4.03	134	292	167	34
44998	16-5-2023 20:22	N 52.25 E 1.62	39	17-5-2023 01:02	N 51.53 E 3.44	169	279	148	32
Median			59			171	258	172	43

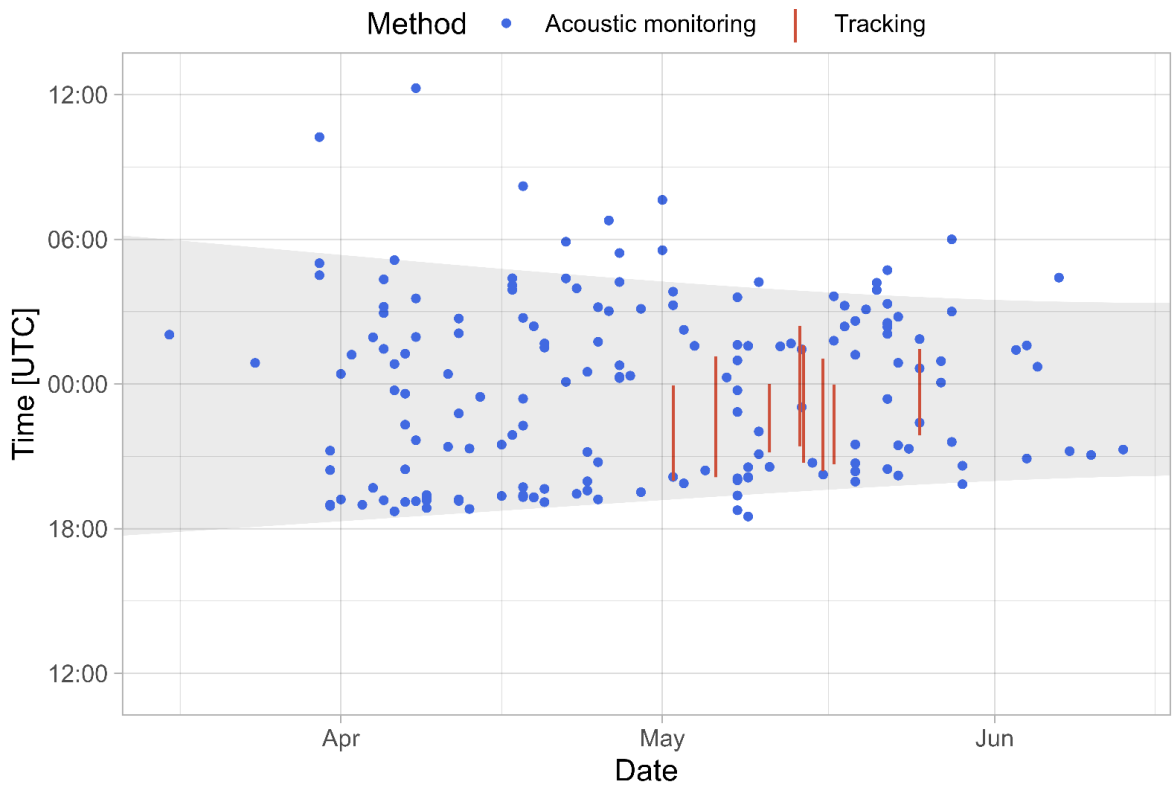

Figure 2: Acoustically recorded bat occurrence throughout the season for all monitoring locations and monitoring years (2018-2021). The time interval between sunset and sunrise is represented by grey. The dots represent the first recording of each individual (n=172). The red bars indicate the duration of single-night crossings over sea from the tracked individuals with known departure time from the east coast of the UK and arrival time at the coast of the European mainland (n=8). Note that the acoustically recorded bats refer to observations in Dutch and Belgian waters, while the crossings over sea include the timeframe of travel from the UK to the European mainland.

2.4.2 Environmental predictors

In the simplified tracking (Eq. 1) and acoustic (Eq. 2) model, the effects of night number, linear and quadratic windspeed were retained, suggesting an increase in departure probability over the migration period and under moderate windspeeds. The effects of wind directions (expressed as harmonic terms) and speeds on the probability of departures differed between tracked bats and the two periods of acoustically detected bats. It should be noted that, in the model output (supplementary file 4), the probability of stay is modelled. A negative coefficient in the linear predictor therefore increases the probability of departure.

The simplified tracking model was:

Eq. 1 Probability of $stay_{i,t} = logit^{-1}$ ($\beta 0 + b_i + \beta 1 \times night_t + \beta 2 \times windspeed_{i,t} + \beta 3 \times windspeed_{i,t}^2 + \beta 4 \times \cos(\theta_{i,t}) + \beta 5 \times \cos(\theta_{i,t}) \times windspeed_{i,t}$)

The simplified acoustic model was:

Eq. 2 Probability of $stay_{i,t} = logit^{-1}$ ($\beta 0 + b_i + \beta 1 \times night_t + \beta 2 \times windspeed_{i,t} + \beta 3 \times windspeed_{i,t}^2 + \beta 4 \times \cos(\theta_{i,t}) + \beta 5 \times \sin(\theta_{i,t}) + \beta 6 \times \sin(2\theta_{i,t}) + \beta 7 \times windspeed_{i,t} \times \cos(\theta_{i,t}) + \beta 8 \times windspeed_{i,t} \times \sin(\theta_{i,t}) + \beta 9 \times windspeed_{i,t} \times \sin(2\theta_{i,t}) + \beta 10 \times period_I + \beta 11 \times period_I \times \sin(\theta_{i,t},)$)

where $b_i \sim N(0, \sigma ind^2)$ are the individual-specific random effects.

In Figure 3, we summarize wind speeds and the relative predicted migration probabilities for observed departures in the tracking model and in each period of the acoustic model. The baseline migration probability differed between the periods, being higher in the May–June period due to the shorter encounter histories. In the figure, we present therefore relative migration probabilities within each period. Specifically, for each directional bin, the median predicted probability is scaled by the sum of median probabilities across all bins, allowing comparison of wind effects independently of baseline differences.

Departures of tracked bats occurred throughout May and June. The model predicted high co-occurrence of departures with moderate westerly winds. Of the 10 individuals with known departure night 8 were observed departing with winds from west or northwest (median windspeed = 7.0 m/s, interquartile range: 5.4 to 11.2 m/s; Fig. 3).

In the acoustic model (Eq. 2), the role of westerly winds was also prominent in the departures recorded in May-June. For bats recorded under winds from west and northwest, median windspeed was 6.6 m/s, interquartile range: 3.0 to 9.9 m/s; n=32; Fig. 3). Bats were also observed in southerly and easterly winds. For bats recorded under winds from southwest, south and southeast, median windspeed was 5.9 m/s; interquartile range: 5.2 to 7.5 m/s; n=19; Fig. 3) and from east, median windspeed was 3.4 m/s; interquartile range 3.4-5.6 m/s; n=7)

Bats from the March-April period were most likely to be detected over the North Sea in stronger winds from southerly directions (median windspeed = 8.5 m/s, interquartile range: 5.9 to 12.7 m/s for the observed departures in winds from southwest, south and southeast; n=68). For both periods, predicted migration was unlikely under winds from north and northeast (Fig. 3).

All other environmental covariates (lunar phase, cloud cover, precipitation, atmospheric pressure change and temperature) showed no statistically significant effect. The output of the analysis can be found in supplementary file 4.

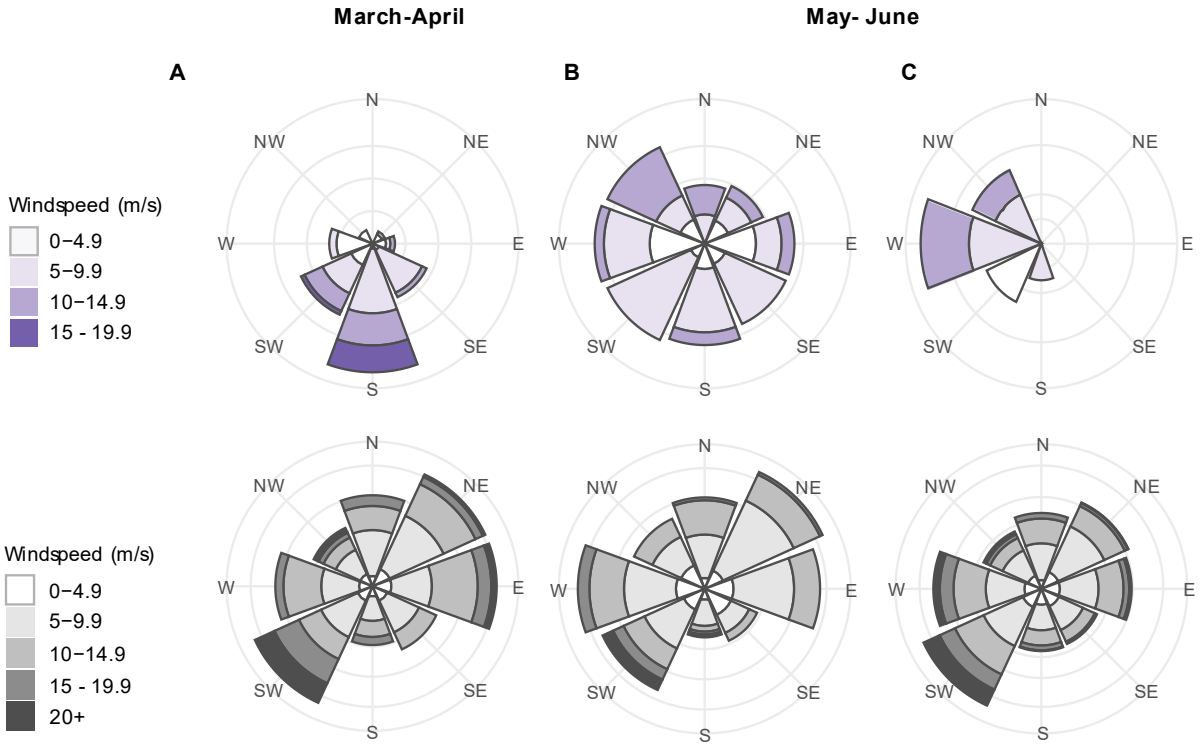

Figure 3. Predicted probability of spring migration over the North Sea as a function of wind conditions at 200 meter above sea level (upper row) and prevailing wind conditions throughout the migration period (lower row) for (A) the acoustic dataset in March–April and (B) May–June, and (C) for the tracking dataset, where migration took place in May–June. The upper-row wind roses represent the directional structure of relative migration probability for each period. Meteorological wind direction (direction from which the wind blows) is divided into 8 compass sectors (45° bins). For each sector, the total bar height represents the median predicted probability of departure, normalized within period. Bars are stacked by wind-speed class, with the purple fill intensity indicating the proportion of observations falling into each wind-speed class within a given direction. The wind roses in the lower row illustrate the directional structure of overall winds during the corresponding migration periods. The height of each bar indicates the proportion of nights with winds originating from each directional bin. Stacks within each bar indicate the proportional distribution of wind-speed classes within each direction. Shades of grey represent wind-speed classes, with lighter shades denoting weaker winds.

2.5 DISCUSSION

In the present study we combined two observation techniques, acoustic monitoring and individual tracking, to improve our understanding of bat migration patterns. Spring tracking data indicated that bats departed the UK's east coast approximately one hour after sunset and reached the Dutch coast about three hours before sunrise, whereas acoustic monitoring showed that most offshore detections occurred close to sunset or sunrise. Both monitoring methods identified wind conditions at 200 m above sea level as a key predictor of Nathusius' pipistrelle spring migration over sea. Tracked bats crossed from the UK to the European mainland in May and June under supportive moderate westerly and north-westerly winds. Similarly, most acoustically recorded bats in May–June were also detected under westerly and north-westerly winds, albeit at lower wind speeds. However, acoustically recorded bats were absent in March–April under these wind conditions. During this earlier period, most acoustic detections were associated with strong southerly winds, while no tracked bats were observed crossing the North Sea. No significant effects were detected for the other environmental variables examined, including precipitation, temperature, cloud cover, atmospheric pressure change and lunar phase.

2.5.1 Seasonal and nocturnal occurrence

The main breeding areas of Nathusius' pipistrelle are located in northeastern Europe and wintering occurs in southern and western Europe, including the UK (Russ, 2022). Migrants generally follow a southwest–northeast route in spring, reversing direction in autumn (Hutterer, 2006; Pētersons, 2004). North Sea crossings from the east coast of the UK to the European mainland are typically routed east to southeast to reduce the over-water distance (Lagerveld et al., 2024).

Our data show that spring migration over the southern North Sea occurs from mid-March until mid-June, and most bats can be expected in April and May (median acoustic occurrence 27 April). The species has been recorded in the German Bight between 20 April and 26 May (median 2 May) (Hüppop and Hill, 2016) and migration over central and northern Europe occurs mainly in May, with the median observation early May in northwest Germany (N 54°) and late May in southwest Finland (N 60–61°) with a difference of 20 days between the two areas (Rydell et al., 2014). Therefore, the seasonal pattern we captured fits well in the pattern from other studies.

The timing of bat occurrence throughout the night differed significantly between the tracking and acoustic datasets. Tracked bats that crossed the North Sea in a single night departed from the UK's east coast about one hour after sunset and arrived at the Dutch coast approximately three hours before sunrise. The sea crossing took around four hours. In contrast, acoustically recorded bats were mostly detected around sunset or sunrise. Since there are no resident bat populations at the North Sea, detections near sunset indicate that

bats used offshore platforms as diurnal stopover sites during their migration over sea (Lagerveld et al., 2023b). Late-night detections, or morning occurrences in daylight hours likely represent individuals seeking daytime shelter.

Another indication that offshore platforms are primarily used as roosting sites, and not as foraging sites, is the generally short duration bats are recorded acoustically and the low proportion of recordings containing feeding buzzes/intense exploration calls.

2.5.2 Environmental predictors

Supportive winds promote bat migratory departures (Dechmann et al., 2017; Hurme et al., 2025; Lagerveld et al., 2024, 2021). Consistent with these studies, our analysis identifies wind at 200 m above sea level as a key determinant of bat migratory movements. Moreover, seasonal differences in the wind conditions under which bats were recorded suggest migration from distinct geographical areas. In March–April, acoustic detections coincided with relatively strong southerly winds (median wind speed = 8.5 m/s, interquartile range: 5.9–12.7 m/s), generally exceeding the maximum range velocity of Nathusius' pipistrelle (7.5 m/s, cf Troxell et al., 2019), which represents the species' typical migratory airspeed. In these conditions a migrating animal has no other option than to follow the general direction of the wind (Alerstam, 1978). Consequently, early spring detections most likely reflect bats that were wind-drifted over the North Sea while migrating from areas south of the acoustic monitoring network (e.g. Channel Area, northern France, Belgium, and southern parts of the Netherlands). Migration from the east coast of the UK to the European mainland in March–April appears to be rare or absent, as none of the tagged bats migrated over sea in this period and acoustic detections during westerly and northwesterly winds were scarce.

All tagged bats crossed the North Sea in May–June, typically under moderate westerly or northwesterly tailwinds (median wind speed = 7.0 m/s, interquartile range: 5.4–11.2 m/s). Similarly, acoustic detections in May–June were predominantly associated with westerly and northwesterly winds, albeit at lower wind speeds (median = 6.6 m/s, interquartile range: 3.0–9.9 m/s), indicating reduced wind support for bats detected acoustically. During May-June, migration probability was also elevated under winds from southerly directions (median = 5.9 m/s; interquartile range: 5.2–7.5 m/s) and from the east (median = 3.4 m/s; interquartile range: 3.4–5.6 m/s). Under these conditions, wind-drifted bats originating from the European mainland appear less likely, instead, it seems more plausible that these observations consist of individuals departing from the UK under crosswinds or low headwinds. In both periods, northerly and northeasterly winds were associated with the lowest migration probabilities.

In addition to wind, several other environmental factors such as precipitation, cloud cover, atmospheric pressure change, temperature and the lunar phase, can influence bat migratory movements. Increased temperatures (Hurme et al., 2025; Pettit and O'Keefe, 2017; True et al., 2021) and decreasing atmospheric pressure (Hurme et al., 2025) trigger spring migration. During autumn migratory departures generally occur under dry conditions (Brabant et al., 2021; Lagerveld et al., 2014, 2023b), whereas precipitation and overcast skies tend to induce stopovers (Cryan and Brown, 2007; Hüppop and Hill, 2016). Autumn migration has also been linked to darker lunar phases (Cryan and Brown, 2007; Lagerveld et al., 2023b). Our analysis of the acoustic dataset revealed no statistically significant effect of precipitation, cloud cover, atmospheric pressure change, temperature and lunar phase. One possible explanation is that bats acoustically recorded on offshore platforms may have landed under a wide range of environmental conditions, including those that are often considered suboptimal for migration.

2.5.3 Methodological implications

Our novel analytical approach – a state-space formulation of the capture-recapture model – has proven to be an effective solution for analyzing bat departure decisions. It enabled the comparable analysis of two datasets collected using different monitoring techniques, and incorporated uncertainties in migration dates of tagged individuals. While these observation techniques were thought to provide contradictory insights into migration patterns, our analysis shows that combining these two observation techniques improves our understanding of bat migration patterns.

Although the acoustic and tracking monitoring results capture the same late spring seasonal migration pattern, both methods have certain limitations and therefore provide information on different fractions of migratory bats. Acoustic detectors at offshore platforms record Nathusius' pipistrelles below elevations of 50 m above sea level (Lagerveld et al., 2023b) and seem to primarily record individuals that landed on these structures as they failed to cross the North Sea in one attempt, e.g. due to less favorable wind conditions (reduced tailwinds, crosswind or headwind), or because they departed from locations further inland. In contrast, tracking data largely represented bats that crossed the North Sea under moderate supportive tailwinds in a single flight. During supportive tailwinds bats generally fly at altitudes too high to be detected acoustically (Lagerveld et al., 2024). Consequently, bats benefiting from stronger tailwinds, may be underrepresented -or even absent- in the acoustic dataset. This implies that curtailment measures relying exclusively on acoustic monitoring (cf Rijkswaterstaat, 2021) underestimate bat migration over sea at higher wind speeds. Tracking data also have limitations: they reflect only bats departing from a specific geographic location -in this study the east coast of the UK - and therefore remain blind to the migration originating from other areas. To reveal the geographic origin of the Nathusius' pipistrelles appearing over the North Sea with

southerly winds will require extensive tracking studies of individuals captured in other regions such as the Channel area, Northern France and Belgium.

2.5.4 Mitigation strategies for offshore wind farms

Although detection ranges of acoustic detectors and Motus receivers differ, both the acoustic and tracking models indicated that wind at 200 m above sea level (representing regional airflow) was a strong determinant of migration probability. Since current models for curtailment of offshore wind farms require environmental parameters that best predict migration (Rijkswaterstaat, 2021), we can recommend wind direction and speed at 200 m above sea level as key candidate parameters for tailoring curtailment measures to protect Nathusius' pipistrelle during spring migration over the southern North Sea. Moreover, acoustic monitoring can capture migration originating from different geographic locations but likely underestimates the part of the population that crosses the North Sea with optimal wind support in a single flight. This suggests that acoustic and tracking data are complementary rather than contradictory, and both monitoring methods should be used together when developing mitigation measures for offshore wind farms.

2.6 Author contributions of statement of responsibility

AUTHOR CONTRIBUTIONS

Sander Lagerveld conceived the ideas and designed the study. Jane Harris, Bart Noort and Sander Lagerveld conducted the fieldwork and collected the data. Julia Karagicheva, Sander Lagerveld, Pepijn de Vries and Eldar Rakhimberdiev analysed the data. Sander Lagerveld and Julia Karagicheva led the writing of the manuscript. Sander Lagerveld, Jane Harris, Martin Poot and Frank van Langevelde acquired funding. All authors contributed critically to the drafts and gave final approval for publication.

ETHICS DECLARATIONS

Bat trapping and tagging was carried out under Natural England project licences 2021-55582-SCI and 2022-63237-SCI

CONFLICT OF INTEREST STATEMENT

We declare that we have no competing interests

DATA AVAILABILITY STATEMENT

Data and analysis scripts are available from Zenodo: https://doi.org/10.5281/zenodo.18485034 (Lagerveld & Karagicheva 2026)

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3 Stopover departure decisions and movement patterns of migratory bats during autumn migration

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3.1 Abstract

Migrating bats alternate between stopover periods and directed flights. When departing from a stopover site, bats select the night, the specific time within the night, and the flight direction to resume migration. Despite their ecological importance, the factors shaping these stopover departure decisions remain poorly understood. To identify the intrinsic and environmental factors driving departure decisions and movement patterns, we tagged *Nathusius' pipistrelles Pipistrellus nathusii* at three coastal locations in the Netherlands and tracked 178 individuals during autumn migration, using the MOTUS Wildlife Tracking System. We examined movement patterns and analysed departure probability in relation to a set of individual and environmental covariates in a Bayesian capture-recapture model in state-space formulation. Additionally, we modelled within-night variation in departure timing. Seasonal patterns were strongly influenced by reproductive behaviour, with decreased migration probability during the mating period. Regardless of their seasonal timing, bats departed under moderate tailwinds and dry conditions, optimizing energy efficiency, while avoiding crosswinds and cloud cover, enhancing navigational safety. Most individuals departed shortly after sunset, whereas headwinds delayed nocturnal departure. Movement patterns were diverse, including

migration towards lower latitudes, coastal barrier movements, and long-distance roundtrips, suggesting the use of multiple movement strategies. Our study demonstrates that migration patterns in bats emerge from the interaction between intrinsic factors and external conditions, and highlights the importance of both energy efficiency and safety in shaping stopover departure decisions. The presence of multiple movement strategies complicates predictions of spatiotemporal occurrence, emphasising the need to account for behavioural variability in conservation planning, for example in the context of wind energy developments.

Keywords

Bat migration, *Nathusius' pipistrelle*, wind farms, curtailment, bat mortality, capture-recapture state-space models, weather, stopover

3.2 Introduction

Several bat species undertake long-distance migrations, traveling hundreds to thousands of kilometres between their summer and winter ranges (Fleming and Eby, 2003). Because such distances cannot be completed in a single flight, bats alternate between migratory flights and stopovers to rest and refuel (Jonasson and Guglielmo, 2016; McGuire et al., 2012). Bats use torpor to conserve energy (Geiser, 2004), enabling them to depart on low fuel loads and use short stopovers in comparison to birds (Clerc and McGuire, 2021; McGuire et al., 2012), which often accumulate high fuel loads during extended stopovers (Alerstam and Lindström, 1990; Schmaljohann and Eikenaar, 2017). When embarking on a migratory flight from a stopover site, bats decide on the specific night, specific time within the night, and direction to depart. These decisions affect energy expenditure, time budget and mortality risk during migration (Alerstam and Lindström, 1990; Hedenström, 2009).

The overall spatiotemporal pattern of migration appears to be genetically controlled as bats likely migrate without guidance of related individuals (Baerwald and Barclay, 2016; Van Schaik et al., 2025) and migration occurs within distinct seasonal timeframes (Fleming and Eby, 2003; Lagerveld et al., 2024, 2023; Pettit and O'Keefe, 2017; Rydell et al., 2014).

In addition to their innate migration program, several intrinsic (e.g. sex and age) and external factors (e.g. environmental conditions) influence migratory decisions. Seasonal timing is both sex-dependent (Jonasson and Guglielmo, 2016; Lagerveld et al., 2024; Pētersons, 2004) and age-dependent (Pētersons, 2004; Strelkov, 1969). Environmental conditions such as wind support (Dechmann et al., 2017; Hurme et al., 2025; Lagerveld et al., 2024, 2021) as well as dry weather (Brabant et al., 2021; Lagerveld et al., 2023, 2014) promote departures, whereas strong headwinds, precipitation and overcast conditions induce stopovers (Hüppop and Hill, 2016). Additionally, bat migratory movements coincide with higher temperatures

(Brabant et al., 2021; Hurme et al., 2025; Lagerveld et al., 2021; Pettit and O'Keefe, 2017; True et al., 2023), atmospheric pressure changes (Hurme et al., 2025), and may be associated with darker phases of the moon (Cryan and Brown, 2007; Lagerveld et al., 2023).

Despite growing knowledge of bat migration, key aspects of stopover departure decisions remain unresolved. In particular, it is unclear whether cloud cover affects departure decisions. Apart from being associated with precipitation, cloud cover may also hinder navigation by obscuring celestial cues. The role of crosswinds is also poorly known. Moreover, the specific departure time within the night is also not well understood. Bats generally depart shortly after sunset (Bach et al., 2022; Lagerveld et al., 2024; McGuire et al., 2012; True et al., 2023), yet it remains unclear whether environmental conditions influence within-night departure timing. To fill parts of these knowledge gaps, we investigated autumn stopover departure decisions in the long-distance migratory *Nathusius' pipistrelle Pipistrellus nathusii*. The species' nursery roosts are primarily located in northeastern Europe, whereas most hibernation sites are distributed across southern and western Europe, including the United Kingdom (Pētersons, 2004; Russ, 2022; Strelkov, 1969). Most migrants are recorded in coastal regions (Ahlén et al., 2009; Ijäs et al., 2017; Voigt et al., 2023). This coastal concentration likely reflects barrier effects, as *Nathusius' pipistrelles* generally follow shorelines to avoid large expanses of open water, and often perform back-and-forth movements along the coast while searching for a suitable location to cross over sea (Lagerveld et al., 2024). Autumn migration coincides with the mating season, during which males establish mating roosts along the flyway and remain there for extended periods (Gerell-Lundberg and Gerell, 1994).

We tagged bats at three locations along the Dutch coast during five autumn seasons (2018-2022) and tracked their movements using the Motus wildlife tracking system (Mitchell et al., 2025; Taylor et al., 2017). With the obtained tracking data, we (I) examined movement patterns, (II) analysed night-to-night departures in relation to the seasonal timing, environmental conditions and individual traits, and (III) analysed the within-night departures, in relation to the departure time relative to sunset and environmental conditions.

3.3 Material & methods

3.3.1 Bat tagging and tracking movements

Bats were captured and tagged over five consecutive autumn seasons (2018–2022), at three coastal sites in the Netherlands: Hoek van Holland (N 51.99, E 4.12), northern North Holland (N 52.84, E 4.71) and the Afsluitdijk (N 53.07, E 5.34). Captured bats were sexed, aged, weighted and measured following (Haarsma, 2008). Individuals assessed to be in poor condition (i.e. visible injuries, lots of parasites, damaged wing membranes) were released immediately.

In total, 566 bats were tagged between 20 August (day 232) and 19 October (day 292), including 369 from bat boxes during the day and 197 at night using Austbat harp traps (Faunatec) and mist nets (Solida Safety line – white). The dataset comprised 103 first-year females, 202 adult females, 91 first-year males and 170 adult males, with similar mean tagging dates across groups (days 255–257).

Tags were attached with skin adhesive (Sauer), ensuring total tag mass remained <5% of the bat's body mass (Aldridge and Brigham, 1988). Bats were released on-site after the adhesive was set (after about 10 min). We used 0.35 g NTQB2-2 tags (2018–2019) and 0.26 g NTQB2-1 tags (2020–2022; LOTEK Wireless) with burst intervals of 5.9–8.9 s, transmitting uniquely coded signals at 150.1 MHz.
Movements were tracked using the Motus Wildlife Tracking System (Mitchell et al., 2025; Taylor et al., 2017), which gradually increased in the study area from 51 receivers in 2018 to 109 receivers in 2022 (Appendix S1). Detection data and receiver metadata were retrieved from www.motus.org (accessed 19 May 2025). To avoid false positives, detections with less than three consecutive signals were excluded. Additional manual filtering was conducted to exclude detections from receivers affected by high levels of radio noise (e.g. in ports);; or otherwise implausible detections (Appendix S2). All analyses were performed in R version 4.5.1 (R Core Team, 2025)

Receiver locations were used as proxies for the location of the bat at the timestamp when the strongest signal was received, except at the departure location where the timestamp of the last signal received was used, as migratory bats typically perform erratic movements prior to the actual departure (McGuire et al., 2012). We recorded both movements within one night as well as movements over multiple nights. Migratory flights (hereafter *flights*) were defined as a directed flight of 30 km or more. Of the 566 tagged bats, 23 individuals (4%) were not detected, 357 (63%) remained within a 30 km of the tagging site and 186 bats (33%) undertook *flights*. Flight bearings were calculated using the R package sf. (Pebesma, 2018). As autumn migration is predominantly south westward, *flights* were classified as *regular* when they were oriented in southern or western directions, and as *return* when oriented in northern or eastern directions.

3.3.2 Environmental data

Weather data were obtained from the Copernicus Climate Data Store (Hersbach et al., 2018) using the R package CopernicusClimate (De Vries, 2025), retrieved 2 July 2025. Data were provided as hourly raster fields (0.25° × 0.25°) and included 2 m air temperature [K], mean sea-level air pressure [hPa], total precipitation [m/h], cloud cover [%], eastward (U) and northward (V) wind speed components [m/s]. Wind data, provided for specific air pressure layers, were converted to altitude layers using the barometric equation (NASA, 1976). We used wind data at 200 m above sea level, as these better represent regional airflow patterns in comparison to near-surface (up to 100-150 m) winds (Garratt, 1992). We calculated the tailwind (wind support in the direction of travel) and crosswind components (wind perpendicular to the

direction of travel), using the bearing between the departure and arrival location. When the bat was also detected in-between, the receiver closer to the departure point was chosen to estimate the bearing of departure. Temperature was converted to °C, precipitation to binary values (0 = dry, 1 = precipitation) and atmospheric pressure change was calculated relative to values 24 hours earlier. Lunar phase [degrees] and moon illumination fraction [%] were derived using the R package suncalc (Thieurmel, 2022).

(I) Movement patterns

We recorded *flights* of 186 bats, including two *flights* by 76 individuals, three *flights* by 17, four *flights* by seven, five *flights* by three, and six *flights* by a single individual. Flights were recorded for 8% of adult males (13 individuals), 43% of first-year males (39 individuals), 52% of first-year females (54 individuals), and 40% of adult females (80 individuals).

(II) Night-to-night departures

Of the 186 tracked bats, 28 initiated their first *flight* on the night of tagging and were excluded as handling may have influenced behaviour and earlier departures could not be ruled out. The remaining 158 bats, including 72 adult females, 49 first-year females, 10 adult males and 27 first-year males, were used to assess minimum stopover duration and the night-to-night departure probability.

Minimum stopover duration at the tagging site was defined as the interval between tagging and the last detection. Individuals tagged during daytime (captured in bat boxes) were assigned as first-time present in the previous night. Differences among the sex and age groups were tested using a Kruskal–Wallis test. Night-to-night departure probability was analysed in relation to seasonal timing, environmental conditions and individual traits, using a Bayesian capture-recapture state-space model in JAGS (Gimenez et al., 2007; Kéry M. and Schaub M., 2011; Royle, 2008), following (Lagerveld et al., 2026) (*under review*). Migratory state of each individual was represented as a time series. Starting from the tagging date, the migratory state was assigned 1 when an individual has not yet departed from the tagging site and 0 on the night when it was detected at its destination. On nights between the first and last detection when an individual was not observed, the migration state was assigned NA (unknown). For these nights, the latent probability of migration was modelled. For individuals with multiple *flights*, only the first was used, representing departure from the stopover site. The dataset included 146 *flights* (92%) in the *regular* migration direction and 12 (8%) *return* flights.

The night-to-night departure probability was modeled as a likelihood of transition between the states in relation with night in year (mean-centered: linear and quadratic terms), environmental conditions and individual traits. Individual-level random intercepts were included to account for repeated observations.

Migration probability was derived as 1−plogis of the linear predictor. Consequently, negative coefficients correspond to increased departure probability, while positive coefficients correspond to decreased departure probability.

Environmental covariates included tailwind and crosswind (both linear and quadratic terms), atmospheric pressure change, temperature, precipitation and cloud cover, averaged between sunset and two hours post-sunset. Temperature was correlated with night in year and was therefore included in the model as residuals from a regression on night in year.

Cloud cover is often associated with precipitation, but may also hinder orientation and navigation by obscuring celestial cues. To separate these overlapping effects, we included a partial interaction term between cloud cover and precipitation. Non-zero precipitation was set as the baseline, enabling the model to estimate the effect of cloudiness under dry conditions. Lunar phase was treated as a cyclic covariate by including both sine and cosine terms. Individual covariates included sex (male/female), age (adult/first-year), along with their interactions with night in year (linear and quadratic terms). Body mass index (BMI) was calculated as a within-sex-age-group residual of individual body mass at tagging on arm length (Appendix S3)

Aiming to define the most influential factors affecting departure decisions, we started with a model that included all candidate covariates and their interactions. To avoid possible spurious outcomes due to the limited sample size/covariate number ratio, we sequentially removed the covariates with the weakest support, based on the overlap of the 95% posterior credible intervals of parameters with zero and the corresponding evidence ratios. Convergence was confirmed for all parameters ($\hat{R} < 1.01$). Model simplification continued until the model with the lowest deviance information criterion (DIC) was obtained. The final model was:

$$\eta_{i,t} = \beta 0 + b_i + \beta 1 day_{i,t} + \beta 2 day_{i,t}^2 + \beta 3 crosswind_{i,t} + \beta 4 crosswind_{i,t}^2 + \beta 5 tailwind_{i,t} + \beta 6 tailwind_{i,t}^2 + \beta 7 drynesst_{i,t} + \beta 8 (cloud_{i,t} \times dryness_{i,t}) + \beta 9 temp_{i,t} + \beta 10 sex_i + \beta 11 age_i + \beta 12 (sex_i \times day_{i,t})$$

with individual random intercept effects:

$b_i \sim N(0, \sigma_{ind}^2)$,

where $p_{i,t} = 1 - logit^{-1}(\eta_{i,t})$ is the probability of migration of individual i on day t.

(III) Within-night departures

The same modelling approach was used to analyse the within-night departure probability. For each individual bat with a known departure time (n = 102), we modelled the hourly probability of a transition between states (not yet departed = 1 versus departed = 0) on the night of departure as a function of time since

sunset, and weather conditions affecting flight conditions (tailwind, crosswind and precipitation), food availability (temperature) and ambient light levels (cloud cover and moon illumination). The encounter histories started one hour before sunset. Two outliers (departures at 315 and 427 min after sunset) were removed from the analysis. The full model was the model with the lowest DIC:

$\eta_{i,t}=\beta 0+b_i+\beta 1 timesincesunset_{i,t}+\beta 2 crosswind_{i,t}+\beta 3 tailwind_{i,t}+\beta 4 dryness_{i,t}+\beta 5(cloud_{i,t}\times dryness_{i,t})+\beta 6 temp_{i,t}+\beta 7 moonillumination$

with individual random intercept effects:

$b_i \sim N(0,\sigma_{ind}^2)$,

where $p_{i,t}=1-logit^{-1}(\eta_{i,t})$ is the probability of migration of individual i on day t.

3.4 RESULTS

3.4.1 Movement patterns

Of the 186 tracked bats, 169 individuals (91%) initiated migration in the regular autumn direction (between south and west-northwest), while 17 individuals (9%) performed return *flights* (north to northeast). Among those initially migrating in the regular direction, 30 individuals (18%) later performed one or more return *flights*. Conversely, five individuals (29%) that initially made return *flights* subsequently migrated in the regular direction. Overall, 139 bats (75%) exclusively followed the regular migration direction, 12 bats (6%) performed only return *flights* and 35 bats (19%) exhibited back-and-forth *flights*. Three individuals were detected in the United Kingdom, while the remaining 183 were recorded solely on the European mainland (Figure 1 and Appendix S4).

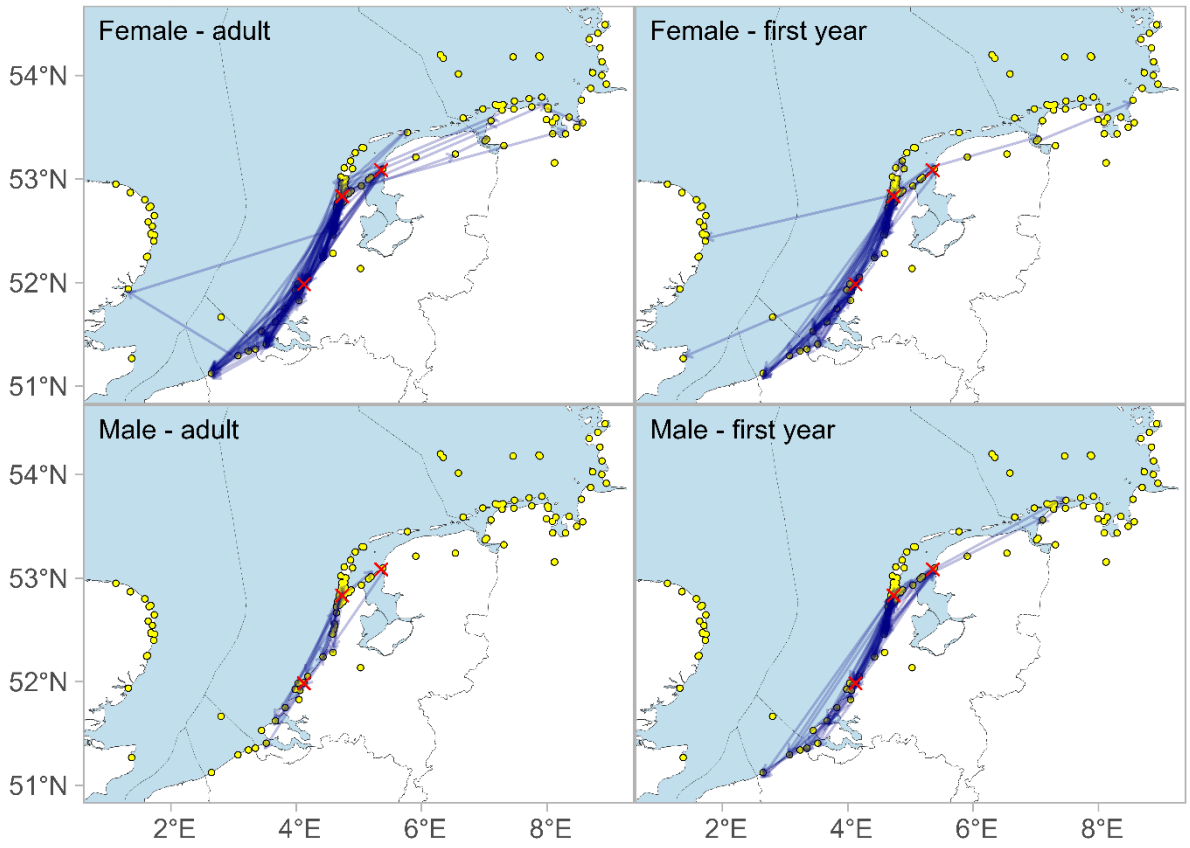

Figure 1 Movements >30 km from the tagging sites (n = 186). Receivers are indicated as yellow dots, tagging locations as red crosses. The flights are represented as straight lines between start and end point, not necessarily reflecting the actual flight paths. See Supplementary file 4 for the movements of each individual.

Among bats exhibiting back-and-forth movements, 26% covered distances exceeding 300 km (Figure 2), including one adult female that travelled at least 715 km within three weeks. This individual travelled from the Afsluitdijk (N53.10 E5.48) to southern Belgium (N51.29 E3.07), subsequently crossed the North Sea to the east coast of the United Kingdom (N51.94 E1.32), and subsequently returned to the tagging site (Figure 1 and Appendix S4: Deployment 42408). We found no evidence that the occurrence of back-and-forth *flights* differed among the sex and age groups (Fisher's exact test, p = 0.19).

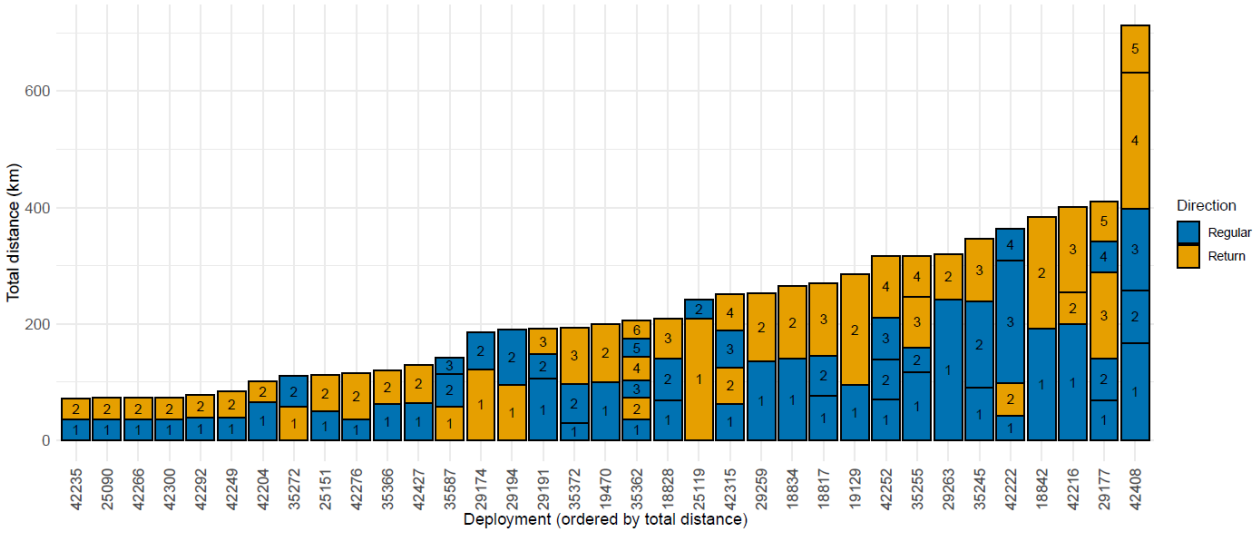

Figure 2: Minimum distance back-and-forth flights by flight number and direction

3.4.2 Night-to-night departures

The overall median minimum stopover duration was two days. A considerable proportion of bats (46%) stayed only one day, while maximum observed duration was 58 days. Stopover duration did not differ significantly among sex and age groups (Kruskal–Wallis: $\chi^2(3) = 5.71$, $p = 0.127$). In general, minimum stopover duration generally increased as the season progressed (Figure 3).

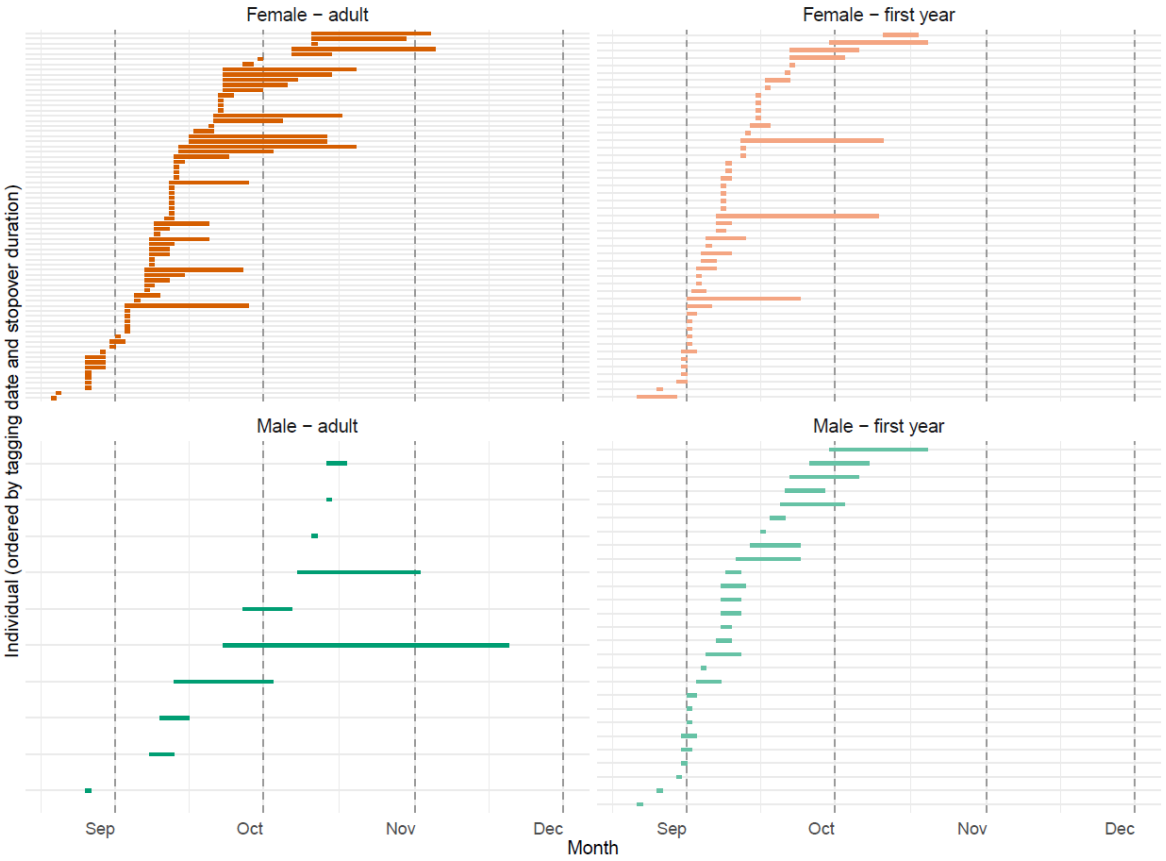

Figure 3: Minimum stopover duration for each individual per sex and age group, ordered by tagging date and stopover duration.

The model showed strong support for a non-linear seasonal pattern with higher departure probability in the beginning and at the end of the migration period ($\beta 2$ = −0.002, 95% CI: −0.003 to −0.001, f =1.00). Males and adults tended to have lower departure probabilities than females and first-year individuals, although these effects were weakly supported (β10 = 0.747, 95% CI: −0.007 to 1.615, f =0.97; β11 = 0.538, CI: -0.134 to 1.274, f =0.94. However, later in the season males had a significantly lower probability of migration (β12 = 0.049, CI: 0.006 to 0.096, f =0.99, Figure 4).

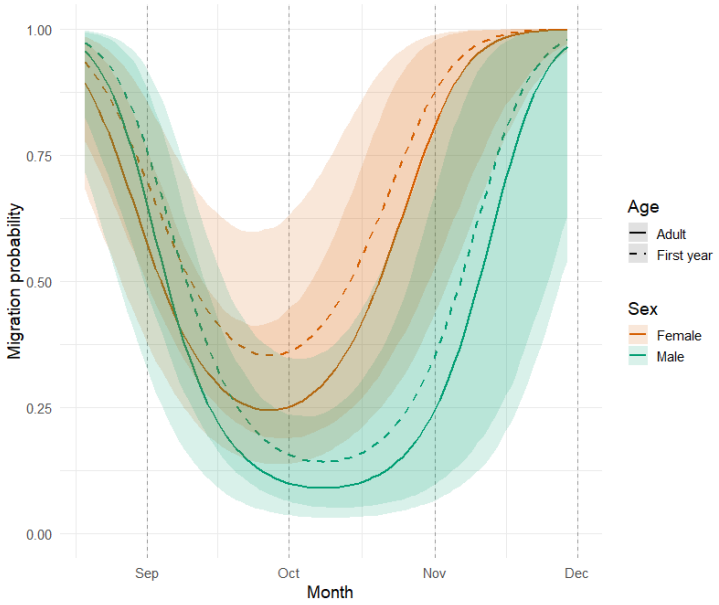

Figure 4: Departure probability throughout the season for each sex and age group

Wind conditions had pronounced non-linear effects on departure decisions (β6 = 0.009, CI: 0.003 to 0.016, f =1.00; β4 = 0.026, CI: 0.017 to 0.036, f =1.00), indicating the highest departure probability during moderate tailwinds and low (near-zero) crosswinds (Figure 5). The maximum migration probability was predicted under tailwinds of 9.9 m/s and crosswinds of 0.9 m/s from the left, which corresponds to eastern winds for most flights (92%) in the dataset.

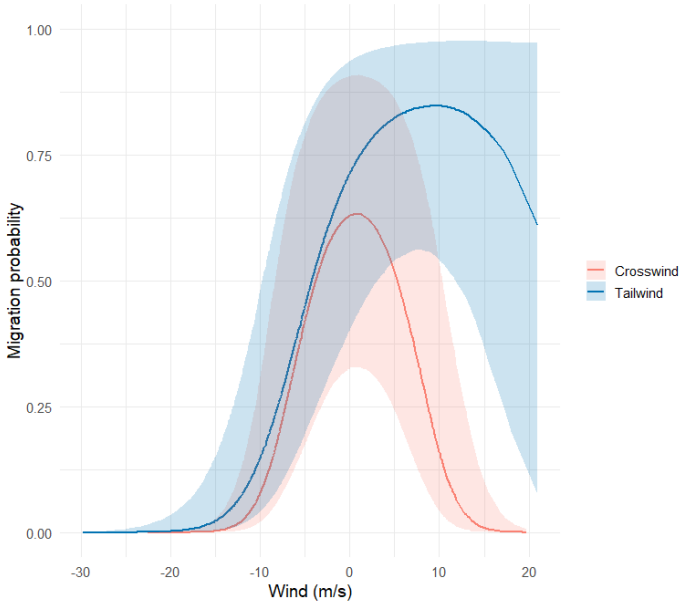

Figure 5: Departure probability depending on tailwind and crosswind

Precipitation strongly reduced departure probability (β7 = −1.151, CI: − -1.951 to −0.344, f =1.00). The positive cloud cover × precipitation interaction (β8 = 1.262, CI: 0.071 to 2.498, f =0.98), showed a statistically significant negative effect of cloud cover under dry conditions on departure probability. Temperature showed a weak, but not significant, effect (β9 = −0.119, CI: −0.300 to 0.056, f =0.91). Substantial individual-level variation was observed (σ_ind = 1.096, CrI: 0.538 to 1.727, f =1.00) (Appendix S5).

3.4.3 Within-night departures

Most bats (88%) departed within two hours after sunset and 9% between 2-3 hours after sunset. The remaining three individuals departed 182, 315 and 427 min after sunset (Figure 6).

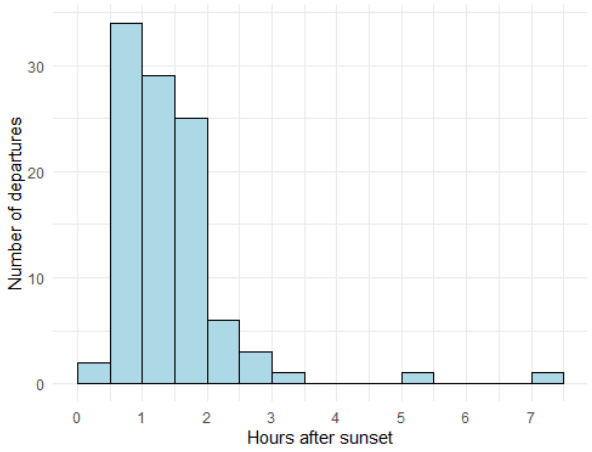

Figure 6: departure time after sunset

The model showed a strong effect of time since sunset on departure probability (β = -24.08, 95% CI: −37.65 to −12.23, f = 1.00), indicating that departures were concentrated early in the night. Tailwind had a clear positive effect (β = −0.80, 95% CI: −1.70 to −0.12, f = 0.99), meaning that increased headwinds delayed departures (Figure 7). Crosswind showed a weaker and uncertain negative effect (β = 0.49, 95% CI: −0.23 to 1.38, f = 0.91), suggesting a tendency to delay nocturnal departures. Other environmental covariates were not supported with wide confidence intervals overlapping with zero. The individual variation was very large (σ_ind = 13.94 (CrI: 6.77–22.61)), suggesting substantial individual heterogeneity not explained by covariates in the model (Appendix S5).

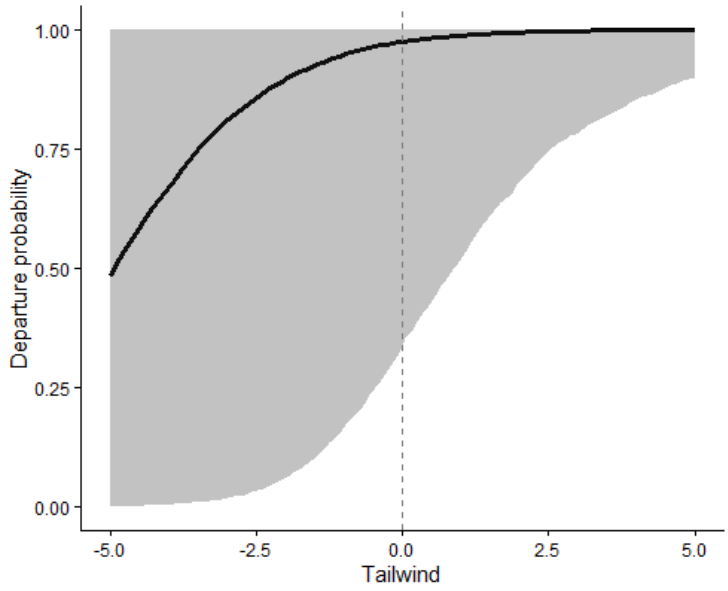

Figure 7: migration probability depending on tailwind. Note that negative tailwind refers to headwind.

3.5 DISCUSSION

We tracked Nathusius' pipistrelles during autumn migration to examine movement patterns and stopover departure decisions at both night-to-night and within-night scales. Movement patterns suggest multiple overlapping strategies, including migration towards hibernation sites, barrier-type movements, and mating-related movements. Seasonal migration probability peaked in late August, declined during the mating period, and increased again from mid-October onwards, indicating that mating activities likely constrain migration during early autumn. Later in the season, females departed earlier than males and first-year bats of both sexes tended to depart earlier than adults. Regardless of timing, bats departed under moderate tailwinds and dry conditions to optimize energy expenditure, while crosswinds and cloud cover were avoided to enhance safety. Bats typically departed soon after sunset, while headwinds delayed nocturnal departure, further highlighting energy-efficiency, even at fine temporal scales.

(I) Movement patterns

Most bats (75%) migrated in the expected southwest direction, whereas 19% showed back-and-forth movements along the coast, and 6% moved in the opposite direction, possibly reflecting return movements where the southwest-bound movement was not recorded. These back-and-forth flights likely reflect barrier movements to find a suitable location to cross over sea (cf Lagerveld et al., 2024). Also in other regions, movements of migratory bats along large expenses of open water have been observed, opposite or perpendicular to the general migration direction (McGuire et al., 2012; Voigt et al., 2023). The observed back-and-forth movements suggest that at least part of the population may attempt to cross the North Sea towards the United Kingdom. The small number of individuals detected there is likely underestimated due to limited receiver coverage and rapid inland dispersal.

We also recorded long-distance roundtrips, including one individual that crossed the North Sea and returned three weeks later. This indicates that some movements are not strictly migratory, but may also be driven by other factors such as mating. Together, these findings suggest that autumn movement patterns reflect migration, barrier and mating-related movements.

(II) Night-to-night departures

Departure decisions were shaped by both intrinsic and environmental factors, with mating behaviour likely structuring seasonal patterns. Adult males were largely sedentary (8% departed), consistent with their role at mating sites, whereas females and first-year bats showed substantially higher departure rates, indicating more transient individuals in these groups. Across all groups, departure probability peaked in late August, declined during September–mid-October, and increased thereafter (Figure 4). This decline coincides with the mating season in western Europe (cf Lina and Reinhold, 1997), during which males establish mating roosts

where they remain extended periods (Gerell-Lundberg and Gerell, 1994) Females visit these roosts for one to several days. Among them, first-year individuals who attain sexual maturity at an age of about three months (Gerell-Lundberg and Gerell, 1994). First-year males, which reach sexual maturity after about one year (Gerell-Lundberg and Gerell, 1994), also join these temporary harems (Van Schaik et al., 2025). The overlap between mating season and reduced migration probability strongly suggest that mating activities constrain migratory movements from early September to mid-October.

In the breeding areas, adult females depart first, subsequently the first-year bats and last the adult males (Strelkov, 1969). At the end of the migration period first-year bats of both sexes tended to depart earlier than adults, with females leaving earlier than males. This pattern suggests that the adult females migrate slower than first-year females, possibly because adult females invest more time in mating activities, resulting in a convergence in departure timing later in the season in the western parts of their range. First-year males migrate more slowly than first-year females and exhibit departure timing similar to that of adult males, which depart last, as has also been observed in other regions (cf Pētersons, 2004; Strelkov, 1969). Departure probability was not related to body mass index, further supporting the idea that departures do not depend on high fuel loads (cf Clerc and McGuire, 2021; McGuire et al., 2012). Weather conditions strongly influenced departures. Bats preferentially departed with moderate tailwinds, confirming the importance of wind support for migratory bats cf Dechmann et al., 2017; Hurme et al., 2025; Lagerveld et al., 2026, 2024, 2021). Numerous studies also identify wind support as a major determinant of migratory departures in songbirds (Brust et al., 2019; Packmor et al., 2020; Rüppel et al., 2023). When songbirds encounter crosswinds during flight over land they often drift sideways, but compensate for drift near the coastline (Horton et al., 2016). Migrating songbirds over sea avoid crosswinds (Packmor et al., 2020). Bats departures peaked in low crosswinds (0.9 m/s) from the left side, which for most of the flights in the dataset (91%) was from the east. This suggests that bats generally avoid crosswinds and actively compensate for drift to minimise the risk of displacement over open water.

Precipitation reduced departure probability, likely due to increased energetic costs (cf Voigt et al., 2011) and reduced foraging and orientation efficiency (Geipel et al., 2019). Similarly, cloud cover decreased migration probability, suggesting that bats prefer clear skies to facilitate orientation. Some species of bats are known to use the Earth's magnetic field for orientation, which is calibrated by the solar azimuth at sunset (Holland et al., 2010; Schneider et al., 2023).

Migratory bat activity is often associated with higher temperatures (Brabant et al., 2021; Hurme et al., 2025; Lagerveld et al., 2021; Pettit and O'Keefe, 2017; True et al., 2023), pointing to a relationship with insect availability, which may further be modulated by the lunar phase (cf Lagerveld et al., 2023). In our study we

found a positive, but not significant, effect of increased temperatures on seasonal departures, while lunar phase had no detectable effect.

Increasing atmospheric pressure generally indicates stable weather and favourable flight conditions over the next few days. Several bird migration studies have observed higher departure probabilities when atmospheric pressure increases (Cooper et al., 2023b; Rüppel et al., 2023; Woodworth et al., 2015). Our results did not show an effect of changes in atmospheric pressure on the departure probability. This may indicate that bats rely on current local weather conditions, rather than taking anticipated future weather into account.

Overall, our findings indicate that the seasonal migration patterns are strongly modulated by reproductive behaviour, while their night-to-night departure decision is based on current atmospheric conditions: tailwinds and dry weather to optimize energy use, clear skies and minimal crosswinds to enhance safety, and possibly higher temperatures to increase foraging opportunities.

(III) Within-night departure timing

Most bats (88%) departed within two hours after sunset, consistent with previous studies (cf. Bach et al., 2022; Lagerveld et al., 2024; McGuire et al., 2012; True et al., 2023). This narrow departure window mirrors patterns observed in migratory songbirds (Cooper et al., 2023a; Klinner et al., 2025; Müller et al., 2016) and suggests shared orientation mechanisms, such as compass calibration at sunset (Cochran et al., 2004; Schneider et al., 2023).

Early departures potentially increase the duration of the migratory flight and the distance covered (Müller et al., 2016). Songbirds embarking on long-distance migratory flight depart generally within two hours after sunset, while individuals performing non-migratory movements away from the stopover site depart later and less synchronously over the course of the night (Cooper et al., 2023a). Bat departure timing showed little variation, with headwinds being the only factor delaying departure. This further highlights the importance of energy efficiency, even at fine temporal scales, and suggests that within-night departure timing is highly constrained.

3.6 CONCLUSION

Our study demonstrates that migration patterns in bats emerge from the interaction between intrinsic factors and external conditions. Seasonal patterns in autumn are strongly shaped by reproductive behaviour, whereas night-to-night departure decisions are primarily driven by immediate atmospheric conditions that optimise energy efficiency and navigational safety. The diversity of observed movements, including migration

towards lower latitudes, coastal barrier movements and long-distance roundtrips, indicates the use of multiple movement strategies, complicating predictions of their spatiotemporal occurrence. Understanding this behavioural variability will be essential for developing effective conservation strategies, particularly in regions facing increasing anthropogenic pressures such as wind energy developments.

Data availability

The data and code supporting this study will be made available upon publication of the manuscript.

Contributions

Study design: Sander Lagerveld, Fieldwork: Karine Stienstra, Bart C.A. Noort and Sander Lagerveld. Data analysis: Julia Karagicheva, Sander Lagerveld, Pepijn de Vries, Eldar Rakhimberdiev. Original draft: Sander Lagerveld and Julia Karagicheva. Editing and review: all authors. Funding: Sander Lagerveld, Martin J.M. Poot, Frank van Langevelde.

Ethics

Fieldwork was conducted under Nature Legislation Permit No. 2018-057682 (Wageningen Marine Research) and in accordance with Animal Welfare Protocols AVD248002016459 / VZZ-18-005 (2018–2020) and AVD24800202114476 / VZZ-2021-001 (2021–2023; Dutch Mammal Society).

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Competing interests

The authors declare that they have no competing interests.

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4 General discussion

4.1 Introduction

During autumn, Nathusius' pipistrelle migrates from its breeding grounds in eastern and northern Europe towards western Europe, where it spends the winter. These movements often involve long-distance flights, with individuals crossing substantial bodies of water such as the Baltic Sea and the North Sea. In spring, the migration is reversed, as the bats return to their breeding areas in the east and north. These bats are exposed to an increased collision risk with the growing number of offshore and onshore wind turbines. Effective protection of Nathusius' pipistrelle populations from additional mortality therefore requires detailed knowledge of the timing, routes, and magnitude of migration as well as environmental drivers of departures. In this report, the available migration data of Nathusius' pipistrelles collected within the Wozep bat research programme 2016 - 2023 were re-examined by integrating telemetry data with passive acoustic monitoring data. This report seeks to synthesise all these findings on bat activity at offshore wind farms, aiming to enhance our understanding of offshore bat occurrence. Its dual objectives are to refine impact assessments and to optimise existing mitigation strategies such as curtailment, with the overarching goal of minimising potential bat fatalities.

We begin by outlining the existing curtailment measures for bats at offshore wind farms in the Netherlands. These measures have been implemented under the precautionary principle. However, no empirical observations of bat collisions at sea have been made to date. We therefore have no direct evidence of how often collisions occur or under which conditions they might take place. This lack of data raises fundamental questions about the effectiveness of current mitigation, which relies entirely on autumn acoustic data. We do not know whether bats are at risk during migration flights or due to local occurrence near turbines during stopovers. However, bats occur and behave in a different context at sea in comparison to land and consequently it seems likely that the collision risks at sea differs from that on land (Lagerveld et al 2020), making offshore-specific observations and the evaluation of specifically these data essential for effective mitigation.

On land the methodology for assessing the fatality rate is rather straightforward. This includes regular carcass searching under the wind turbines and adjusting the number of fatalities for causes of imperfect detection. Offshore, however, carcass searching is virtually impossible and therefore a model-based or technical solution is the only available option (Lagerveld et al 2020). In relation to the application of shutdown and curtailment provisions within the Dutch sector of the North Sea, it is important to recognise that no empirical data exist on the actual number of bat collisions, nor on the specific conditions under which such events occur.

This uncertainty equally applies to the automated start–stop systems currently in use for nocturnally migrating songbirds. In the absence of direct empirical data, both for birds and bats, risk assessment and mitigation have therefore relied on theoretical models (e.g. stochastic collision models for birds) and indirect indicators of activity (e.g. acoustic detections of bat presence).
The analyses presented in this report, which for the first time combine telemetry and acoustic detector data, have revealed clear limitations of acoustic data alone. They highlight why the effectiveness of mitigation measures based solely on acoustic monitoring must be questioned. We therefore summarise the most relevant new findings from these analyses and assess their implications for current mitigation practices.

Finally, we examine why no empirical evidence of offshore bat collisions has yet been obtained. This serves two purposes: first, to clarify why the current curtailment approach, while the best available, may not be fully effective; and second, to identify the key knowledge gaps that must be addressed to demonstrate whether the mitigation measures achieve their intended effect. In this context, we provide an overview of what is currently known about the migration system and the factors influencing bat presence at sea near offshore wind farms, distinguishing between spring and autumn movements, while also highlighting where

knowledge remains lacking due to technical limitations. We also draw a comparison with the start-stop procedure used for nocturnally migrating songbirds, which similarly follows a precautionary principle under the assumption that higher migration intensities lead to more collisions; however, like the current bat curtailment system, this approach lacks empirical validation.

In developing the recommendations, we will indicate priorities in terms of both practical action and timing. We recognise that several critical knowledge gaps cannot be resolved in the short term. The current mitigation system therefore represents the best available approach following the precautionary principle. Nevertheless, this should not preclude regular evaluation, as continued assessment is essential to ensure that the measures remain justified and effective as new evidence emerges.

4.2 Current curtailment in Dutch offshore windfarms

Given that the mitigation toolkit for offshore environments is strongly constrained by ecological, technical, and logistical uncertainties, the Dutch government, following the precautionary principle, applies in autumn a fixed curtailment procedure based on a combination of time, wind speed and temperature criteria. The specific regulatory prescription currently applied to mitigate potential bat collisions at Dutch offshore wind farms is detailed below. These provisions apply to several designated wind farm zones and serve as the basis for current operational shutdown measures. For the offshore wind farm sites of Borssele, Hollandse Kust South, Hollandse Kust North and Hollandse Kust West, the following condition applies:

Table 4.1 Current operational shutdown criteria in autumn: the cut-in wind speed (m/s) per wind direction at hub height of the turbines in combination with the air temperature, for the offshore wind farm sites of Borssele, Hollandse Kust South, Hollandse Kust North and Hollandse Kust West, based on Boonman (2018).

Temperature (°C)	N	NNE	NE	E	ESE	SSE	S	SSW	SW	W	WNW	NNW
<11	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0
11–15	3.5	4.5	5.5	6.0	5.5	5.5	3.5	3.5	3.5	3.0	3.0	3.0
>15	3.5	4.5	5.5	6.0	5.5	5.5	4.0	3.5	3.5	3.0	3.0	3.0

Measures to prevent collision fatalities of bats at rotor height:
a) During nights (between sunset and sunrise) in the period from 25 August to 10 October, the cut-in wind speed at hub height of the turbines is additionally adjusted according to air temperature and wind direction, as presented in Table 4.1.
b) When the wind speed is below the cut-in wind speed defined under (a), the permit holder shall reduce the number of rotor revolutions per minute per turbine to fewer than two during the nights referred to in a.
c) Measurements of wind speed, wind direction and temperature, as well as calculations of sunset and sunrise, are to be performed per turbine, with a measurement interval not exceeding twenty minutes. The most recent interval measurement shall determine whether the measures described under a and b are to be applied.
d) The permit holder shall, within two months after the period referred to in (a), submit a report to the Minister of Economic Affairs and Climate Policy describing how compliance with this condition has been ensured.

4.3 New insights on spring migration of Nathusius' pipistrelles

Our results reveal the presence of two distinct cohorts of migrating bats that differ in their wintering origins and migratory contexts. One cohort consists mainly of individuals originating from the United Kingdom, representing seasonal migration supported by westerly winds. The other cohort appears to originate from the European mainland (e.g. Belgium/France) and includes individuals that likely have been drifted seaward during migration over land by strong southerly winds. The differing migratory circumstances suggest that bats observed offshore in spring represent different cohorts.

Acoustic monitoring data primarily captures bats during stopovers or while travelling under suboptimal conditions. Individuals migrating under more favourable conditions, particularly when supported by stronger tailwinds and potentially flying at higher altitudes, are likely to remain undetected, as they move beyond the detection range of acoustic sensors. It also remains uncertain whether bats in active migration are echolocating (Corcoran et al. 2018, 2021, Chiu et al 2008), which further complicates the interpretation of offshore acoustic records.

Both analytical approaches reconfirm that bats preferentially migrate with tailwinds, though the data indicate that bats exploit stronger tailwinds than previously assumed. In autumn the vast majority of Nathusius' pipistrelles is acoustically recorded in low wind speeds at 10 m asl between 2-3 m/s (cf (Brabant et al., 2021; Lagerveld et al., 2023, 2021, 2014). These observations are the basis for the current Dutch curtailment procedure (Table 4.1). However, in the acoustic spring dataset (Chapter 2, Figure 3) migration peaked in March and April with median southern winds of 8.5 m/s (at 200 m asl), whereas in May and June it peaked with western or northwestern winds of (median) 6.6 m/s. Also in autumn (Chapter 3, Figure 4) maximal migration probability of tagged animals was predicted with moderate tailwind of 9 m/s and at low crosswind blowing from the east side (for 91% of the bats in the dataset). Tracked bats over the North Sea in spring have also been observed in higher wind speeds compared to acoustically recorded individuals. In the tracking model in Chapter 2, Figure 3, the predicted probability of migration in May-June even peaked with wind speeds of (median) 7.0 m/s from the west, though the number of tracked animals involved is small. Our study therefore reconfirms that bats generally use moderate tailwinds during migration, while acoustically recorded migratory bats refer to individuals traveling in suboptimal conditions, such as low tailwinds, crosswinds or headwinds. Consequently, wind is the primary driver shaping bat migration patterns.

4.4 New insights on autumn migration of Nathusius' pipistrelles

We analysed the departure decisions of 178 Nathusius' pipistrelles captured at an autumn migration stopover site in the Netherlands and equipped with MOTUS transmitters. We show that tailwinds and crosswinds, precipitation and cloud cover are the major weather factors affecting the day-to-day departure decisions in Nathusius pipistrelles, while the within-night departure was affected by headwinds. Additionally seasonal departure timing was associated with sex and, possibly, age.

Individuals tagged early in the migratory period typically remained at the site for one or a few days, whereas those captured later often stayed much longer. These longer stopovers are likely related to mating activities. The variation in stopover duration contributed to the two distinct peaks in departure probability observed at the beginning and end of the season. At the nightly scale, variation in departure timing was limited: most bats departed within two hours after sunset; departures were delayed under headwinds.

Also in this study we observed back-and forth movements along the coast, a behaviour typical of bats encountering large water bodies along their route. However, in some cases we observed return movements over very large distances, including one individual which migrated to the UK, and returned three weeks later after a roundtrip of at least 715 km to the area where it was tagged. Consequently, movements over larger distances in autumn not necessarily reflect exclusively migration to the hibernacula. As the mating season overlaps with the autumn migration period, this may imply that at least a portion of these movements may be motivated by reproductive behaviour. Another cause of extensive return flights may be to return to an area previously visited to winter. These movement patterns indicate multiple overlapping strategies such as migration to hibernation sites, barrier movements, and mating-related movements. Migration probability peaked in late August, dropped during mating, and rose again from mid-October, suggesting mating limits migration in early autumn.

Our analysis focused on individuals observed to depart on long-distance flights, which could only be detected along the coastal array of MOTUS receivers. The final destinations of these bats beyond the array remain unknown. A more comprehensive understanding of migration routes, and particularly the locations, timing, and numbers of North Sea crossings, will require a significant expansion of the MOTUS receiver network outside the Netherlands.

4.5 Assumptions of current curtailment for nocturnal songbird and bat migration

A widely held assumption in avian and bat collision risk assessment is that periods of high migratory intensity inherently correspond to elevated numbers of turbine-related fatalities. However, this relationship remains largely unverified by empirical data (e.g. Hüppop et al., 2020; Cryan & Barclay, 2009; Voigt et al., 2015). Collision probability is mediated by multiple interacting factors, including geographical location, species, flight altitude, weather conditions, turbine design and operation, and behavioural responses such as avoidance or attraction. Consequently, high migration fluxes do not necessarily translate into proportionally higher collision rates. A more nuanced understanding of these mechanisms is essential to ensure that mitigation measures are appropriately targeted.

For birds, it has become common practice to assume that periods of intense migratory passage at rotor height coincide with the highest collision risk. Curtailment procedures for nocturnal songbird migration are based on a predictive model with horizontal radar data of bird movements at rotor height only. Implicitly, this assumption presumes a proportional relationship between the intensity of migration and the number of fatalities, as estimated through stochastic collision models. In these models, the estimated number of potential collisions depends on the combined characteristics of the migratory bird species (body size, flight speed) and of the turbines (dimensions and type, determining the height coverage of the rotor swept area and the rotational velocity of the blades). The model further incorporates the vertical distribution of migration over the rotor plane, informed by radar measurements and/or GPS-tagged birds, and a series of avoidance parameters describing the extent to which birds circumvent the wind farm as a whole (macro avoidance), individual turbines (meso avoidance), and finally the rotor blades themselves (micro avoidance).

Radar data can provide useful information on macro- and meso-scale avoidance behaviour, but the final stage, close to the rotor, remains a major unknown. Radar systems cannot observe this zone directly due to clutter caused by turbine reflections. Moreover, with the radar systems currently in operation, it is presumably not possible to distinguish bats with certainty within the general bird migration stream. GPS-tagging of birds or bats also has its limitations in battery capacity preventing an employment of high frequency GPS measurements in the order of magnitude necessary to record avoidance flight movements within a wind farm, let alone close to the rotor. Consequently, the actual avoidance behaviour near the blades remains highly speculative. It is therefore entirely possible that the real collision dynamics differ substantially from current model based assumptions. Indeed, peak migration nights that trigger offshore turbine shutdowns typically coincide with favourable weather conditions such as tailwinds, enabling many birds and bats (Lagerveld et al 2024b) to fly above rotor height. Nevertheless, given the very large numbers of migrant songbirds involved, a considerable absolute number of songbirds will still traverse the rotor swept zone. Visibility during such events is often good, which may enable birds to perceive and evade the rotor at the last moment more effectively than is currently assumed.

Pre-construction acoustic monitoring can be used to assess the species-specific bat presence/absence over time in the area concerned. However, it is not a good predictor for the actual fatality rate. Hein et al. (2013) reviewed fatality data from 12 windfarms in the US and showed that there is no significant relationship between pre-construction acoustic measurements of bat activity and the number of post-construction fatalities, possibly due to attraction to turbines once they are built and/or the changes in site use due to an alteration of the habitat.
Post-construction acoustic bat activity on land is in general a good predictor for the fatality rate when the relationship between acoustic activity and the number of fatalities has been validated (Kunz et al. 2007, Baerwald & Barclay 2009 & 2011). However, results may be biased when wind turbines with different dimensions are used for the reference data, and when reference data is gathered at locations with different species compositions, environmental conditions, and in different seasons (Lagerveld et al 2020). The offshore fatality rate is currently unknown, and therefore it is not possible at this stage to validate curtailment measures offshore using acoustic data.

To advance our understanding of collision risks for bat and nocturnal songbird migration at offshore wind farms, empirical research into flight behaviour in these environments is imperative. Only through direct

observation, either by tracking individual bats or deploying thermal imaging technology, can we begin to unravel the frequency and circumstances under which collisions occur. While research on songbirds appears more advanced, the current state of knowledge remains fundamentally similar: we simply do not know the true extent or dynamics of collision events. The knowledge on songbirds relies heavily on theoretical stochastic collision modelling, yet the actual incidence and conditions of collisions remain unquantified. Thus, the effectiveness of the curtailment measures presently implemented remains unvalidated. Ultimately, the critical knowledge gap on collisions persists. Addressing this gap is essential to inform evidence-based mitigation strategies and ensure the coexistence of renewable energy infrastructure with bat and bird conservation.

4.6 Consequences of the new insights for curtailment measures

Given the current state of prevailing technical limitations offshore we give an overview in Figure 4.1 of all presented knowledge about spring migration over the North Sea to summarize the even more complex situation for bats compared to nocturnal migrating songbirds, because besides continuous migration flights over sea bats stop over at wind turbines with potential extra risks on collisions.

During spring, the migration of Nathusius' pipistrelles across the North Sea likely follows two main patterns: regular crossings from the UK to the European mainland, and drifted migrations from the mainland influenced by strong southerly winds., respectively. The timing and occurrence of sea crossings are determined by a combination of intrinsic factors, environmental conditions, and geographic constraints, notably the sea acting as a natural barrier. Offshore wind farms and platforms may serve either as temporary refuges or ecological traps. The ultimate fate of individuals recorded on such offshore structures, however, remains entirely unknown.

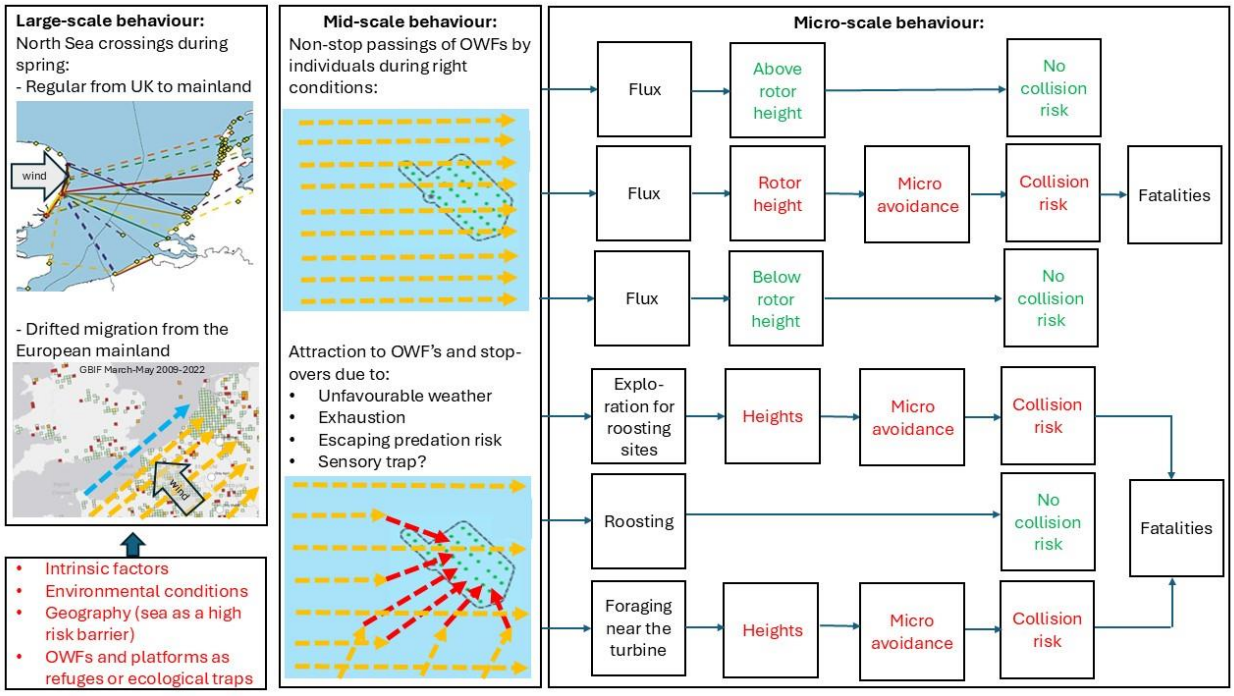

Figure 4.1 Schematic summary of the current understanding of Nathusius' pipistrelle spring migration over the North Sea and its occurrence at offshore wind turbines, illustrating the scale, influencing factors, behaviours, and associated potential collision risks. The autumn situation is described in the text.

At a mid-scale level, individuals may pass OWFs non-stop under favourable conditions, with collision risk confined to the rotor-swept area, while altitudes above or below the rotors are generally safe. Less favourable weather (e.g. low tailwinds, crosswinds or headwinds), exhaustion, daylight (predation risk) or sensory cues (skyglow or illumination) may lead to attraction to OWFs. Two additional phenomena may contribute to collision risk: turbines as foraging places, and sites for resting. During these behaviours bats may venture in the dangerous rotor-swept area.

During autumn, the migration pattern is largely the reverse of spring. However, the limited number of MOTUS receivers along the UK coast limits our understanding based on combined telemetry and passive acoustic monitoring. Sea crossings are known to occur, although the available data likely provide a conservative estimate. Bats may travel also parallel to the coast over the sea, either as drifted individuals or deliberately crossing sections of sea to follow the shortest route. Comprehensive studies employing multiple complementary techniques simultaneously are required to better characterise autumn migration.

4.6.1 Autumn

In autumn, the turbine shutdown procedure offshore in the Netherlands have so far been based solely on acoustic monitoring, which mainly reflects activity of low-flying individuals, rather than the higher-flying migratory bats now also detected during spring migration through telemetry. Acoustic monitoring is conducted at an altitude of about 20 m above sea level, and likely provides limited insight into actual migration dynamics during peak migration periods. It seems plausible that bats detected at low altitude represent individuals flying under suboptimal migratory conditions, whereas peak migration events likely involve larger numbers of bats flying at higher altitudes that may entirely escape detection by bat detectors.

4.6.2 Spring

During the peak migration period in May, the migrating population includes pregnant females returning from the United Kingdom to the European mainland en route to their maternity areas. This group represents a crucial demographic subgroup within the population and provides a strong argument for assigning high priority to curtailment measures also during the spring migration period (Lagerveld et al. 2024b). The absence of curtailment measures in spring, contrasting with their application in autumn, warrants reconsideration. From a precautionary perspective, it can be reasoned that curtailment should be considered for the period May, taking into account the meteorological conditions under which migration occurs from the UK across the North Sea.

Another new finding reported in chapter 2 concerns the drift of bats onto the North Sea during strong southern winds. If this represents a regular migratory phenomenon, it is plausible that the largest proportion of the European population of Nathusius' pipistrelle overwinter in Western Europe, with western part of Belgium and France potentially serving as a source of bats crossing the North Sea during spring. In this period, bats appear to undertake broad-front migration over land, with a subset near the Northwestern coast of France and also Belgium continuing over the sea when aided by tailwinds or drifted by crosswinds.

When designing or adapting shutdown provisions, it is important to account for differences in hinterland geography and the associated wind direction and strength influencing migration, as found in the spring with combining acoustic and telemetry data. This aspect warrants further consideration for the autumn period as well. An open question remains whether coastal-parallel movements occur along the Dutch coastline (Lagerveld 2024b), or whether easterly winds can cause drift of inland migratory flows towards the sea.

4.7 Interpreting new insights on bat migration over the North Sea: knowledge gaps and research priorities

The recent integration of acoustic monitoring with telemetry data has yielded novel insights into the spring migration of bats across the North Sea. While data in autumn are less extensive and such combined analysis of acoustic observations and tagged individuals are not made (Lagerveld et al. 2023a, Lagerveld et al. 2024a), we expect that the key insights derived from these analyses on spring data will largely apply to the autumn period as well. While these findings advance our understanding of migratory behaviour, they also reveal critical discrepancies between methodologies and challenge existing predictive factors for migration.

However, the current state of knowledge does not yet allow us to definitively address the specific questions raised regarding the implications for effect assessments and curtailment strategies, as basic knowledge gaps exist on the occurrence of collisions, population sizes and dynamics, and the influence of environmental factors on flight altitudes ultimately determining collision risks.

Key uncertainties and research needs

1. Effect assessments and flight altitude
The new data suggest that bats employ diverse migratory strategies, including variations in flight altitude and timing. However, it remains unclear how these findings should inform effect assessments, particularly whether low-flying individuals face increased risks, or if the majority migrate at safer altitudes above the turbines in tailwind conditions. The relationship between observed flight heights and model-based altitude predictions also requires further validation. Only through direct empirical research, combining thermal imaging and tracking, can we resolve these uncertainties and refine collision risk models.

2. Environmental influences: wind, moonlight, and seasonality
While the study confirms that bats preferentially migrate with tailwinds and avoid crosswinds or adverse weather, the role of moonlight and seasonal differences (e.g., spring vs. autumn wind conditions) remains ambiguous. Earlier studies suggested conflicting results regarding lunar influence, and the interplay between wind patterns at 200m altitude and migratory behaviour is not yet understood. Targeted field studies are essential to clarify these relationships and improve predictive accuracy.

3. Overwintering and coastal concentrations
The potential for overwintering in Belgium/France, and its implications for offshore migration rates, is another critical gap. Coastal regions are confirmed as migration hotspots due to barrier effects and stopover behaviour, yet the collision risks in coastal wind farms, where many projects are sited, are poorly quantified. Systematic monitoring in these high intensity zones for migratory bats is urgently needed to assess both occurrence and risk.

4. Curtailment and mitigation strategies
Current autumn curtailment measures lack empirical validation for offshore contexts, and spring migration, now recognised as a high-risk period, remains unaddressed so far. Our study's findings underscore the need for:

- Immediate review of curtailment thresholds, particularly for tailwind conditions and spring migration.
- Development of "rules of thumb" for spring curtailment, pending further data.
- Expansion of the MOTUS network and tagging studies in France/Belgium to clarify offshore movements from mainland wintering sites.
- Thermal camera-based collision monitoring to quantify actual collision rates.
- Behavioural studies on attraction to wind farms, including experimental and observational research into sensory mechanisms (visual and auditive) and lighting effects vs insect attraction/availability.

A precautionary path forward
Our study's innovative combination of acoustic and telemetry data has exposed both the complexity of bat migration and the limits of current knowledge. The recommended research pathways, spanning curtailment evaluations, spatial-temporal monitoring, flight path modelling, collision studies, and coastal risk assessments, represent the viable means to bridge these gaps. Until these steps are taken, effect assessments will remain speculative, and mitigation measures, cannot be guaranteed as effective.

4.8 Near future research prospects

To date, no monitoring system has been capable of directly measuring flight behaviour in the immediate vicinity of offshore turbine rotors. However, recent advances in remote sensing now make such measurements possible. For the first time, since spring 2025, thermal imaging cameras are being deployed on an offshore turbine in the Netherlands, providing the ability to record close, range flight trajectories and interactions. In autumn 2025 the three-year project BirdSafe has been started with six extra turbines

equipped with thermal camera's. This technology holds promise for quantifying both bat and bird movements and collisions in the offshore environment.

With the start of the first thermal camera projects in Dutch offshore windfarms we are getting close to develop a more empirical approach of curtailment procedures, in which fatalities are being monitored using measurement equipment that is able to detect the actual event, as well as the species involved. The application to monitor bat (and bird) fatalities should ideally consist of (Lagerveld et al 2020):
1. A combination of radar, which detects approaching flying objects and identifies the potential relevant ones (bats and birds) and thermal cameras, in order to obtain footage to assess collisions/barotrauma, as well as for the identification and at least separation of bats and birds. Furthermore, thermal cameras may be used to record a falling corpse from the rotor swept area. This set up is e.g. currently applied in BirdSafe.
2. A combination of ultrasonic detector (bat detector) to record bat echolocation and social calls and subsequently for the identification of individual bat species, and a bird sound recorder to record flight calls and subsequently for the identification of bird species. With this extension of a research set up BirdSafe would be suitable to fully include bats.

As another example, currently a five-year NWA project POWER is being developed and will investigate two main topics: collision risk in relation to environmental conditions, and the potential attraction of migrating bats by offshore wind turbines. In addition, a re-analysis of existing data and integrating new tracking approaches, POWER aims to improve the knowledge on offshore bat movements. Selected bats will be equipped with advanced sensors to test how environmental factors influence detection and migration behaviour. In parallel, experimental lighting setups will be used to assess whether and why bats are attracted to OWT warning lights. In support of these goals, POWER will establish a common framework for evaluating and improving monitoring technologies used to study the movement of birds and bats offshore. This Aerial Tracking Toolbox will integrate four major technology groups: optical and thermal cameras, audio loggers, radar systems, and GPS/RF telemetry.

5 Conclusions

Our study's innovative combination of acoustic and telemetry data has yielded interesting new findings on bat migration over the North Sea, but also exposed both the complexity of bat migration and the limits of current knowledge to implement into effect studies and curtailment strategies. Existing curtailment measures, lack empirical validation. Closing this knowledge gap is vital for developing effective, evidence-based mitigation strategies that balance renewable energy expansion with wildlife conservation.

To assess collision risks for bats at offshore and also coastal wind farms, direct empirical research is essential. Neither acoustic monitoring nor current knowledge based on tagged animals can reliably predict actual collision rates at sea. The recommended research pathways, spanning curtailment evaluations, spatial-temporal monitoring, flight path modelling, collision studies, and coastal risk assessments, are needed to bridge these gaps. Until these steps are taken, effect assessments will remain speculative, and mitigation measures, cannot be guaranteed as effective.

Below the key findings of the two analyses presented in this report are:

5.1 Different migratory cohorts in spring

Our results identify two distinct cohorts of spring migrating bats, differing in wintering origins and migratory contexts. One cohort primarily originates from the United Kingdom, representing large-scale late spring migration aided by westerly tailwinds. The other appears to come from the European mainland (e.g. Belgium/France) and may include individuals drifted seaward during broad-front land migration under southerly winds in early spring. These findings indicate that offshore observations reflect multiple migratory strategies.

5.2 Detection limitations in acoustic monitoring

Acoustic monitoring mainly detects bats during stopovers or under suboptimal conditions. Individuals migrating under favourable conditions, especially with strong tailwinds or at higher altitudes, are likely undetected. It also remains unclear whether actively migrating bats echolocate.

5.3 Environmental drivers identified

Bats in autumn preferentially depart under moderate tailwinds and dry conditions to optimizing energy efficiency, and avoid crosswinds and cloud cover to enhance navigational safety. Precipitation reduced departure probability, likely due to increased energetic costs and reduced foraging and orientation efficiency. We found a positive, but not significant, effect of increased temperatures on seasonal departures, while lunar phase had no detectable effect.

5.4 Seasonal and nocturnal patterns

Spring (March–June): Early spring migration (March–April) primarily involves individuals drifting from the European mainland (Belgium/France), while later migration (May–June) consists largely of bats originating from the United Kingdom. Telemetry data indicate that (likely pregnant) female bats predominantly cross in

May from the UK to the European mainland (Lagerveld et al 2024b), highlighting this period as particularly important for curtailment measures.

Autumn (August-November): Migration probability peaked in late August, dropped during mating, and rose again from mid-October, suggesting mating limits migration in early autumn. These movement patterns along the coast indicate multiple overlapping strategies such as migration to hibernation sites, barrier movements, and mating-related movements. At the end of the migration period females left earlier than males, and first year bats of both sexes tended to depart earlier than adults. Nearly all departures occur within two hours after sunset, although headwinds can delay departures. Overall, our findings indicate that the seasonal migration patterns in autumn are strongly modulated by reproductive behaviour, while their night-to-night departure decision is based on current atmospheric conditions.

This new knowledge leads to a number of recommendations in terms of next steps in mitigation measurements and future research presented in the following section.

6 Recommendations

From a precautionary perspective, the highest priority is to evaluate the current autumn curtailment measures and to develop corresponding strategies for the spring migration period. These actions can be implemented most quickly as mitigation measure. Following this, expanding the MOTUS network and conducting tagging studies along the coasts of France and Belgium, based on the outcomes of the curtailment evaluation, is recommended to rapidly increase our understanding of occurrence at sea of bats wintering on the mainland. In contrast, research on collision risk and potential attraction to offshore wind farms is relatively complex, relying on two relatively long-term academic projects that are already underway and partially operational. Consequently, these topics have the lowest priority in terms of timing, with their development proceeding autonomously.

6.1 Curtailment

A systematic review and evaluation of current curtailment practices is required to evaluate their actual effectiveness in reducing bat collision risk at offshore wind farms. Based on recent insights into bat migration and flight behaviour presented in this report, there is a clear rationale for extending the range of curtailed wind speeds during the autumn migration period, as bats appear to migrate under stronger tailwind conditions than previously assumed. In addition, practical "rules of thumb" should be developed for curtailment during spring migration, when information on offshore bat activity remains extremely limited. To achieve this, it is recommended to initiate a dedicated expert consultation process to refine and align curtailment strategies with the latest empirical evidence and modelling results.

6.2 Occurrence in space and time

Further research is needed to improve our understanding of spatial and temporal patterns of offshore bat occurrence at the North Sea. In particular, targeted tagging studies in northern France and Belgium during spring would provide crucial information on potential offshore movements from continental Europe towards the Dutch part of North Sea. Complementary monitoring in the northern North Sea, combining both acoustic and tracking methods as proven to be successful in reconstructing spatial origin and migratory pathways, is also recommended to assess the extent and timing of bat activity in the more northern offshore regions in the Dutch EEZ, given an expanding MOTUS network with sufficient coastal and offshore coverage, not only in the Dutch EEZ.

6.3 Flight paths

The routes taken by migratory bats during offshore migration influence their risk of becoming victims of offshore wind turbines. Flight paths are likely largely determined by wind, as bats adjust their flight direction, speed, and altitude to wind conditions. If flight paths can be reliably predicted based on wind conditions, and possibly other environmental factors, mitigation measures could likely be made more specific. This would improve bat protection while avoiding unnecessary curtailment. Predicting or modeling flight paths may also help to identify potential departure areas. This will be particularly useful for acoustically detected bats north of the Wadden Islands, as their origen is currently unknown.

6.4 Collision risk

To directly investigate collision risk, the use of thermal camera-based monitoring systems, such as those developed under the WIS-BirdSafe programme, should be considered to be applied on the short term to more offshore operating and future windfarms. These first two projects implementing these systems are now operational and provide a valuable opportunity to evaluate the detectability and frequency of bat collisions at offshore turbines under varying environmental conditions. The two ongoing projects will need to be further adapted for bat research through e.g. the deployment of passive acoustic bat detectors, which is planned to take place within the framework of the POWER project.

6.5 Attraction to offshore wind farms

Further research into the potential attraction of bats to offshore wind farm structures and lighting/skyglow is strongly recommended. This includes experimental studies investigating the underlying behavioural and sensory mechanisms driving attraction, for which a dedicated research proposal is currently being developed within the POWER project framework.

6.6 Coastal wind farms

Although ecological effects of coastal wind farms are not studied within the Wozep progam, this study reconfirms the importance of coastlines. Most migratory bats are recorded in coastal regions (Ahlén et al., 2009; Ijäs et al., 2017; Pētersons, 2004; Voigt et al., 2023). This coastal concentration is due to barrier effects, as Nathusius' pipistrelles follow shorelines to avoid large expanses of open water, and often perform back-and-forth movements along the coast while searching for a suitable location to cross the sea (Lagerveld et al., 2024). Movements during stopovers and mating activities result in additional flight activity.
Many wind farms have been constructed along the coast due to higher energy yields, even though this area is of great importance for migratory bats (and birds). It is therefore recommended to conduct further research into the spatiotemporal occurrence of bats and their collision risk in the coastal zone.

7 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system, certified since February 27, 2001 by DNV. ISO 9001 is an international standard for quality management, focused on the continuous improvement of processes and ensuring customer satisfaction.

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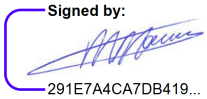
Justification

Report: C041/26
Project Number: 4315100245

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. M.J. Baptist Colleague scientist
Signature:	
Date:	May 4, 2026

Approved:	A.M. Mouissie, PhD Business Manager Projects
Signature:	
Date:	May 4, 2026

Annex 1 Supplementary files analysis 1 (chapter 2)

A1.1 Supplementary file 1: Trapping and tagging effort, processing MOTUS data and tracking results

A1.1.1 Trapping and tagging

Table SF1-1: trapping sessions

Date	Location	Start time [UTC]	End time	Duration [h]	Harp traps	Mist nets	Team*
29-03-21	Minsmere	18:25	22:00	03:35	2	3	JH, SP, EP
30-03-21	Minsmere	18:35	22:30	03:55	2	2	JH, SP, EP
04-04-21	Minsmere	18:45	21:30	02:45	2	2	JH, SP, EP
18-04-21	Minsmere	19:30	21:30	02:00	2	3	JH, SP, EP
19-04-21	Minsmere	19:20	21:00	01:40	2	2	JH, SP, EP
20-04-21	Minsmere	19:15	23:00	03:45	2	3	JH, SP, EP
27-04-21	Minsmere	19:15	23:34	04:19	3		JH, SP, EP
02-05-21	Minsmere	19:30	23:00	03:30	3		JH, SP, EP
07-05-21	Minsmere	19:30	21:55	02:25	3		JH, SP, EP
08-05-21	Minsmere	19:30	02:00	06:30	3		JH, SP, EP
10-05-21	Minsmere	19:35	00:30	05:00	3		JH, SP, EP
11-05-21	Minsmere	19:35	02:00	06:30	3		JH, SP, EP
12-05-21	Minsmere	19:40	23:45	04:05	3		JH, SP, EP
14-05-21	Minsmere	19:40	02:00	06:20	3		JH, SP, EP
05-04-22	Minsmere	19:40	23:00	03:20	3		JH, SP, EP
13-04-22	Minsmere	19:00	23:50	04:50	3		JH, SP, EP
14-04-22	Minsmere	19:00	00:30	05:30	3		JH, SP, EP
18-04-22	Minsmere	19:00	00:33	05:33	3		JH, SP, EP
19-04-22	Minsmere	19:15	22:00	02:45	3		JH, SP, EP, HP
30-04-22	Minsmere	19:30	00:00	04:30	5		JH, SP, EP, HP, ND
01-05-22	Minsmere	19:30	23:30	04:00	5		JH, SP, EP, HP, ND
04-05-22	Landguard	19:35	00:30	04:25	3		JH, SP, EP, HP
05-05-22	Landguard	19:35	00:30	04:25	3		JH, SP, EP, HP
10-05-22	Minsmere	19:50	01:30	05:40	3		JH, SP, EP, HP
30-03-23	Minsmere	18:25	21:55	03:30	4		JH, HP, ND
17-04-23	Minsmere	19:00	21:00	02:00	4		JH, HP, ND
22-04-23	Minsmere	19:05	23:30	04:25	5		JH, HP, ND
28-04-23	Minsmere	19:20	01:35	06:15	5		JH, HP, ND
29-04-23	Benacre	19:20	00:30	05:20	5		JH, HP, LP
30-04-23	Minsmere	19:30	02:30	07:00	5		JH, SP, EP, HP
01-05-23	Minsmere	19:30	02:00	06:30	5		JH, SP, EP, HP
02-05-23	Benacre	19:30	22:30	03:00	5		JH, SP, EP, HP
03-05-23	Minsmere	19:30	02:30	07:00	5		JH, SP, EP, HP
05-05-23	Benacre	19:30	01:00	05:30	5		JH, SP, EP, HP
07-05-23	Minsmere	19:30	02:30	07:00	5		JH, SP, EP, HP, ND
10-05-23	Minsmere	20:00	02:30	06:30	5		JH, SP, EP, HP

* JH = Jane Harris, SP = Sue Parsons, EP = Ewan Parsons, HP = Huma Pearce, ND = Nathan Duszynski, LP = Lotty Packman

Bats were trapped and tagged at Minsmere (N 52.24 E 1.62), Benacre National Nature Reserve (N 52.39 E 1.71) and the Landguard Bird Observatory (N 51.94 E 1.32). In total 36 trapping sessions were undertaken, lasting on average 4.5 hours (Table SF1-1).

Bats were captured with no. 2 and no. 3 Austbat harp traps (Faunatec, Australia) and mist nets (Solida, Germany) in combination with AT100 acoustic lures (Binary Acoustic Technology, United States) playing the advertisement calls of male Nathusius' pipistrelle. Traps were checked every 20 minutes, or sooner, mist nets were monitored continuously. Of each individual information on biometry (forearm length), sex, age (when possible) and reproductive status was gathered using the criteria described by Haarsma, 2008. Subsequently, a visual check for pregnancy, injuries, parasites or aberrations in fur and wing membranes was executed. Pregnant females, judged to be less than 2 weeks to parturition, were released immediately. Individuals lacking visible injuries, low ectoparasite load, healthy fur and wing membranes were qualified suitable for tagging. They were tagged only, when their weight exceeded 6 g. This minimum was employed, in accordance with Natural England guidance for the capture and marking of bats (guidance note WML-G39), to ensure that the weight of the radio-transmitter should not exceed 5% of the individual's body weight. To attach the radio-transmitter, fur was lightly clipped between the shoulder blades to create a small pocket (8 mm x 4 mm). The transmitter was affixed using medical adhesive (Torbot Group, United States). To ensure the transmitter was properly attached, tagged bats were held in cloth bags on heat pads and released as soon as the adhesive was set (after about 10 min). A total of 139 Nathusius' pipistrelles were trapped, of which 122 individuals were tagged.

A1.1.2 Processing of MOTUS data

Receiver metadata and transmitter detection data were retrieved (19 May 2025) from www.motus.org, using the Motus R package (Birds Canada, 2022). Detections with run lengths < 3 were filtered out, in accordance with the MOTUS R Book (Birds Canada, 2022). In addition, unlikely detections were removed from specific receivers at locations with high levels of radio noise (table SF1-2). The location of a receiver that detects the radio transmitter is used as an estimate for the bat's current location. If multiple receivers detect a signal from a particular transmitter within 30 seconds and are less than 10 km apart, the receiver with the strongest signal is considered the best approximation of the bat's location. When a bat moved from one receiver to another we assigned the departure and arrival timestamps when the strongest signals were received.

Tabe SF1-2: false positives

Deployment	Detections removed	Reason
43047	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.
43048	18/5/2023 26_Utlandshörn (#10968)	Detections during daylight hours
43052	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.
43046	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.
42442	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.
44997	all detections 123_Norderney 2 (#10283)	Lots of detections during a prolonged time (also during daylight hours)
31911	all detections WUR Texel NIOZ (#10258)	Multiple false positives of various species due the presence of many running (non-deployed) tags at the NIOZ office, very close to the receiver
31912	all detections WUR Texel NIOZ (#10258)	Multiple false positives of various species due the presence of many running (non-deployed) tags at the NIOZ office, very close to the receiver
31901	all detections Rysum 1 (#10282)	Multiple false positives of various species due the presence of many deployed tags in the immediate vicinity
31907	all detections Rysum 1 (#10282)	Multiple false positives of various species due the presence of many deployed tags in the immediate vicinity
31909	all detections 125_Norderney 4 (#10285)	Multiple false positives of various species due the presence of many deployed tags in the immediate vicinity
38491	12/6/2021 127_Woldsee 1 (#10555)	Multiple false positives of various species due the presence of many deployed tags in the immediate vicinity
31902	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.
39000	all detections 17_Fedderwardersiel (#11191)	A receiver in an area with a lot of radio activity nearby. Lots of detections during a prolonged time, also during daylight hours and from other deployments.

31905	19/5/2021 Minsmere2 (#12367)	Tag found in Sparrowhawk pellet and retrieved. Remarkably it was still functioning (and not switched off) and subsequently detected by several receivers over the next few days during fieldwork activities.
	21/5/2021 BM3-NPip_tracking (#11931)	
	23/5/2021 FB-Testing (#12097)	

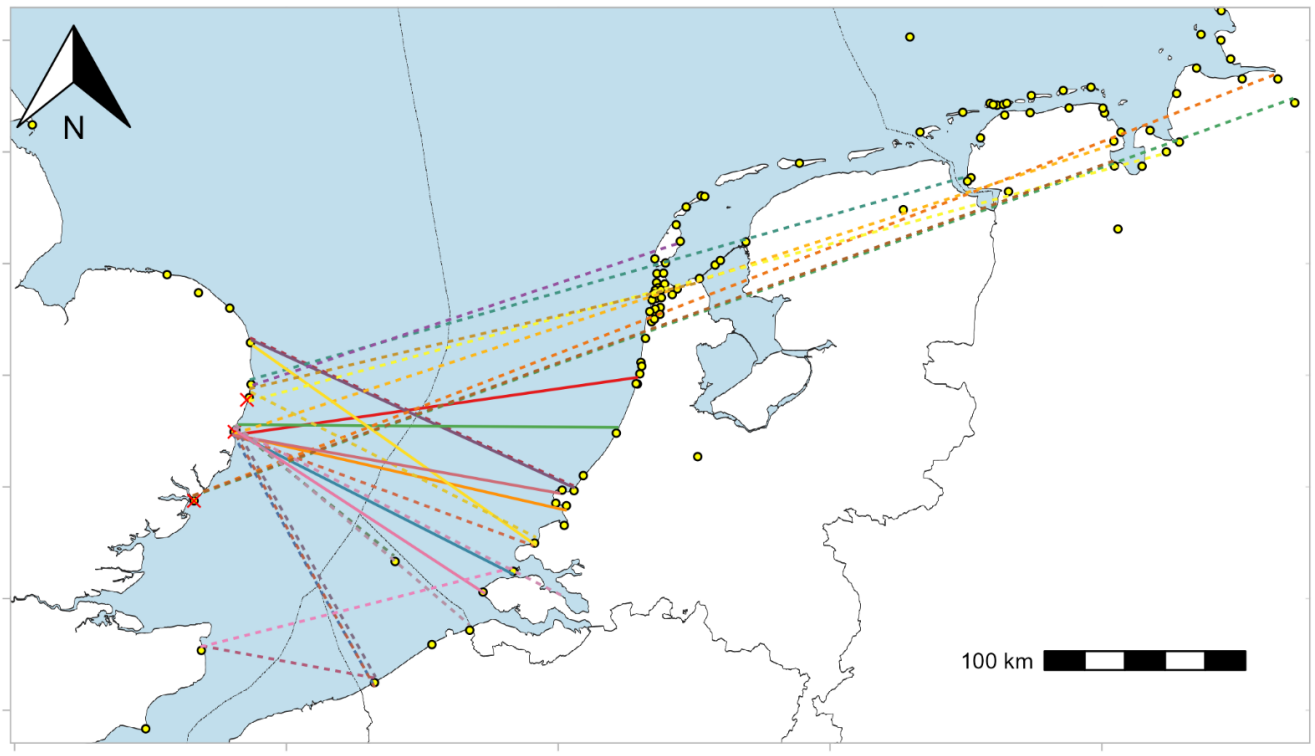
A1.1.3 Tracking results

In total, 122 bats were tagged, comprising 18 males and 104 females. The number of individuals tagged differed across years, with 20 in 2021, 24 in 2022, and 78 in 2023. Table SF1-3 shows where and when each individual (deployment) was tagged, its last detection in the UK and the first documented arrival on the European mainland.

Table SF 1-3: Time and location of tagging, last UK detection and first detection at the European mainland

Deployment	Sex	Tagged [UTC]	Lat/Long	Last UK [UTC]	Lat/Long	First mainland [UTC]	Lat/Long	Comments	Link
31861	F	2021-03-29 21:50	N 52.246 E 1.618	2021-05-02 20:13	N 52.247 E 1.615	2021-05-02 23:57	N 52.506 E 4.601	crossing night 2021-05-02	https://motus.org/data/tagDeployment?id=31861
31862	M	2021-04-20 21:00	N 52.247 E 1.619	2021-06-04 00:55	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31862
31863	M	2021-05-02 21:55	N 52.246 E 1.618	2021-06-04 23:14	N 52.247 E 1.615		N 52.247 E 1.615		https://motus.org/data/tagDeployment?id=31863
31864	M	2021-05-08 20:55	N 52.246 E 1.618	2021-06-13 22:52	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31864
31911	F	2021-05-08 22:25	N 52.246 E 1.618	2021-05-12 20:50	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31911
31912	F	2021-05-08 23:55	N 52.246 E 1.618	2021-05-12 23:25	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31912
31899	F	2021-05-09 00:20	N 52.246 E 1.618	2021-05-10 21:17	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31899
31900	F	2021-05-10 22:05	N 52.247 E 1.619	NA	NA			tag found detached 2021-05-10	https://motus.org/data/tagDeployment?id=31900
31901	F	2021-05-11 00:05	N 52.247 E 1.619	2021-05-25 00:45	N 52.247 E 1.615	2021-05-26 23:55	N 51.116 E 26.324	crossing night of 24, 25 or 26 May	https://motus.org/data/tagDeployment?id=31901
31902	F	2021-05-11 00:45	N 52.247 E 1.619	2021-05-16 22:23	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31902
31903	F	2021-05-11 22:00	N 52.247 E 1.619	2021-05-18 22:34	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31903
31904	F	2021-05-11 22:55	N 52.247 E 1.619	2021-05-17 20:42	N 52.247 E 1.615	2021-05-17 23:59	N 51.623 E 1.619	crossing night 2021-05-17	https://motus.org/data/tagDeployment?id=31904
31905	F	2021-05-12 01:52	N 52.247 E 1.619	NA	NA			Predated	https://motus.org/data/tagDeployment?id=31905
31906	F	2021-05-12 22:15	N 52.247 E 1.619	2021-05-29 00:41	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31906
31907	F	2021-05-13 00:35	N 52.247 E 1.619	2021-05-19 21:28	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31907
31908	F	2021-05-14 22:45	N 52.247 E 1.619	2021-05-25 21:20	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31908
31909	F	2021-05-15 00:15	N 52.247 E 1.619	2021-05-22 23:28	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=31909
31910	F	2021-05-15 00:35	N 52.247 E 1.619	2021-05-18 21:25	N 52.247 E 1.615	2021-05-20 21:22	N 53.369 E 7.011	first detection Germany early evening 2021-05-20. Consequently, crossing was in the night of 18 or 19 May	https://motus.org/data/tagDeployment?id=31910
31898	F	2021-05-15 01:40	N 52.247 E 1.619	2021-05-25 22:01	N 52.247 E 1.615	2021-05-26 01:22	N 51.991 E 4.124	crossing night 2021-05-25	https://motus.org/data/tagDeployment?id=31898
31897	F	2021-05-15 20:30	N 52.247 E 1.619	2021-05-24 21:55	N 52.247 E 1.615	2021-05-28 21:07	N 51.991 E 4.124	first detection in Netherlands early evening 2021-05-28. Consequently, crossing was in the night of 24, 25, 26 or 27 May	https://motus.org/data/tagDeployment?id=31897
38458	F	2022-04-13 20:20	N 52.247 E 1.619	2022-05-03 20:19	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38458
38459	F	2022-04-13 20:20	N 52.247 E 1.619	2022-05-02 20:15	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38459
38460	F	2022-04-13 21:40	N 52.247 E 1.619	2022-05-04 23:00	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38460
38491	F	2022-04-18 21:20	N 52.247 E 1.619	2022-04-20 22:02	N 51.940 E 1.327				https://motus.org/data/tagDeployment?id=38491
38492	F	2022-04-19 00:30	N 52.247 E 1.619	2022-05-01 23:23	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38492
35904	F	2022-04-22 20:45	N 52.247 E 1.619	2022-05-05 20:33	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=35904
35902	F	2022-04-30 20:50	N 52.247 E 1.619	2022-05-06 20:29	N 52.247 E 1.615	2022-05-07 01:09	N 52.247 E 4.433	crossing night 2022-05-06	https://motus.org/data/tagDeployment?id=35902
38862	F	2022-04-30 20:50	N 52.247 E 1.619	2022-05-04 20:32	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38862
38863	F	2022-05-01 18:00	N 52.247 E 1.619	2022-05-06 20:10	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38863
35903	M	2022-05-01 19:30	N 52.247 E 1.619	2022-05-24 21:46	N 52.247 E 1.615	2022-05-25 22:58	N 51.632 E 2.765	crossing night 2022-05-25 (detected at sea)	https://motus.org/data/tagDeployment?id=35903
38864	F	2022-05-01 20:45	N 52.247 E 1.619	2022-05-01 23:31	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38864
38865	F	2022-05-01 21:30	N 52.247 E 1.619	2022-05-06 23:26	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38865
38866	F	2022-05-01 22:00	N 52.247 E 1.619	2022-05-02 00:19	N 52.247 E 1.615	2022-05-06 21:02	N 53.100 E 4.898	crossing in the night of 2, 3, 4 or 5 May (crossing in the night of 1 May unlikely given the late detection , and early evening detection in the Netherlands on 6 May)	https://motus.org/data/tagDeployment?id=38866
38867	F	2022-05-01 22:00	N 52.247 E 1.619	2022-05-03 01:48	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38867
38872	F	2022-05-01 22:25	N 52.247 E 1.619	2022-05-06 20:52	N 51.362 E 1.375	2022-05-09 22:43	N 51.116 E 2.632	crossing in the night of 6, 7, 8 or 9 May	https://motus.org/data/tagDeployment?id=38872
38868	F	2022-05-01 22:30	N 52.247 E 1.619	2022-05-06 21:15	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=38868
38873	F	2022-05-01 22:30	N 52.247 E 1.619	2022-05-02 21:54	N 52.247 E 1.615	2022-05-06 20:22	N 51.759 E 3.845	crossing in the night of 2, 3, 4 or 5 May (early evening detection 6 May in the Netherlands)	https://motus.org/data/tagDeployment?id=38873
35905	F	2022-05-01 23:45	N 52.247 E 1.619	2022-05-06 20:07	N 52.247 E 1.615	2022-05-09 22:21	N 51.1156 E 2.638	crossing was in the night of 6, 7 or 8 May (crossing in the night of 9 May highly unlikely, given the low groundspeed of 16 km/h)	https://motus.org/data/tagDeployment?id=35905
35901	F	2022-05-05 22:15	N 51.938 E 1.320	2022-05-05 22:28	N 51.938 E 1.320	2022-05-13 01:45	N 53.300 E 5.078	first detection in Netherlands late night 2022-05-13. Consequently, crossing was in the night of 5, 6, 7, 8, 9, 10, 11 or 12 May	https://motus.org/data/tagDeployment?id=35901
38998	F	2022-05-05 23:05	N 51.938 E 1.320	2022-05-06 23:25	N 51.938 E 1.320				https://motus.org/data/tagDeployment?id=38998
39000	F	2022-05-05 23:10	N 51.938 E 1.320	2022-05-16 21:19	N 52.656 E 1.729				https://motus.org/data/tagDeployment?id=39000
39001	F	2022-05-05 23:40	N 51.938 E 1.320	2022-05-06 21:03	N 51.938 E 1.320	2022-05-11 23:06	N 53.630 E 9.589	crossing in the night of 6, 7, 8, 9 or 10 May (given the evening detection in Germany on 11 May)	https://motus.org/data/tagDeployment?id=39001
39006	M	2022-05-10 21:40	N 52.247 E 1.619	NA	NA			tag detached 2022-05-17	https://motus.org/data/tagDeployment?id=39006
39007	F	2022-05-11 02:10	N 52.247 E 1.619	2022-05-11 21:10	N 52.247 E 1.615	2022-05-12 00:00	N 51.893 E 4.037	crossing night 2022-05-11	https://motus.org/data/tagDeployment?id=39007
45000	M	2023-03-30 20:00	N 52.247 E 1.619	2023-04-29 20:16	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=45000
42291	M	2023-04-28 21:30	N 52.247 E 1.619	2023-05-27 23:46	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=42291
42267	F	2023-04-28 22:00	N 52.247 E 1.619	2023-05-28 02:10	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=42267
42210	F	2023-04-28 23:15	N 52.247 E 1.619	2023-04-30 21:17	N 52.459 E 1.740				https://motus.org/data/tagDeployment?id=42210
43266	F	2023-04-29 00:15	N 52.247 E 1.619	2023-05-07 23:56	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=43266
43271	F	2023-04-29 00:30	N 52.247 E 1.619	2023-04-29 20:50	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=43271
43270	F	2023-04-29 01:00	N 52.247 E 1.619	2023-04-29 20:01	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=43270
43272	F	2023-04-29 01:15	N 52.247 E 1.619	2023-05-04 22:08	N 52.459 E 1.740	2023-05-05 23:14	N 52.934 E 5.039	crossing night 2023-05-04, as detected relatively early in the night in the Netherlands about 25 km inland on 5 May	https://motus.org/data/tagDeployment?id=43272
42325	F	2023-04-29 22:30	N 52.387 E 1.707	2023-05-10 21:03	N 52.459 E 1.740				https://motus.org/data/tagDeployment?id=42325
43051	F	2023-04-29 22:50	N 52.387 E 1.707	2023-05-10 21:04	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=43051

Deployment	Sex	Tagged [UTC]	Lat/Long	Last UK [UTC]	Lat/Long	First mainland [UTC]	Lat/Long	Comments	Link
43047	F	2023-04-30 00:15	N 52.387 E 1.707	2023-04-30 00:25	N 52.386 E 1.708	2023-05-08 22:28	N 53.501 E 8.475	crossing in the night of 1 - 7 May (30 April unlikely and 8 May not feasible, as detected relatively early in the evening in Germany)	https://motus.org/data/tagDeployment?id=43047
43054	F	2023-04-30 21:30	N 52.247 E 1.619	2023-05-14 23:13	N 52.801 E 1.583				https://motus.org/data/tagDeployment?id=43054
43053	F	2023-04-30 22:00	N 52.247 E 1.619	2023-05-24 01:15	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=43053
43273	F	2023-04-30 22:15	N 52.247 E 1.619	2023-05-04 21:47	N 51.938 E 1.320	2023-05-08 22:05	N 53.437 E 8.092	crossing in the night of 4, 5, 6 or 7 May	https://motus.org/data/tagDeployment?id=43273
42265	F	2023-04-30 22:45	N 52.247 E 1.619	2023-05-09 20:50	N 50.917 E 0.965			this bat crossed from Dunwich to Koksijde in the night of 2023-05-01, and returned to the UK (Dungeness) the same night!	https://motus.org/data/tagDeployment?id=42265
43049	M	2023-04-30 23:15	N 52.247 E 1.619	2023-05-10 21:09	N 52.400 E 1.727	2023-05-11 20:01	N 51.749 E 3.826	crossing night 2023-05-10	https://motus.org/data/tagDeployment?id=43049
43048	F	2023-04-30 23:45	N 52.247 E 1.619	2023-05-04 21:55	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=43048
43050	M	2023-05-01 00:15	N 52.247 E 1.619	2023-05-04 20:50	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=43050
43052	F	2023-05-01 00:45	N 52.247 E 1.619	2023-05-14 21:30	N 52.801 E 1.583				https://motus.org/data/tagDeployment?id=43052
43046	F	2023-05-01 00:50	N 52.247 E 1.619	2023-05-14 21:25	N 52.646 E 1.736	2023-05-15 02:24	N 51.749 E 3.826	crossing night 2023-05-14	https://motus.org/data/tagDeployment?id=43046
42438	F	2023-05-01 01:15	N 52.247 E 1.619	2023-05-04 22:45	N 52.253 E 1.628	2023-05-28 00:41	N 53.548 E 8.088	crossing in the night between 4 - 27 May (given the detection in Germany in the night of 28 May)	https://motus.org/data/tagDeployment?id=42438
43055	F	2023-05-01 01:30	N 52.247 E 1.619	2023-05-05 20:24	N 52.801 E 1.583				https://motus.org/data/tagDeployment?id=43055
42440	F	2023-05-01 22:00	N 52.247 E 1.619	2023-05-04 22:41	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=42440
42442	M	2023-05-01 22:10	N 52.247 E 1.619	2023-05-04 22:13	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=42442
43058	F	2023-05-01 21:50	N 52.247 E 1.619	2023-05-08 20:14	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=43058
43056	M	2023-05-01 22:50	N 52.247 E 1.619	2023-05-14 20:45	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=43056
43057	F	2023-05-01 22:55	N 52.247 E 1.619	2023-05-10 21:25	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=43057
42237	F	2023-05-02 01:00	N 52.247 E 1.619	2023-05-26 22:42	N 52.801 E 1.583				https://motus.org/data/tagDeployment?id=42237
45001	F	2023-05-02 02:30	N 52.247 E 1.619	2023-05-02 03:00	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=45001
43269	F	2023-05-02 21:00	N 52.387 E 1.707	2023-05-16 21:35	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=43269
45002	F	2023-05-03 21:00	N 52.247 E 1.619	2023-05-04 22:03	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=45002
45003	M	2023-05-03 21:45	N 52.247 E 1.619	2023-05-04 23:36	N 52.459 E 1.740				https://motus.org/data/tagDeployment?id=45003
45004	F	2023-05-03 23:30	N 52.247 E 1.619	2023-05-27 23:08	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=45004
45005	F	2023-05-04 01:00	N 52.247 E 1.619	2023-05-15 21:55	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45005
45006	F	2023-05-04 01:45	N 52.247 E 1.619	2023-05-23 22:58	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45006
45008	F	2023-05-04 01:50	N 52.247 E 1.619	2023-05-19 22:59	N 51.599 E 0.936				https://motus.org/data/tagDeployment?id=45008
45009	F	2023-05-04 01:55	N 52.247 E 1.619	2023-06-02 23:20	N 51.938 E 1.320				https://motus.org/data/tagDeployment?id=45009
45010	M	2023-05-04 02:00	N 52.247 E 1.619	2023-06-02 22:15	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45010
45011	F	2023-05-04 02:05	N 52.247 E 1.619	2023-05-13 23:08	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=45011
45012	F	2023-05-04 02:15	N 52.247 E 1.619	2023-05-08 00:57	N 52.801 E 1.583				https://motus.org/data/tagDeployment?id=45012
45013	F	2023-05-04 02:20	N 52.247 E 1.619	2023-05-15 20:57	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45013
45014	F	2023-05-04 02:30	N 52.247 E 1.619	2023-05-05 20:37	N 52.247 E 1.615	2023-05-17 21:44	N 51.489 E 4.057	crossing in the night between 5 - 16 May (given the relatively early detection at Yerseke in the evening of 17 May)	https://motus.org/data/tagDeployment?id=45014
45016	F	2023-05-04 02:30	N 52.247 E 1.619	2023-05-05 20:50	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45016
45017	F	2023-05-05 21:10	N 52.387 E 1.707	2023-05-10 21:02	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=45017
45018	F	2023-05-05 21:20	N 52.387 E 1.707	2023-05-15 21:11	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=45018
45019	F	2023-05-05 21:30	N 52.387 E 1.707	2023-05-05 23:21	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=45019
45020	F	2023-05-05 22:00	N 52.387 E 1.707	2023-05-05 23:38	N 52.459 E 1.740				https://motus.org/data/tagDeployment?id=45020
45021	F	2023-05-05 22:15	N 52.387 E 1.707	2023-05-05 23:15	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=45021
45022	F	2023-05-05 22:30	N 52.387 E 1.707	2023-05-06 00:24	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=45022
45023	F	2023-05-05 22:45	N 52.387 E 1.707	2023-05-28 00:36	N 51.938 E 1.320				https://motus.org/data/tagDeployment?id=45023
45024	F	2023-05-05 22:50	N 52.387 E 1.707	2023-05-17 01:44	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=45024
45025	F	2023-05-06 00:30	N 52.387 E 1.707	2023-05-08 22:20	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45025
45026	F	2023-05-07 20:45	N 52.247 E 1.619	2023-05-15 20:35	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=45026
45027	F	2023-05-07 21:45	N 52.247 E 1.619	2023-05-23 23:35	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=45027
45028	F	2023-05-07 21:50	N 52.247 E 1.619	2023-05-21 21:12	N 52.253 E 1.628	2023-05-25 00:13	N 51.358 E 3.349	crossing in the night of 21, 22, 23 or 24 May	https://motus.org/data/tagDeployment?id=45028
45029	F	2023-05-07 22:10	N 52.247 E 1.619	2023-06-02 22:05	N 51.938 E 1.320				https://motus.org/data/tagDeployment?id=45029
44980	F	2023-05-07 22:30	N 52.247 E 1.619	2023-05-15 20:52	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44980
44981	M	2023-05-07 22:45	N 52.247 E 1.619	2023-06-04 01:34	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44981
44982	F	2023-05-07 22:50	N 52.247 E 1.619	2023-05-20 02:22	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=44982
44984	F	2023-05-07 22:55	N 52.247 E 1.619	2023-05-10 21:08	N 52.253 E 1.628	2023-05-14 22:34	N 51.124 E 2.648	crossing in the night of 10, 11, 12, 13 or 14 May	https://motus.org/data/tagDeployment?id=44984
44983	M	2023-05-07 23:00	N 52.247 E 1.619	2023-05-19 20:49	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44983
44988	F	2023-05-07 23:10	N 52.247 E 1.619	2023-05-08 00:40	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=44988
44987	F	2023-05-07 23:20	N 52.247 E 1.619	2023-05-22 20:44	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44987
44986	F	2023-05-07 23:30	N 52.247 E 1.619	2023-05-15 22:05	N 50.917 E 0.965				https://motus.org/data/tagDeployment?id=44986
44989	F	2023-05-08 00:40	N 52.247 E 1.619	2023-05-14 23:06	N 51.938 E 1.320				https://motus.org/data/tagDeployment?id=44989
44990	F	2023-05-08 01:10	N 52.247 E 1.619	2023-05-08 01:35	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=44990
44991	F	2023-05-08 01:20	N 52.247 E 1.619	2023-05-11 02:25	N 51.2678 E 1.3743				https://motus.org/data/tagDeployment?id=44991
44992	F	2023-05-08 02:00	N 52.247 E 1.619	2023-05-14 21:11	N 52.247 E 1.615				https://motus.org/data/tagDeployment?id=44992
44993	F	2023-05-08 02:40	N 52.247 E 1.619	2023-05-08 21:05	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44993
44995	F	2023-05-10 22:45	N 52.247 E 1.619	2023-05-20 21:47	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44995
44996	F	2023-05-10 22:50	N 52.247 E 1.619	2023-05-21 22:49	N 52.386 E 1.708				https://motus.org/data/tagDeployment?id=44996
45007	M	2023-05-10 22:50	N 52.247 E 1.619	2023-06-11 00:25	N 51.2678 E 1.3743	2023-06-15 00:27	N 51.622 E 3.669	crossing in the night of 11, 12, 13, 14 or 15 June	https://motus.org/data/tagDeployment?id=45007
44994	F	2023-05-11 01:00	N 52.247 E 1.619	2023-05-14 20:58	N 52.253 E 1.628	2023-05-15 01:36	N 51.983 E 4.116	crossing night 2023-05-14	https://motus.org/data/tagDeployment?id=44994
44997	F	2023-05-11 01:40	N 52.247 E 1.619	2023-05-16 21:21	N 52.400 E 1.727				https://motus.org/data/tagDeployment?id=44997
44998	F	2023-05-11 02:10	N 52.247 E 1.619	2023-05-16 20:22	N 52.253 E 1.628	2023-05-17 01:02	N 51.529 E 3.447	crossing night 2023-05-16	https://motus.org/data/tagDeployment?id=44998
44999	F	2023-05-11 02:40	N 52.247 E 1.619	2023-05-17 22:32	N 52.646 E 1.736				https://motus.org/data/tagDeployment?id=44999
45015	M	2023-05-11 02:45	N 52.247 E 1.619	2023-05-14 23:18	N 52.459 E 1.740				https://motus.org/data/tagDeployment?id=45015
44985	M	2023-05-11 02:45	N 52.247 E 1.619	2023-06-04 00:42	N 52.253 E 1.628				https://motus.org/data/tagDeployment?id=44985



A total of 27 bats was detected on the European mainland, excluding deployment 42265. This individual crossed the North Sea in the night of 1 May 2023 twice: from Dunwich (UK) to Koksijde in Belgium (min. 144 km) and back to Dungeness (UK) (min. 120 km). Figure SF1-1 shows the movements between the last detection in the UK and the first detection on the European mainland. Note that the shortest distance between the receivers is shown, which not necessarily reflects the actual flight path between the receivers.

Figure SF 1-1: Movements of Nathusius' pipistrelles included in the analysis (n=27). MOTUS receivers are indicated as yellow dots, tagging locations in red. Solid lines represent movements occurring within a single night, while dotted lines indicate movements over multiple nights.

A1.2 Supplementary file 2: Acoustic monitoring equipment, monitoring locations and raw data processing

A1.2.1 Equipment

Acoustic bat activity was monitored with an Avisoft - UltraSoundGate 116Hnbm in combination with a omnidirectional electret ultrasound microphone FG-DT50 (Avisoft Bioacoustics, Germany). The settings of the UltraSoundGate recording software (RECORDER v. 4.2.29) are shown in Table SF2-1.

Table SF2-1 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 horizontal-mounted microphone was enclosed in a waterproof box (figure SF2-1) and connected with the soundgate through a S/FTP Cat 7 Marine Approved network cable at the monitoring locations Petrogas P9-A (Horizon) and Petrogas Q1-A (Helder). At all other monitoring locations a 2Triple x 0.75mm2 (CI2 TCC) RFOU(I)S1/S6 EPR/ICM/ZHAL/TCWB/ZHAL BLUE 250v cable was used.
The performance of the equipment was checked once per week at the monitoring locations with internet connectivity (C-Power, Belwind, Lichteiland Goeree, Dana P11-B, Luchterduinen, Petrogas P9-A, PAWP, Petrogas Q1-A, Neptune K12-B & Neptune L10A-AC). The performance of the equipment at locations without internet connection (Europlatform, Wintershall P6-A & Wintershall K13-A) could not be checked regularly. At all locations, the microphones were replaced just before the spring migration season (late February/early March), and subsequently recalibrated by the manufacturer (Avisoft Bioacoustics).

A1.2.2 Monitoring locations

We monitored at four offshore high voltage stations (OHVS) in wind farms (C-Power, Belwind, Luchterduinen, and PAWP), two measurement platforms (Europlatform and Lichteiland Goeree) and seven gas production platforms (Dana P11-B, Petrogas P9-A, Wintershall P6-A, Petrogas Q1-A, Wintershall K13-A, Neptune K12-BP and Neptune L10A-AC). The microphone was positioned at heights between 15 and 33 meters above sea level (mean height 21 meters). If technically feasible, the microphone was orientated in an easterly direction to minimize salt spray during strong westerlies (table SF2-2).

Figure SF2-1: Acoustic monitoring at Lichteiland Goeree

Table SF2-2 Geographical location of the monitoring locations, height and orientation of the microphones

Monitoring location	Longitude	Latitude	Height above sea level [m]	Orientation microphone [degrees from N]
C-power OHVS	2.99	51.57	15	60
Belwind OHVS	2.81	51.69	20	90
Europlatform	3.27	51.99	15	90
Lichteiland Goeree	3.66	51.92	15	90
Dana P11-B	3.34	52.35	25	90
Luchterduinen OHVS	4.17	52.40	15	90
Petrogas P9-A (Horizon)	3.74	52.55	33	45
PAWP OHVS	4.23	52.58	15	90
Wintershall P6-A	3.75	52.75	23	110
Petrogas Q1-A (Helder)	4.09	52.92	25	200
Wintershall K13-A	3.22	53.05	25	130
Neptune K12-BP	3.89	53.34	20	135
Neptune L10A-AC	4.20	53.40	17	90

Monitoring was executed from March until June during four consecutive years (2018-2021). In some cases downtime occurred due to malfunctioning equipment or logistical problems. The effective monitoring periods are shown in table SF2-3.

Table SF2-3 Effective monitoring periods per location per year

Monitoring location	2018	2019	2020	2021
C-power OHVS	01/03 - 30/06	01/03 - 30/06	21/06 - 30/06	01/03 - 30/06
Belwind OHVS	01/03 - 30/06	01/03 - 30/06	01/03 - 30/06	-
Europlatform	06/03 - 30/06	01/03 - 30/06	01/03 - 17/05	26/05 - 30/06
Lichteiland Goeree	06/03 - 30/06	09/05 - 30/06	24/06 - 30/06	03/03 - 10/03 22/04 - 02/05
Dana P11-B	-	01/03 - 27/06	01/03 - 06/06	01/03 - 30/06
Luchterduinen OHVS	04/04 - 30/06	01/03 - 30/06	06/04 - 12/06	05/03 - 07/05
Petrogas P9-A (Horizon)	-	01/03 - 30/06	01/03 - 08/06	06/03 - 30/06
PAWP OHVS	01/03 - 30/06	01/03 - 30/06	04/03 - 30/06	01/03 - 30/06
Wintershall P6-A	18/03 - 30/06	01/03 - 30/06	01/03 - 04/06	16/03 - 30/06
Petrogas Q1-A (Helder)	-	01/03 - 30/06	01/03 - 30/06	01/03 - 12/05
Wintershall K13-A	-	01/03 - 30/06	-	-
Neptune K12-BP	01/03 - 30/06	01/03 - 30/06	18/03 - 31/05	20/03 - 17/06
Neptune L10A-AC	01/03 - 30/06	01/03 - 30/06	21/03 - 08/04	-

A1.2.3 Processing of raw acoustic data

Bats use echolocation to capture prey and to get an image of their environment. Wind gusts or maintenance and production activities at offshore platforms, however, also produce ultrasonic sounds. The first step in post-processing raw acoustic data is the separation of recordings with bat calls from recordings with other sound sources. We extracted bat call recordings from the raw acoustic data with the cross-correlation function of Avisoft SASlab Pro, version 5.2.14 (Avisoft bioacoustics), using recordings of reference calls of Nathusius' pipistrelle (n = 8), Common pipistrelle P. pipistrellus (n = 4), Pond bat Myotis dasycneme (n = 4), Common noctule Nyctalus noctula (n = 18), Serotine bat Eptesicus serotinus (n = 5) and the Nyctaloid group (n = 31, including the genera Nyctalus, Vespertilio, Eptesicus). Subsequently, each bat call was individually assessed and identified to the lowest possible taxonomic level, according to the criteria of (Barataud, 2020). Using visual inspection of the spectrograms of the recordings, feeding buzzes/intense exploration echolocation calls were identified (cf. Barataud, 2020), and subsequently verified by listening to the recordings.

A1.3 Supplementary file 3: Acoustic bat activity

Figure SF3-1 shows the bat occurrence of the 172 distinguished individuals for all monitoring locations throughout the season and the night for each monitoring year.

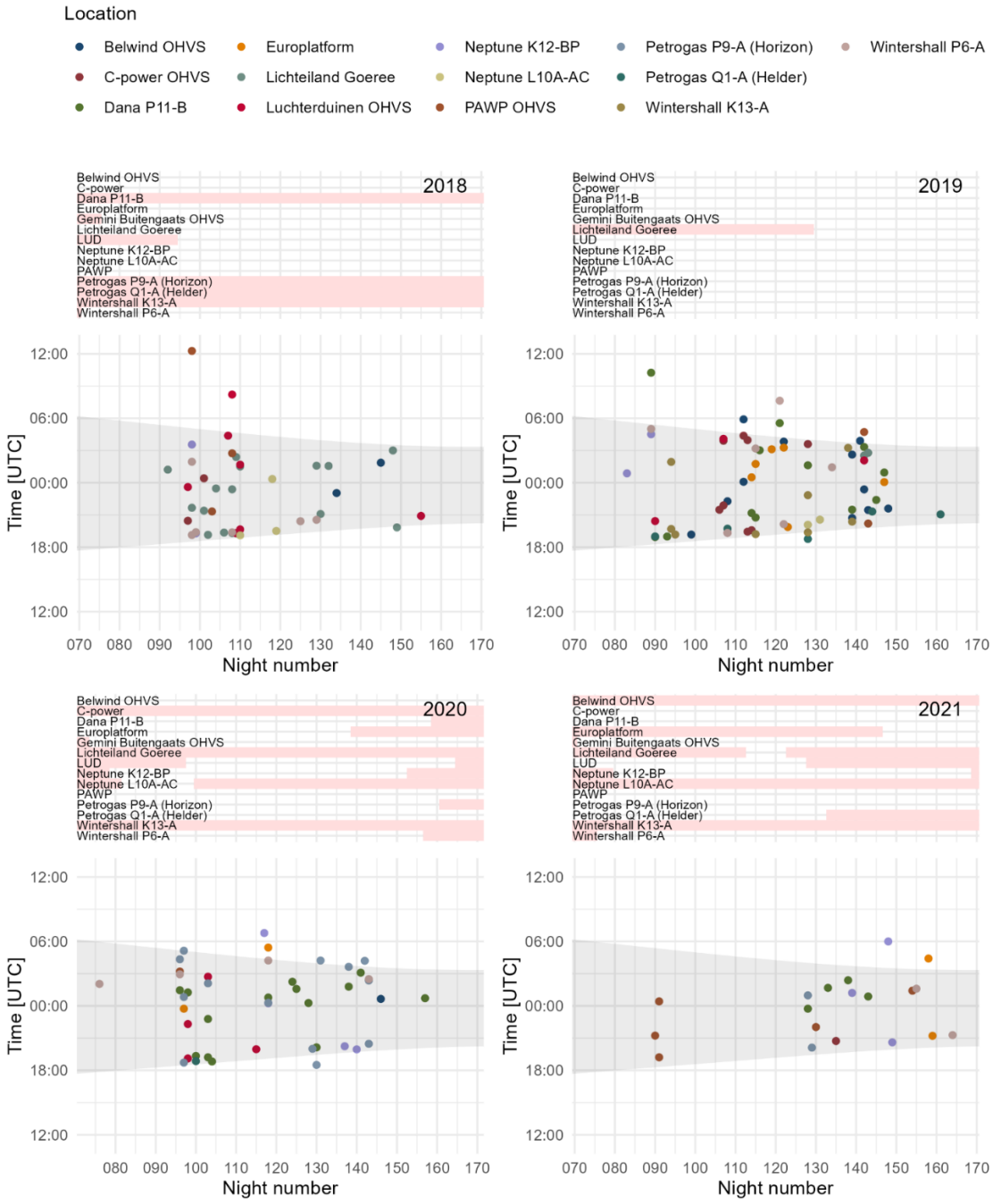


Figure SF3-1: Bat occurrence throughout the night (time interval between sunset and sunrise is represented by grey) and the season for all monitoring locations (2018-2021). The effective monitoring periods per location are indicated in the headers with a white background, whereas the pink background indicates no monitoring. The dots represent the timestamp of the first recording of each individual.

Figure SF3-2 shows the bat occurrence in the first half of the night (until midnight) in relation to the sunset and figure SF3-3 shows the occurrence in the second half of the night (after midnight) in relation to the sunrise. The timestamp of the first recording of each individual is used to determine the timeframe between sunset and sunrise respectively.

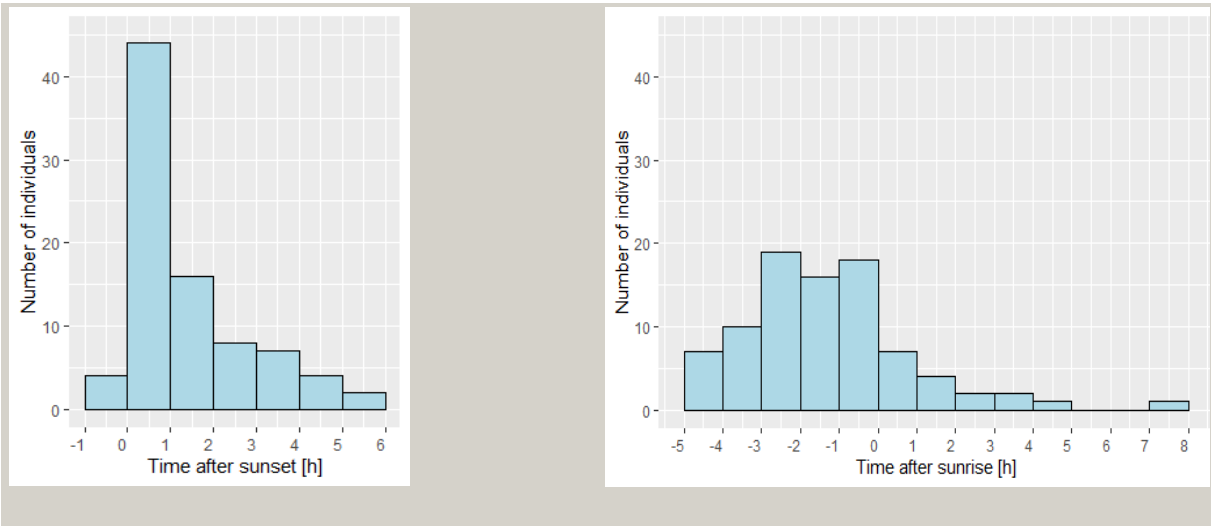


Figure SF3-2: Histogram of bat occurrence before midnight [UTC] in relation to sunset, using the timestamp of the first recording for each individual

Figure SF3-3: Histogram of bat occurrence after midnight [UTC] in relation to sunrise, using the timestamp of the first recording for each individual

Figure SF3-4 shows the staging times of the distinguished individual bats.

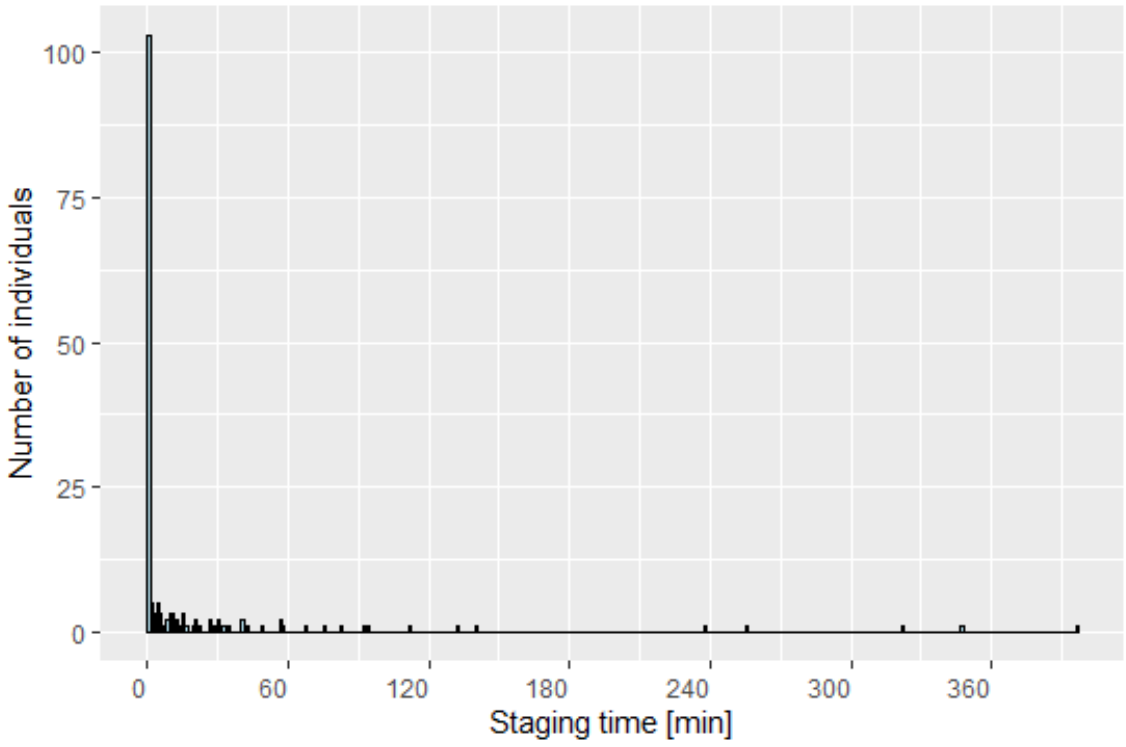


Figure SF3-4: Histogram of staging times.

Figures SF3-5 – SF3-48 show the recorded acoustic presence of Nathusius' pipistrelle per monitoring location for each year. A total of 2777 Nathusius' pipistrelle recordings were obtained of which 152 (5.5%) contained feeding buzzes/intense exploration calls. Blue dots refer to recordings with exclusively echolocation calls, while red dots represent recordings with one or more feeding buzzes/intense exploration echolocation calls. The effective monitoring period is indicated by a white background, whereas a pink background indicates no monitoring. The time interval between sunset and sunrise is represented by grey. See supplementary file 1 for details on the monitoring locations.

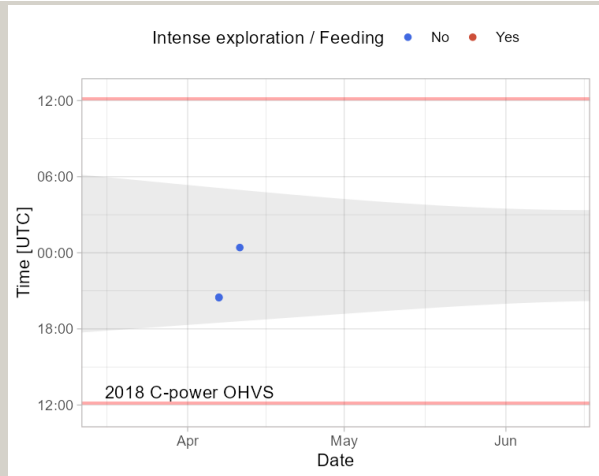


Figure SF3-5: Recorded acoustic presence of Nathusius' pipistrelle - spring 2018 at C-Power OHVS

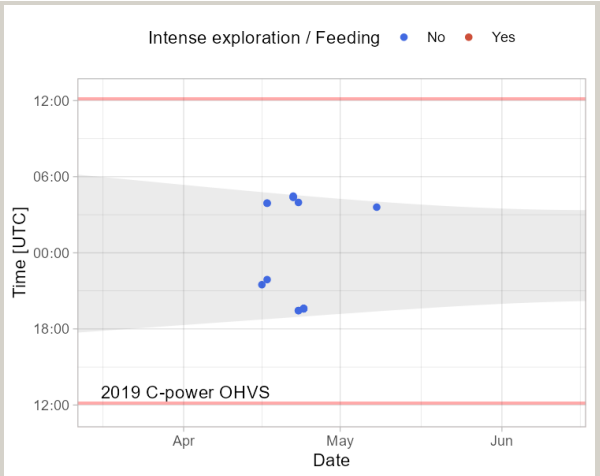


Figure SF3-6: Recorded acoustic presence of Nathusius' pipistrelle - spring 2019 at C-Power OHVS

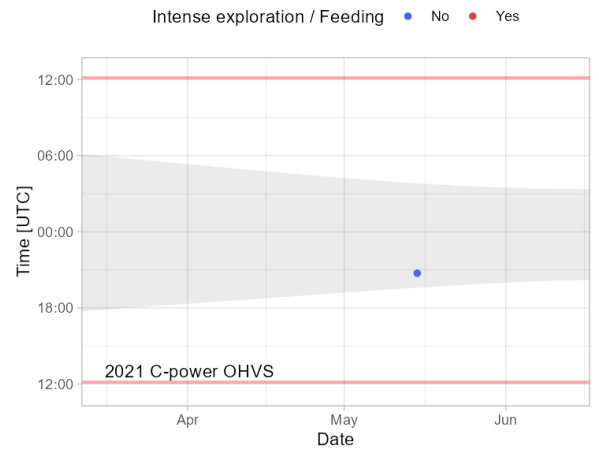


Figure SF3-7: Recorded acoustic presence of Nathusius' pipistrelle - spring 2021 at C-Power OHVS

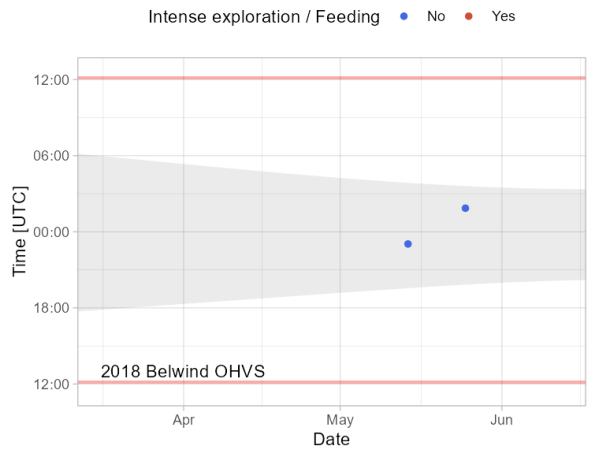


Figure SF3-8: Recorded acoustic presence of Nathusius' pipistrelle - spring 2018 at Belwind OHVS

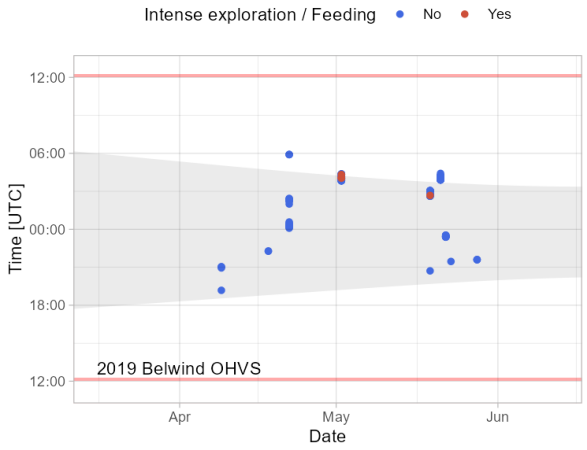


Figure SF3-9: Recorded acoustic presence of Nathusius' pipistrelle - spring 2019 at Belwind OHVS

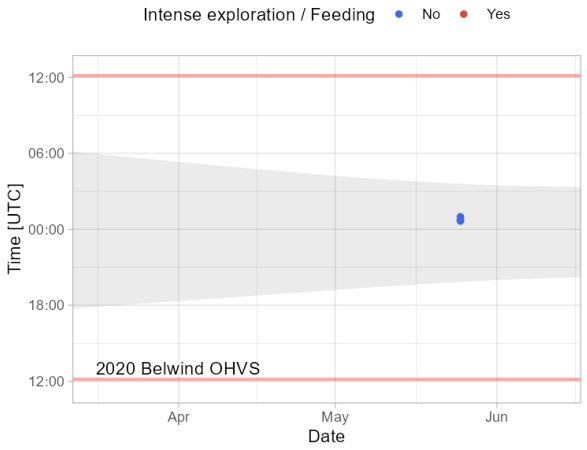


Figure SF3-10: Recorded acoustic presence of Nathusius' pipistrelle - spring 2020 at Belwind OHVS

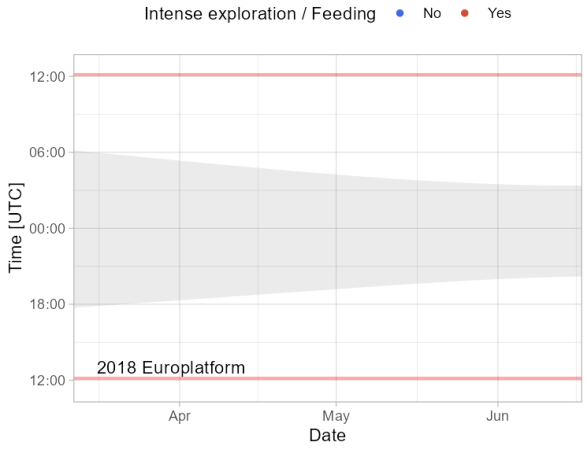


Figure SF3-11: Recorded acoustic presence of Nathusius' pipistrelle - spring 2018 at Europlatform

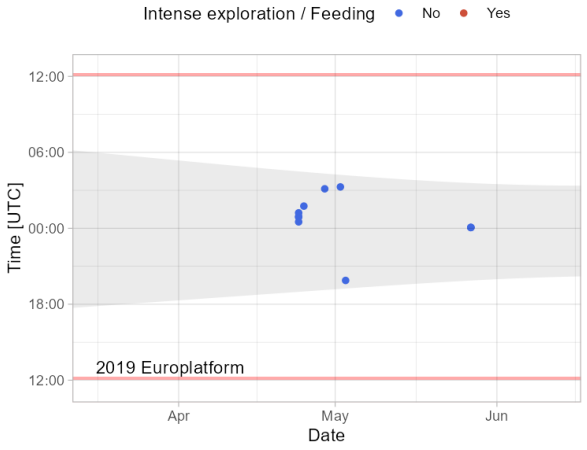
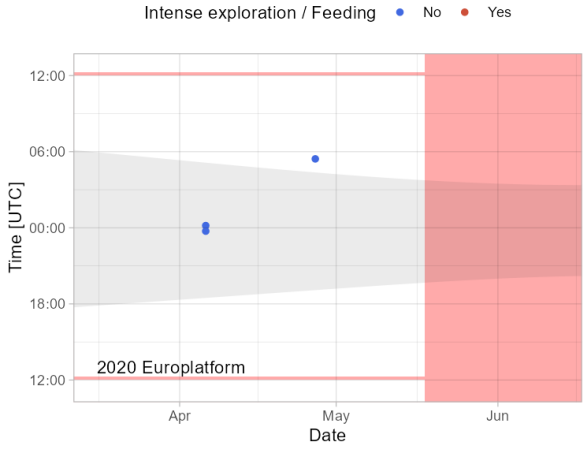


Figure SF3-12: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Europlatform



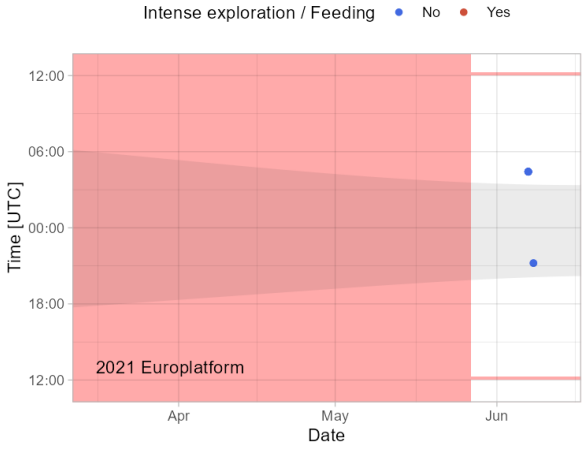


Figure SF3-13: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Europlatform

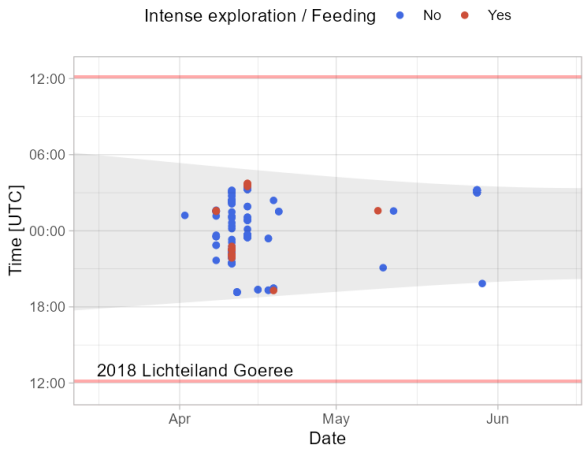


Figure SF3-14: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Europlatform

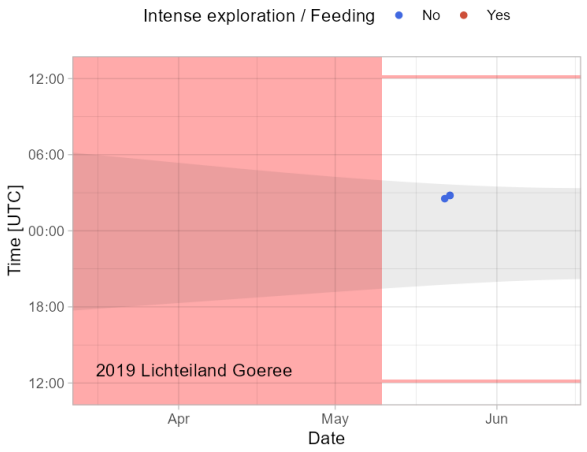
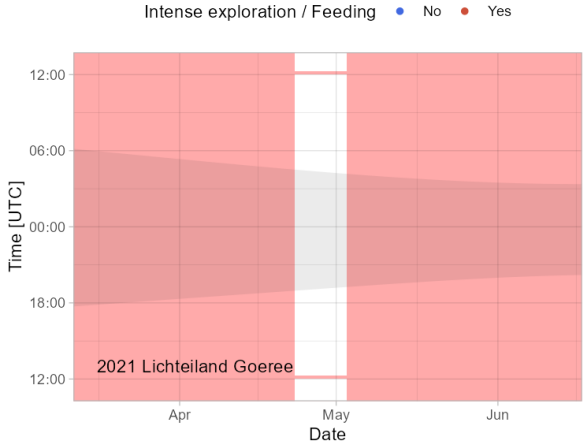


Figure SF3-15: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at Lichteiland Goeree

Figure SF3-16: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Lichteiland Goeree



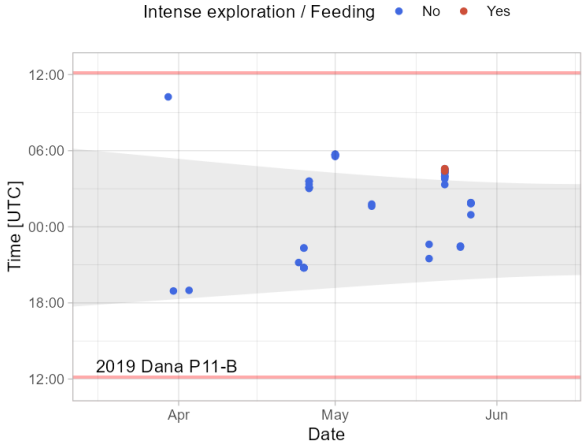


Figure SF3-17: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Lichteiland Goeree

Figure SF3-18: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Dana P11-B

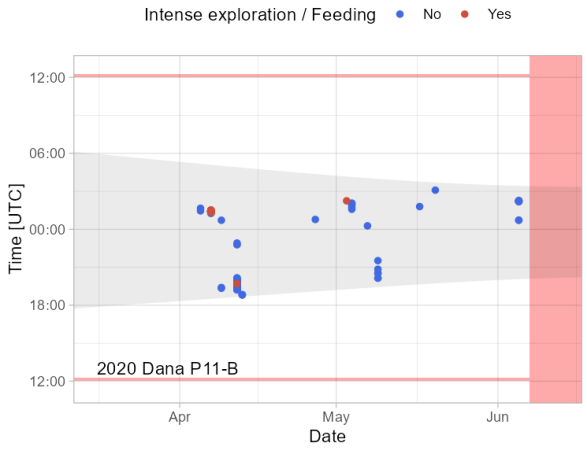


Figure SF3-19: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Dana P11-B

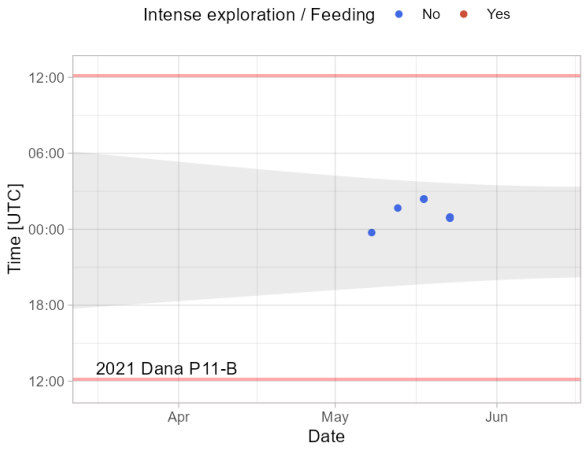


Figure SF3-20: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Dana P11-B

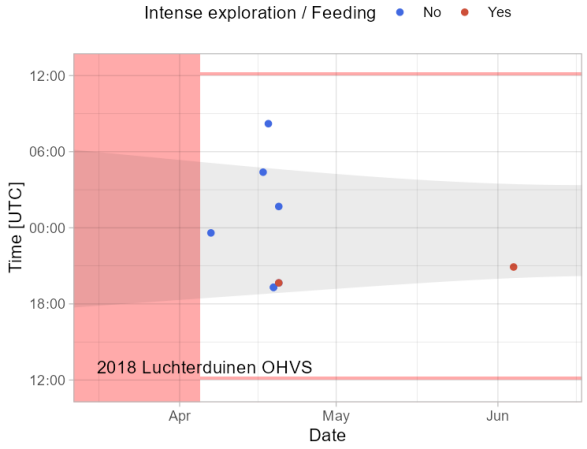


Figure SF3-21: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at Luchterduinen OHVS

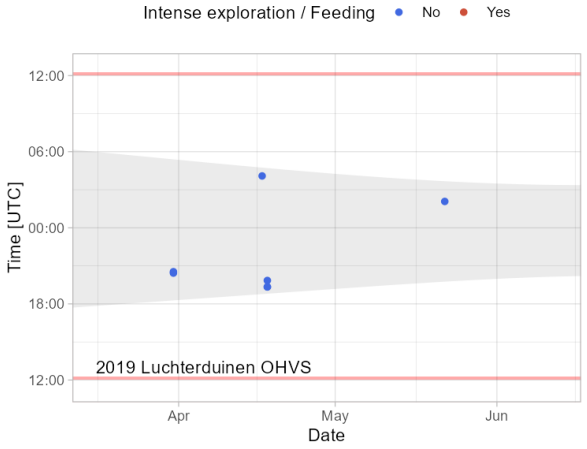


Figure SF3-22: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Luchterduinen OHVS

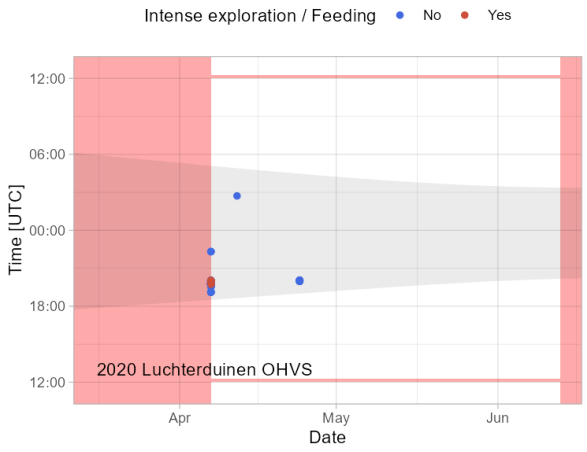


Figure SF3-23: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Luchterduinen OHVS

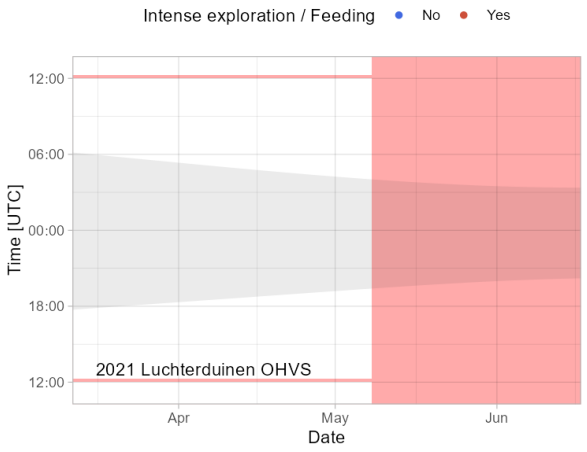


Figure SF3-24: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Luchterduinen OHVS

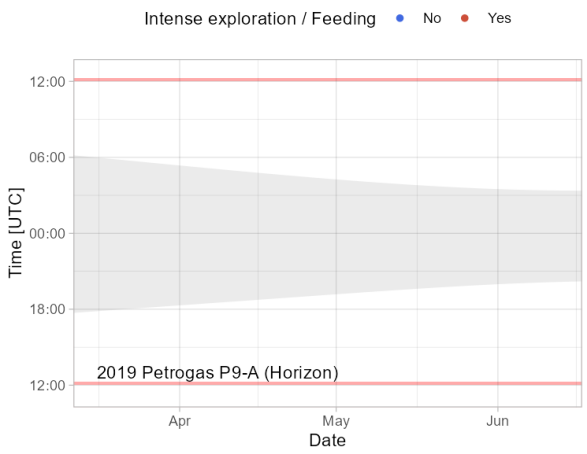


Figure SF3-25: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Petrogas P9-A (Horizon)

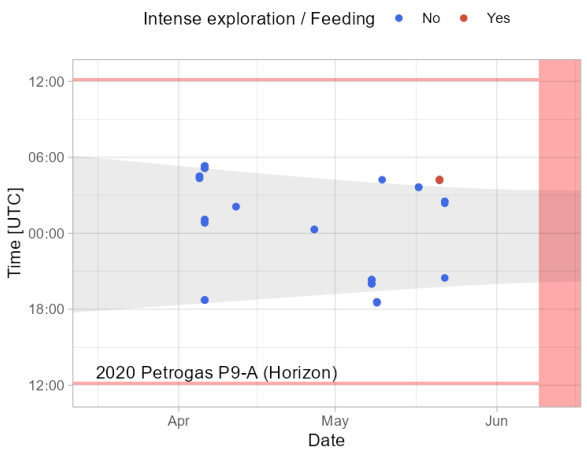


Figure SF3-26: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Petrogas P9-A (Horizon)

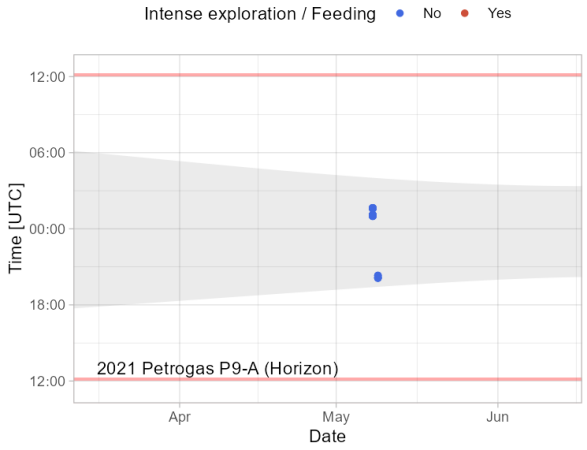


Figure SF3-27: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Petrogas P9-A (Horizon)

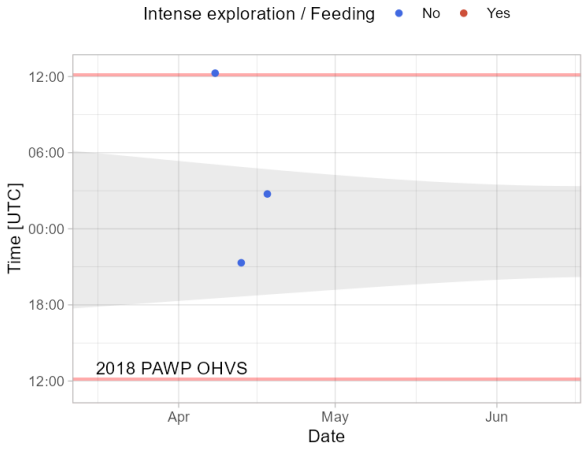
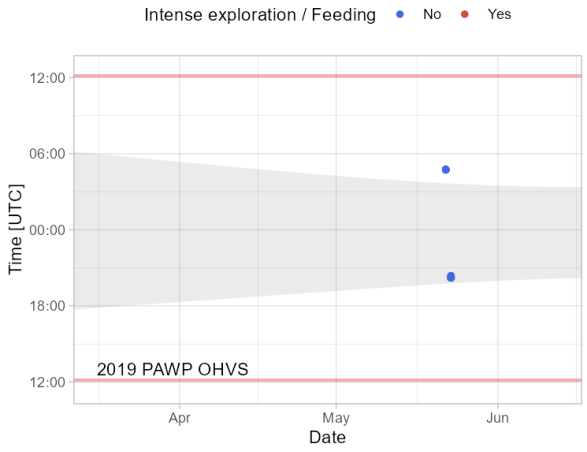


Figure SF3-28: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at PAWP



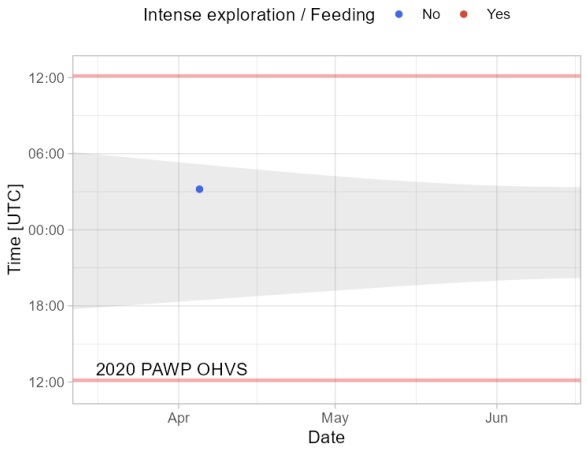


Figure SF3-29: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at PAWP

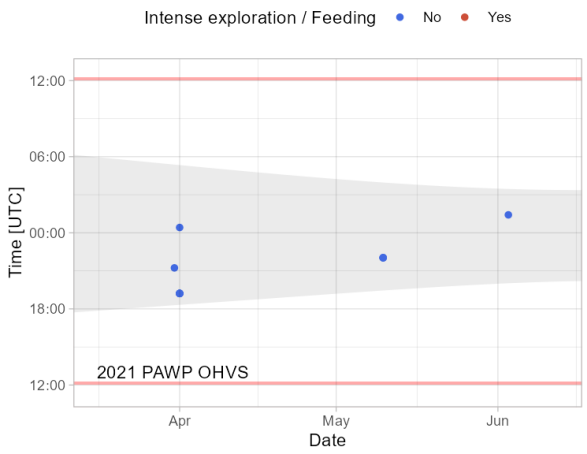


Figure SF3-30: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at PAWP

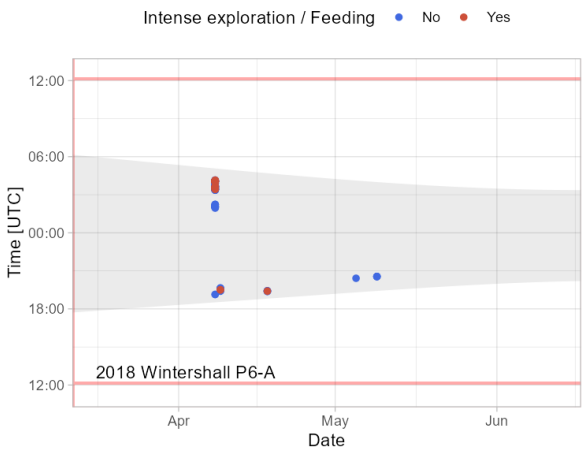


Figure SF3-31: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at PAWP

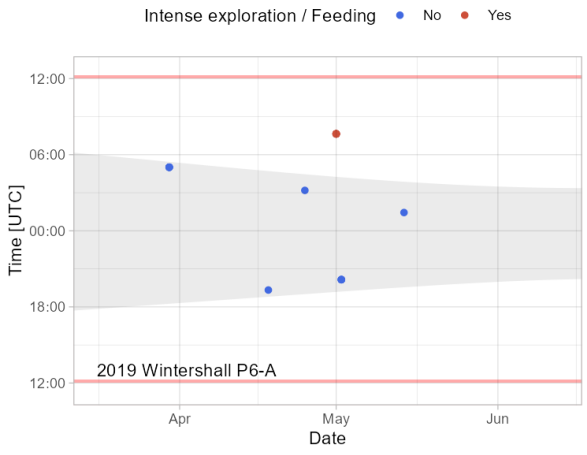


Figure SF3-32: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at Wintershall P6-A

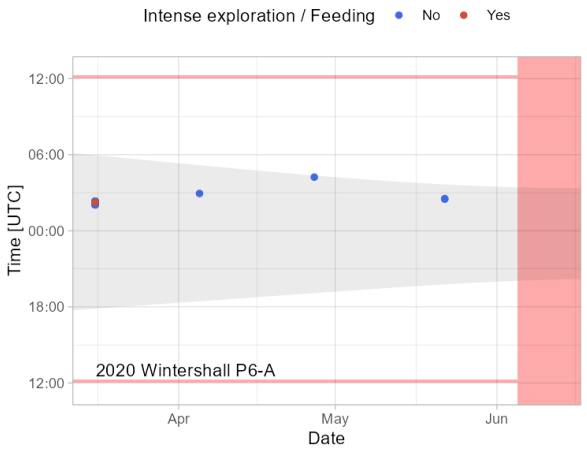


Figure SF3-33: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Wintershall P6-A

Figure SF3-34: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Wintershall P6-A

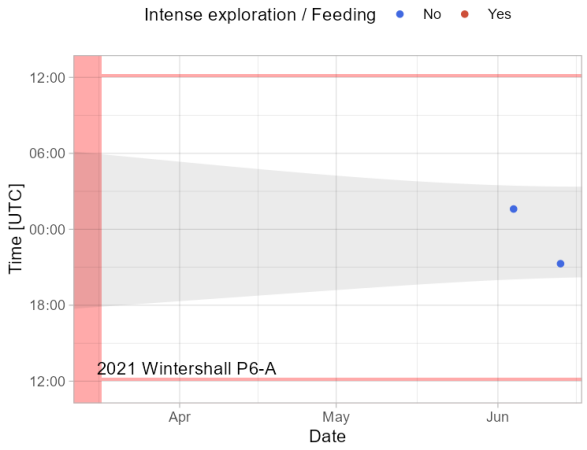


Figure SF3-35: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Wintershall P6-A

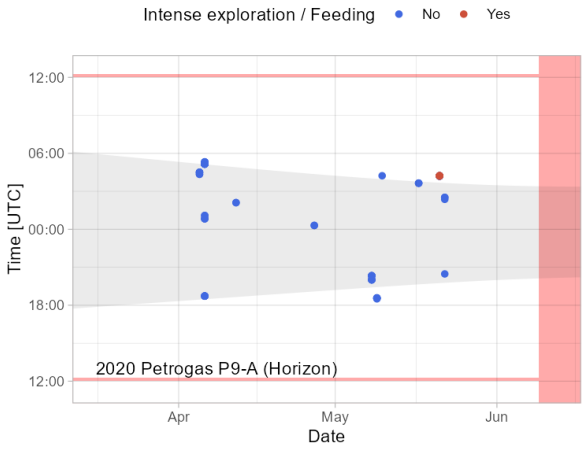


Figure SF3-36: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Petrogas Q1-A (Helder)

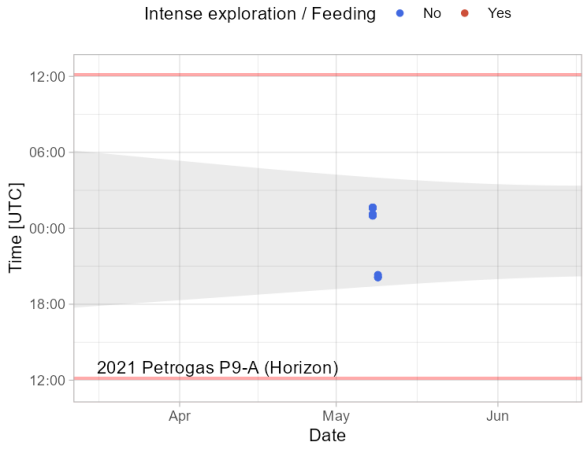


Figure SF3-37: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Petrogas Q1-A (Helder)

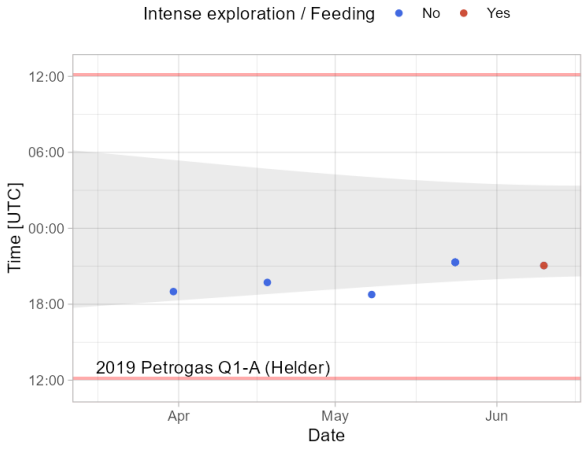
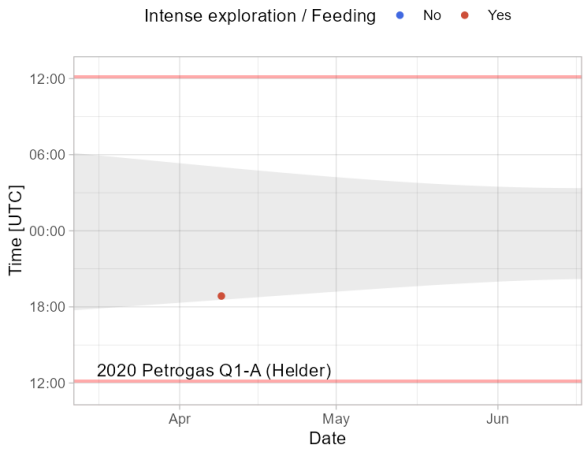


Figure SF3-38: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Petrogas Q1-A (Helder)



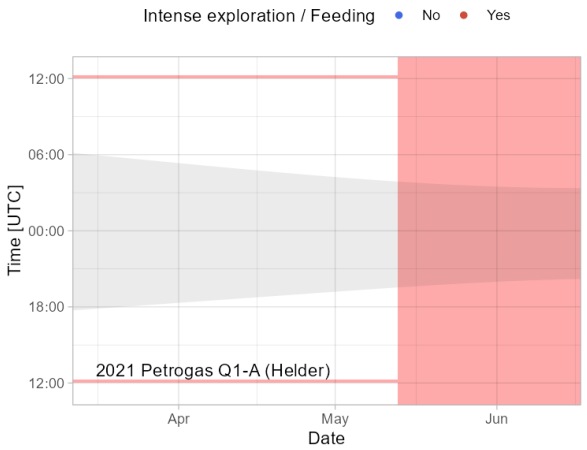


Figure SF3-39: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Petrogas Q1-A (Helder)

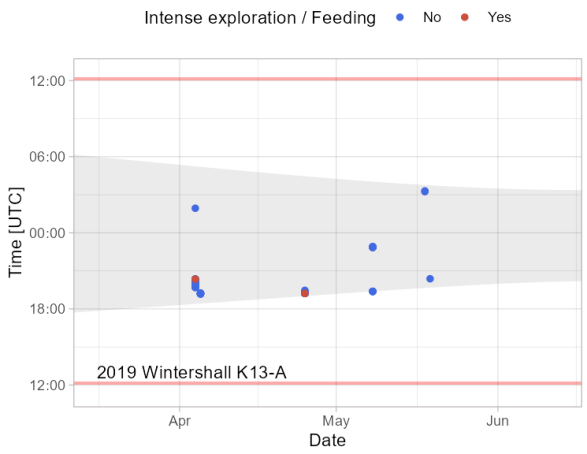


Figure SF3-40: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Petrogas Q1-A (Helder)

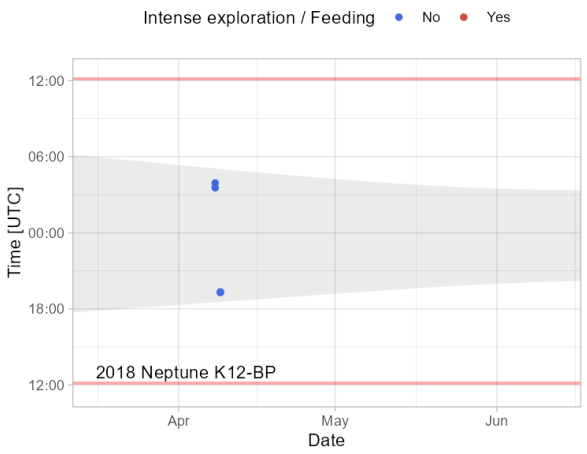
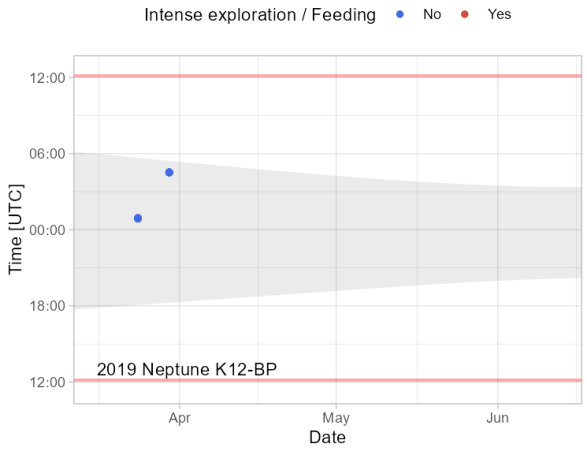


Figure SF3-41: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Wintershall K13-A

Figure SF3-42: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at Neptune K12-BP



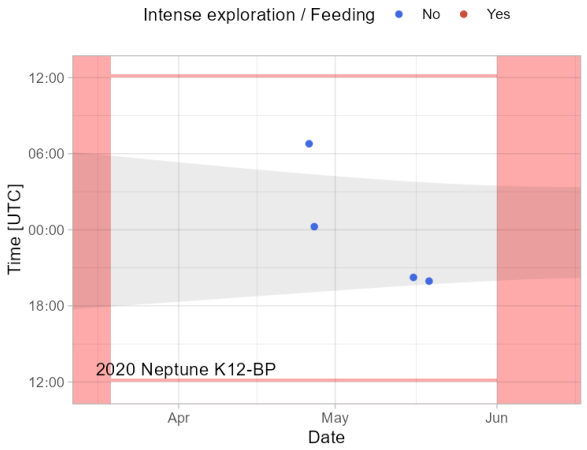


Figure SF3-43: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Neptune K12-BP

Figure SF3-44: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Neptune K12-BP

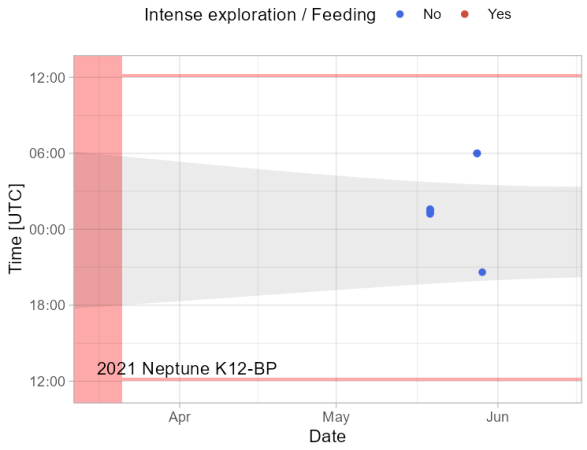


Figure SF3-45: Recorded acoustic presence of Nathusius' pipistrelle – spring 2021 at Neptune K12-BP

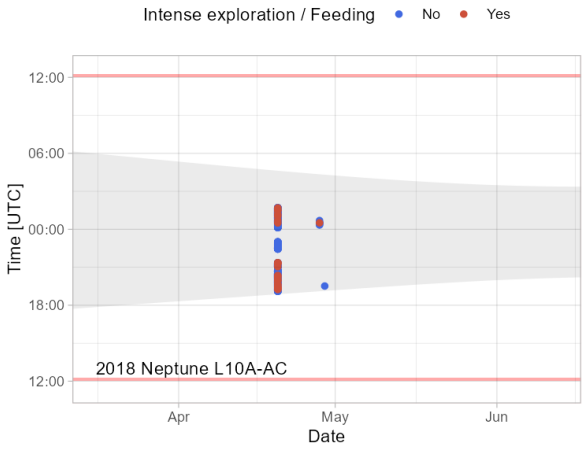


Figure SF3-46: Recorded acoustic presence of Nathusius' pipistrelle – spring 2018 at Neptune L10A-AC

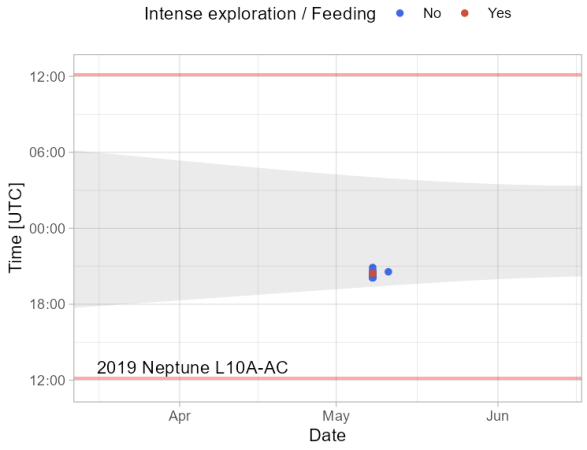


Figure SF3-47: Recorded acoustic presence of Nathusius' pipistrelle – spring 2019 at Neptune L10A-AC

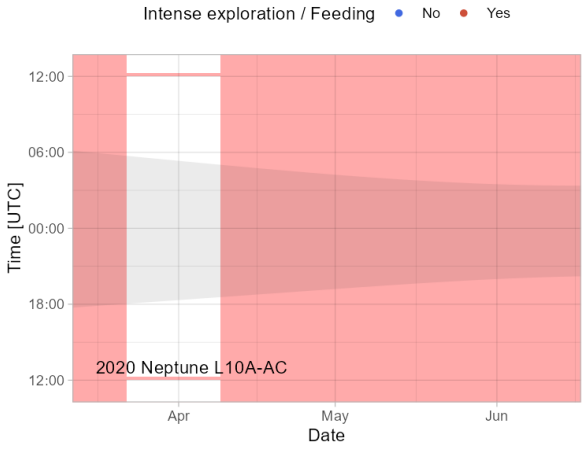


Figure SF3-48: Recorded acoustic presence of Nathusius' pipistrelle – spring 2020 at Neptune L10A-AC

A1.4 Supplementary file 4: tracking and acoustic model output

A1.4.1 Tracking model

The initial fully-parameterized tracking model included the covariates:

- night number (time)
- night number (time) quadratic
- wind speed
- wind speed quadratic
- cos θ
- sin θ
- cos 2θ
- sin 2θ
- wind speed x cos θ
- wind speed x sin θ
- wind speed x cos 2θ
- wind speed x sin 2θ
- sigma individual

Covariates were sequentially removed based on the weakest support (whether the 95% posterior credible interval of their beta parameters overlapped zero). The order in which the covariates were dropped:

1. wind speed x sin θ
2. night number (time) quadratic
3. wind speed x cos 2θ
4. cos 2θ
5. sin θ
6. wind speed x sin 2θ
7. sin 2θ

Convergence was confirmed in the final model for all parameters ($\hat{R} < 1.01$). Table SF1 includes the parameter estimates, Gelman–Rubin convergence diagnostic ($\hat{R}$), effective sample size (n.eff) and the posterior probability the parameter (f). Figure SF1 shows the posterior distributions of the estimated betas.

Table SF1: tracking model output

Parameter	mean	sd	2.50%	25%	50%	75%	97.50%	Rhat	n.eff	overlap0	f
beta0	7.908506	3.461004	3.095676	5.502024	7.245227	9.586554	16.649177	1.005886	1564	0	0.999989
beta_time	-0.10353	0.072163	-0.29351	-0.1357	-0.08685	-0.05325	-0.012592	1.006374	1598	0	0.993097
beta_windspeed	-0.26119	0.272129	-0.83509	-0.43505	-0.2461	-0.0721	0.2294419	1.001039	7461	1	0.833563
beta_windspeed_sq	0.027186	0.014957	0.002991	0.016196	0.025506	0.036461	0.0606411	1.001055	7111	0	0.989615
beta_cos1	-0.12127	0.474875	-1.05341	-0.44134	-0.12106	0.199483	0.8080528	1.000068	95972	1	0.600618
beta_windspeed_cos1	-0.28899	0.123348	-0.56066	-0.36421	-0.27851	-0.20252	-0.076828	1.001009	7260	0	0.997944
sigma_ind	1.233672	0.877877	0.068365	0.600998	1.074548	1.67111	3.3967427	1.00464	1977	0	1
deviance	77.23698	11.75003	53.83714	69.27368	77.4748	85.34155	99.633265	1.001587	4442	0	1

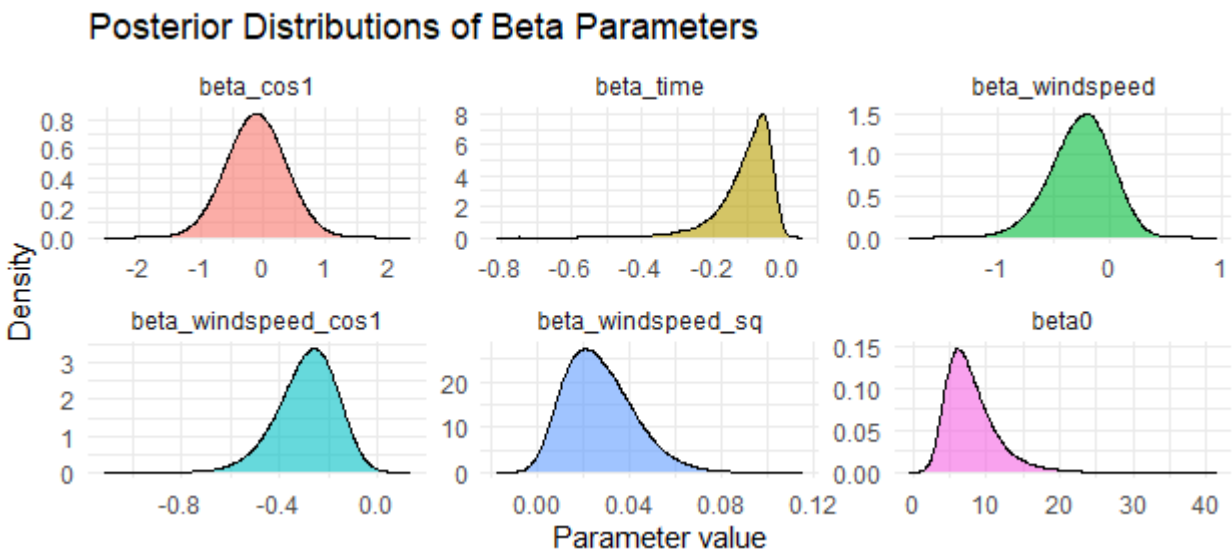


Figure SF1: posterior distributions of the estimated betas - tracking model.

A1.4.2 Acoustic model

The initial fully-parameterized acoustic model included the covariates:

- night number (time)
- night number (time) quadratic
- wind speed
- wind speed quadratic
- cos θ
- sin θ
- cos 2θ
- sin 2θ
- wind speed x cos θ
- wind speed x sin θ
- wind speed x cos 2θ
- wind speed x sin 2θ
- period
- period x cos θ
- period x sin θ
- period x cos 2θ
- period x sin 2θ
- precipitation
- atmospheric pressure change
- residual temperature on night number (time)
- cloud cover
- lunar phase x cos θ
- lunar phase x sin θ
- lunar phase x cos 2θ
- lunar phase x sin 2θ
- sigma individual

Covariates were sequentially removed based on the weakest support (whether the 95% posterior credible interval of their beta parameters overlapped zero and on the corresponding evidence ratio). The order in which the covariates were dropped:

1. lunar phase x sin 2θ
2. lunar phase x sin θ

3. period x cos θ
4. lunar phase x cos θ
5. lunar phase x cos 2θ
6. cloud cover
7. precipitation
8. period x sin 2θ
9. period x cos 2θ
10. atmospheric pressure change
11. night number (time) quadratic
12. residual temperature on night number (time)
13. wind speed x cos 2θ
14. cos 2θ

Convergence was confirmed in the final model for all parameters ($\hat{R} < 1.01$). Table SF2 includes the parameter estimates, Gelman–Rubin convergence diagnostic ($\hat{R}$), effective sample size (n.eff) and the posterior probability the parameter (f). Figure SF2 shows the posterior distributions of the estimated betas.

Table SF2: acoustic model output

parameter	mean	sd	2.50%	25%	50%	75%	97.50%	Rhat	n.eff	overlap0	f
beta0	7.915514	1.320688	5.800598	6.979426	7.75788	8.68458	10.9106285	1.004915	2086	0	1
beta_time	-0.20207	0.048745	-0.312797	-0.23044	-0.19624	-0.16726	-0.1248131	1.005554	1829	0	1
beta_period	6.272837	1.668535	3.629972	5.082138	6.071495	7.237223	10.0798604	1.00533	1875	0	1
beta_windspeed	-0.00558	0.085554	-0.179137	-0.06214	-0.00336	0.053146	0.15614617	1.000292	24327	1	0.515823
beta_windspeed_sq	0.011136	0.00517	0.001587	0.007543	0.010928	0.014509	0.02182917	1.000367	18703	0	0.990168
beta_cos1	0.405202	0.312451	-0.2074	0.195046	0.405007	0.615116	1.0188709	1.000064	104926	1	0.903169
beta_sin1	-0.45249	0.415183	-1.280823	-0.72889	-0.44766	-0.17072	0.34926753	1.000097	76622	1	0.863472
beta_sin2	-0.70931	0.330528	-1.356355	-0.93125	-0.7102	-0.48785	-0.0576457	1.000069	104508	0	0.983371
beta_windspeed_cos1	-0.16542	0.048392	-0.26298	-0.1974	-0.16459	-0.1324	-0.0729943	1.00017	39532	0	0.999832
beta_windspeed_sin1	-0.20913	0.052289	-0.314409	-0.24372	-0.20816	-0.17349	-0.1092526	1.000241	27969	0	0.999994
beta_windspeed_sin2	0.157952	0.045772	0.068905	0.127031	0.157629	0.188542	0.24861888	1.000092	76624	0	0.999759
beta_sin1_period	1.437895	0.38167	0.703627	1.179013	1.432165	1.690717	2.20316383	1.00007	97788	0	0.999952
sigma_ind	1.574849	0.548115	0.672951	1.190297	1.516872	1.895804	2.80418905	1.004859	2012	0	1
deviance	870.3318	55.22984	756.3681	833.9633	872.7028	909.3069	970.85913	1.003421	2374	0	1

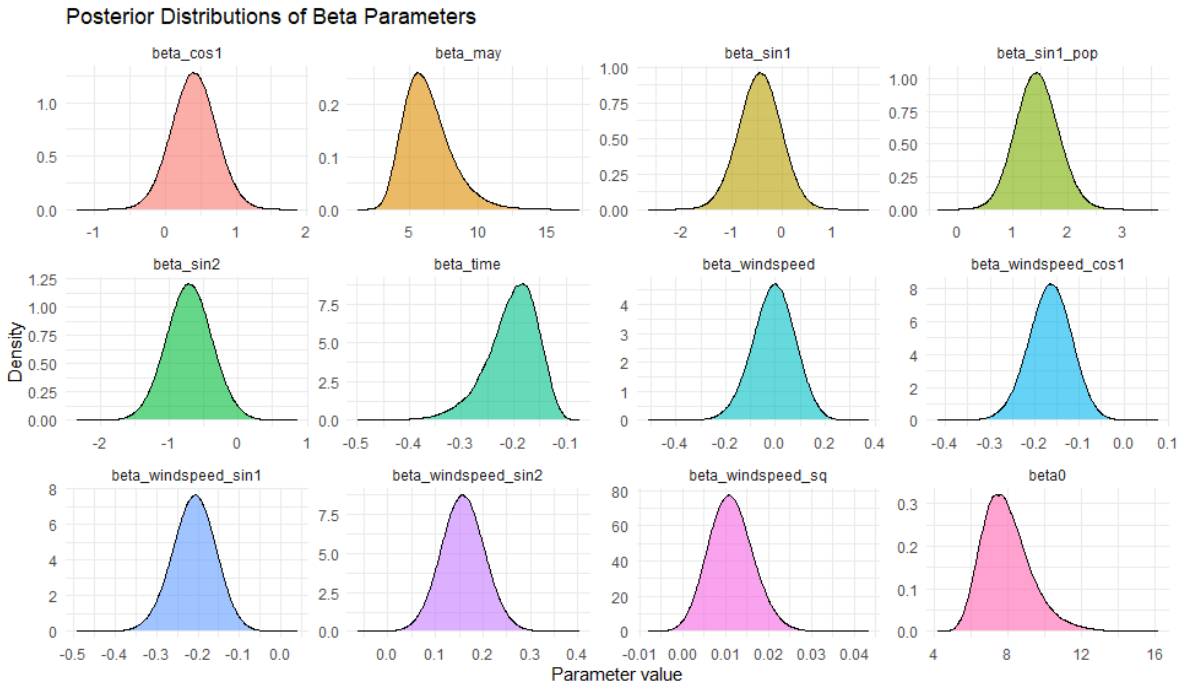


Figure SF2: posterior distributions of the estimated betas – acoustic model.

Annex 2 Supplementary files analysis 2 (chapter 3)

A2.1 Supplementary file 1: southern North Sea Motus receiver network

The Motus Wildlife Tracking System (www.motus.org) is an international collaborative research network that employs automated radio telemetry. It is specifically designed to track the movements of smaller animals, such as bats and birds, during a prolonged period of time without the need to recapture them. Motus is therefore widely used for migration studies. The system operates through a network of stationary automated receiving stations and lightweight coded VHF radio tags, used to identify and track individual animals. In Europe 150.1 MHz is used as common frequency, while 166 MHz is used in Northern & Southern America. Motus is a program of Birds Canada in partnership with collaborating researchers and organizations. Figures SF 1-5 show the development of the receiver network in the southern North Sea area from 2018 - 2022. Generally receivers are located along coastlines and are virtually absent from inland locations. The highest receiver coverage is in northwestern Germany and along the Westcoast of the Netherlands.

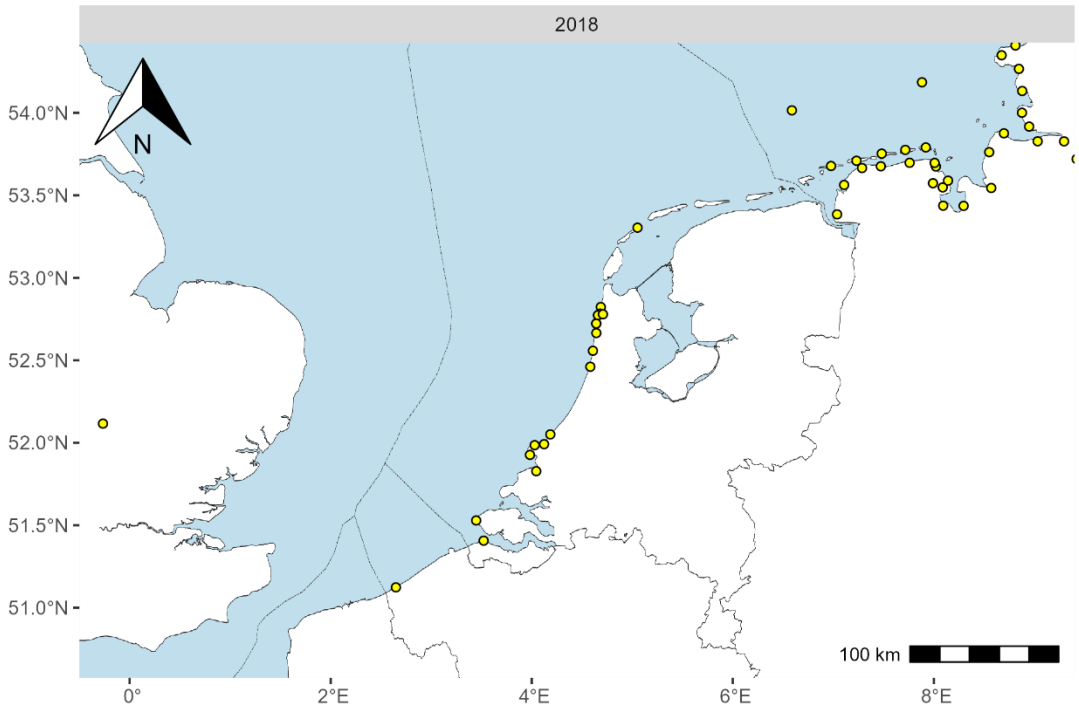


Figure SF1-1: Operational receivers (n=51) in December 2018

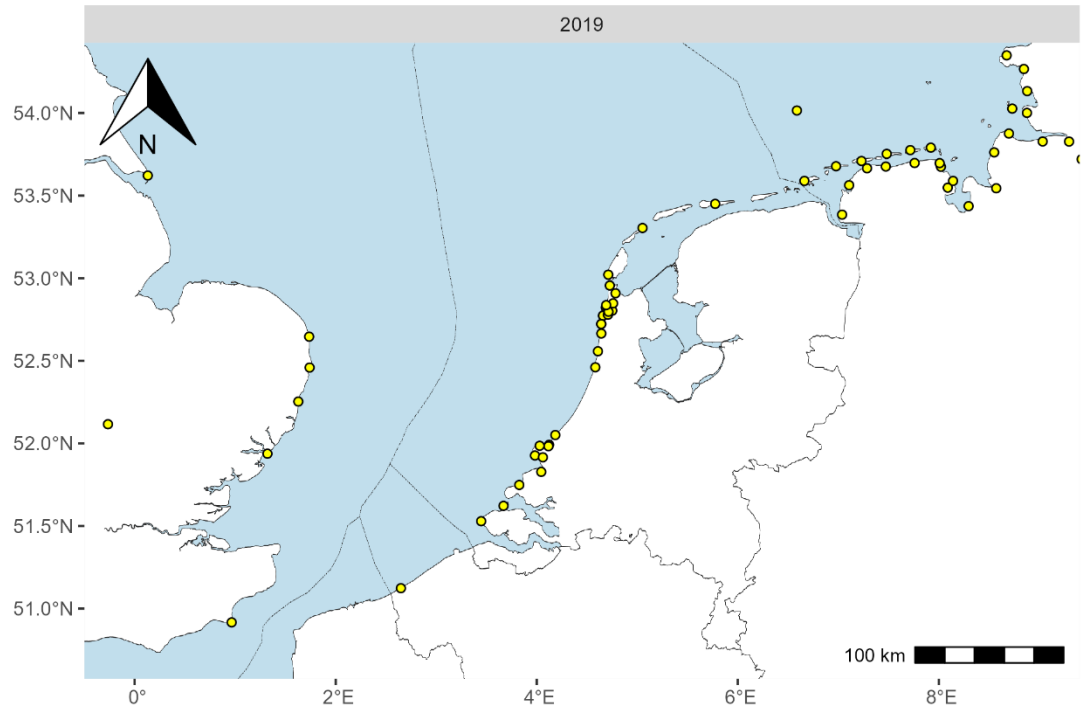


Figure SF1-2: Operational receivers (n=61) in December 2019

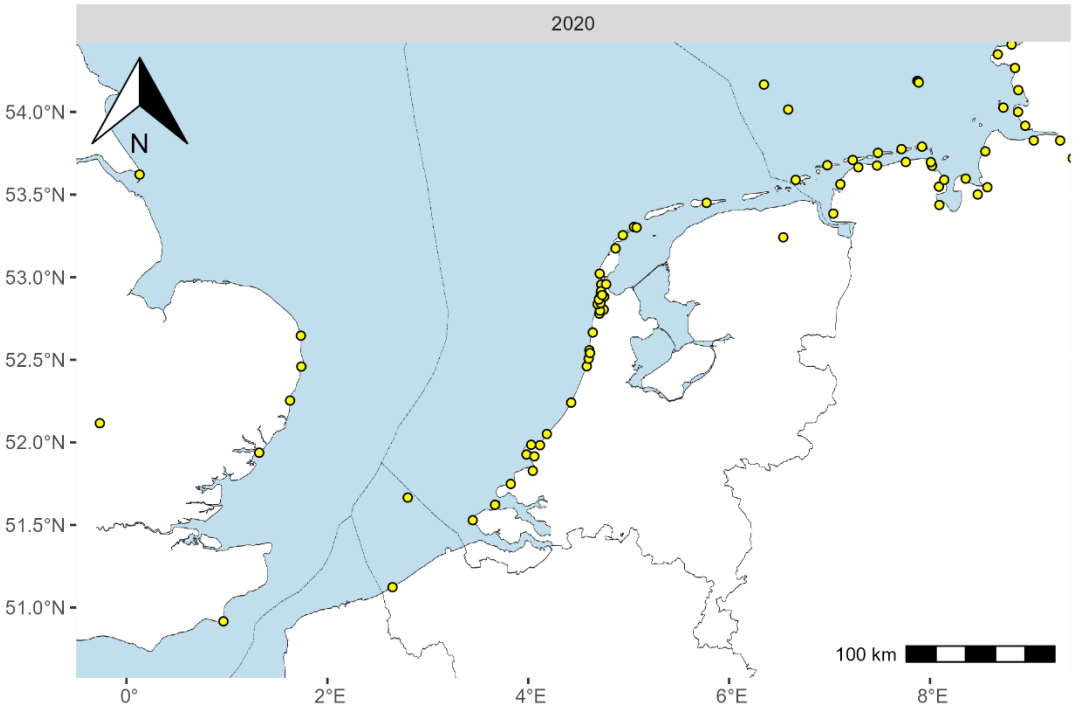


Figure SF1-3: Operational receivers (n=79) in December 2020

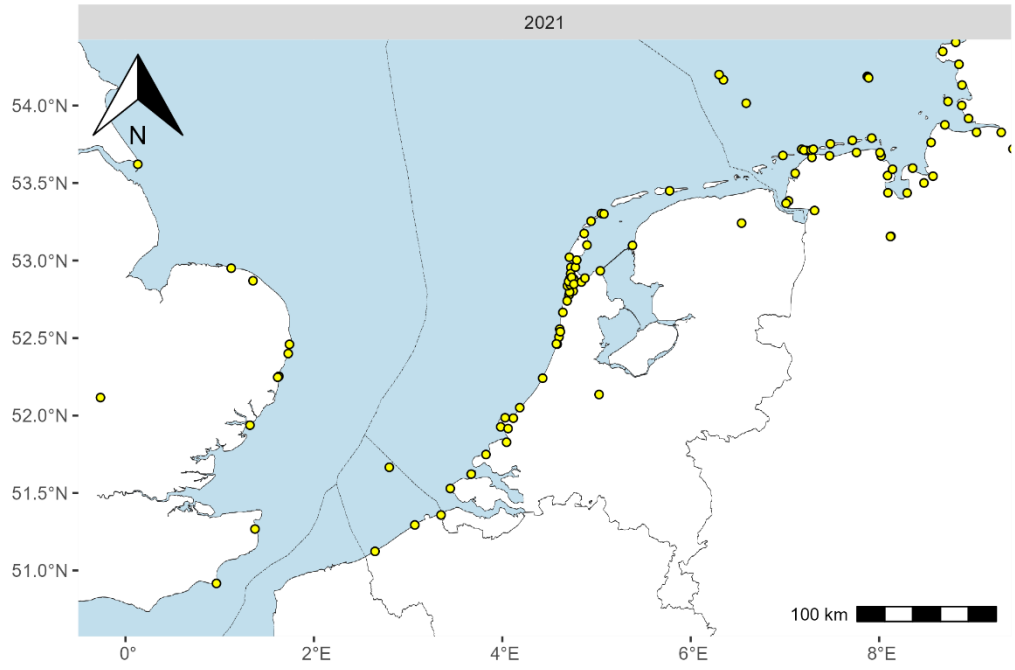


Figure SF1-4: Operational receivers (n=103) in December 2021

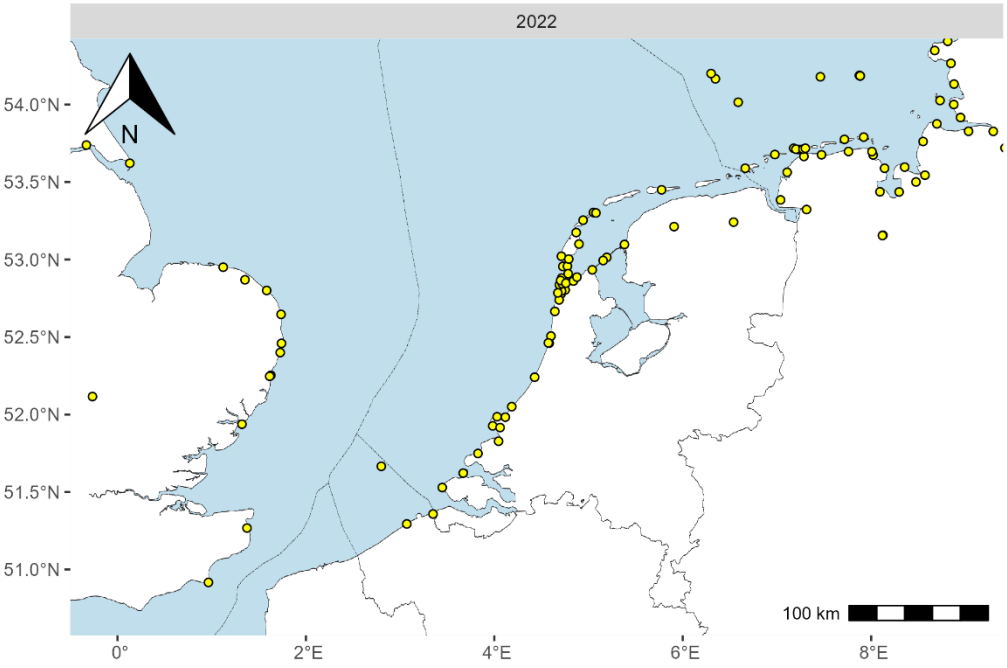


Figure SF1-5: Operational receivers (n=109) in December 2022

A2.2 Supplementary file 2: removal of false positives

Detections with run lengths < 3 were filtered out, in accordance with the MOTUS R Book (Birds Canada, 2022). In addition, unlikely detections were removed from specific receivers at locations with high levels of radio noise (table SF1-2).

Tabe SF2-1: false positives

Year	Tag Deployment	Receiver Deployment	Receiver	Date	Comments
2018	18817	4130	Bremerhaven	all	lots of false positives on this receiver in 2018
2018	18817	4315	Castricum aan zee	all	lots of false positives on this receiver in 2018 (likely caused by cell phone mast)
2018	18818	5023	29_Sillenstede	all	unlikely (one detection during daylight hours)
2018	18840	4315	Castricum aan zee	all	lots of false positives on this receiver in 2018 (likely caused by cell phone mast)
2018	18840	4638	Den Helder Vuurtoren	all	during daylights hours
2018	18840	4454	Ijmuiden vuurtoren	all	lots of false positives on this receiver from 31/10 onwards (also tags from abroad)
2018	18840	4469	13_Ruthenstrom	all	during daylights hours
2018	18840	4130	Bremerhaven	all	lots of false positives on this receiver in 2018
2018	18844	4315	Castricum aan zee	all	lots of false positives on this receiver in 2018 (likely caused by cell phone mast)
2018	18852	4367	26_Utlandshörn	after 30-9-2018 00:00	detections of a dropped off tag after 2018-09-29
2018	18859	4454	Ijmuiden vuurtoren	all	1 unlikely, 1 during daylight hours
2018	18859	4315	Castricum aan zee	all	lots of false positives on this receiver in 2018 (likely caused by cell phone mast)
2018	18861	4892	Huiberts	after 5-9-2018 00:00	detections of a dropped off tag after 2018-09-04
2018	19022	4711	Noorderhaven Julianadorp	after 7-10-2018 00:00	detections of a dropped off tag after 2018-10-06
2018	19023	3702	23_Carolinensiel	all	unlikely
2018	19023	4892	Huiberts	after 13-9-2018 00:00	detections of a dropped off tag after 2018-09-12
2018	19092	4532	HelgolandFG1	all	1 unlikely (15/10, together with deployment 19119)
2018	19093	4817	Jomfruland Bird Observatory	all	late season unlikely detections (also during the day) in Norway
2018	19093	4817	Jomfruland Bird Observatory	all	unlikely (in Norway), also during daylight hours
2018	19095	3943	08_Büsum	all	false positives of 5 tags on the same day (9/10/2018)
2018	19099	3943	08_Büsum	all	false positives of 5 tags on the same day (9/10/2018)
2018	19099	3943	08_Büsum	all	false positives of 5 tags on the same day (9/10/2018)
2018	19100	4556	116_Borkum 1	all	unlikely
2018	19100	4556	116_Borkum 1	all	unlikely
2018	19101	3943	08_Büsum	all	false positives of 5 tags on the same day (9/10/2018)
2018	19107	3943	08_Büsum	all	false positives of 5 tags on the same day (9/10/2018)
2018	19119	4532	HelgolandFG1	all	1 unlikely, (15/10, together with deployment 19092)
2018	19120	4310	ECN	after 15-10-2018 00:00	detections of a dropped off tag after 2018-10-14
2019	25079	5624	Single RX receiver_2 (Lund)	all	unlikely (in Sweden), also during daylight hours
2019	25079	5376	Ekologihuset	all	unlikely (in Sweden), also during daylight hours, and during the time frame it was detected in the Netherlands
2019	25099	5624	Single RX receiver_2	all	unlikely (one detection during daylight hours)
2019	25136	4532	HelgolandFG1	all	1 unlikely (10/9 during daylight hours)
2019	25169		all receivers	all	detections of a dropped off tag after 2019-09-04
2019	25177	5503	Callantsoog Inland	after 27-8-2019 00:00	detections of a dropped off tag after 2019-08-26
2019	25179	5463	t Zand	after 18-9-2019 00:00	detections of a dropped off tag after 2019-09-17
2019	25179	5621	Eendekooi 't Zand	after 18-9-2019 00:00	detections of a dropped off tag after 2019-09-17
2019	25181		all receivers	all	detections of a dropped off tag after 2019-09-04
2019	25220	5621	Eendekooi 't Zand	after 25-9-2019 00:00	detections of a dropped off tag after 2019-09-24
2019	26144	5621	Eendekooi 't Zand	after 1-10-2019 06:00	detections of a dropped off tag after 2019-10-01 06:00
2019	26146	5621	Eendekooi 't Zand	after 29-9-2019 01:30	detections of a dropped off tag after 2019-09-29 01:30
2019	26155	5376	Ekologihuset	all	unlikely (in Sweden), during daylight hours
2019	29197	4892	Huiberts	after 16-9-2020 05:00	detections of a dropped off tag after 2019-09-16 05:00

Tabe SF2-1: false positives (continued)

Year	Tag Deployment	Receiver Deployment	Receiver	Date	Comments
2020	29174	6185	120_HelgolandFG1	all	numerous false positives of various tags from several countries from 24/10/2020 onwards
2020	29206	5463	t Zand	after 17-9-2020 00:00	detections of a dropped off tag after 2020-09-16 05:00
2020	29206	5621	Eendekooi 't Zand	after 17-9-2020 00:00	detections of a dropped off tag after 2020-09-16 05:00
2020	29213	5376	Ekologihuset	all	unlikely (one detection in southern Sweden)
2020	29214	7341	Castricum Ringbaan	all	from 7/11 onwards, numerous false positives of various tags from several countries, caused by the presense of several tags at the ringing site
2020	29215	7341	Castricum Ringbaan	all	numerous false positives of various tags from several countries from 6/11/2020 onwards
2020	29217	4711	Noorderhaven Julianadorp	after 4-10-2020 00:00	detections of a dropped off tag after 2020-10-04
2020	29220	7315	Vlieland Kazerne	all	Likely caused by tagged songbirds present al this location (08/11/2020)
2020	29224	7341	Castricum Ringbaan	all	numerous false positives of various tags from several countries from 6/11/2020 onwards
2020	29229	7341	Castricum Ringbaan	all	numerous false positives of various tags from several countries from 6/11/2020 onwards
2020	29230	7341	Castricum Ringbaan	all	numerous false positives of various tags from several countries from 6/11/2020 onwards
2020	29231	7341	Castricum Ringbaan	all	from 7/11 onwards, numerous false positives of various tags from several countries, caused by the presense of several tags at the ringing site
2020	29232		all receivers	all	detections of a dropped off tag after 2020-10-22
2020	29233	6185	120_HelgolandFG1	all	numerous false positives of various tags from several countries from 24/10/2020 onwards
2020	29244	6133	Callantsoog Inland	after 22-9-2020 00:00	detections of a dropped off tag after 2020-09-21
2020	29275	7341	Castricum Ringbaan	all	from 7/11 onwards, numerous false positives of various tags from several countries, caused by the presense of several tags at the ringing site
2020	29280	7341	Castricum Ringbaan	all	from 7/11 onwards, numerous false positives of various tags from several countries, caused by the presense of several tags at the ringing site
2021	35236	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2021	35249	4892	Huiberts	after 14-9-2021 00:00	detections of a dropped off tag after 2021-09-13
2021	35252	4711	Noorderhaven Julianadorp	after 16-9-2021 00:00	detections of a dropped off tag after 2021-09-15
2021	35259	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2021	35269	4711	Noorderhaven Julianadorp	after 12-9-2021 00:00	detections of a dropped off tag after 2021-09-11
2021	35567	7709	Safari	all	unlikely, detections in the same period in the tagging area
2021	35568	7668	Kennemerwind	after 25-9-2021 00:00	detections of a dropped off tag after 2021-09-24
2021	35572	7692	Norderney 3	all	unlikely, probably caused by the presense of various tagged northern wheatears
2021	36044	4892	Huiberts	after 28-9-2021 00:00	detections of a dropped off tag after 2021-09-27
2021	36052	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2021	36052	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	36331	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42200	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42201	7230	Vogelzand	after 2-9-2022 05:00	detections of a dropped off tag after 2022-9-2 05:00
2022	42205	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42212	4711	Noorderhaven Julianadorp	after 15-9-2021 00:00	detections of a dropped off tag after 2022-09-14
2022	42214	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42214	7315	Vlieland Kazerne	all	Likely caused by tagged songbirds present al this location (21/10/2022)
2022	42216	7315	Vlieland Kazerne	all	unlikely (4/11), caused by tagged songbirds present al this location
2022	42217	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42222	7709	Safari	all	same day detections in Noord Holland
2022	42222	7709	Safari	all	same day detections in Noord Holland
2022	42224	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42234	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards

Tabe SF2-1: false positives (continued)

Year	Tag Deployment	Receiver Deployment	Receiver	Date	Comments
2022	42252	7315	Vlieland Kazerne	all	during daylight hours (19/10), caused by tagged songbirds present al this location
2022	42256	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42256	9047	Caister-on-Sea Lifeboat	all	numerous false positives of various tags from several countries from 30/11/2022 onwards
2022	42258	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42259	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42261	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42261	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42263	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42264	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42295	4892	Huiberts	after 11-11-2022 00:00	detections of a dropped off tag after 2022-11-10
2022	42303	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42308	4892	Huiberts	after 26-9-2022 05:00	detections of a dropped off tag after 2022-09-26 05:00
2022	42311	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42312	4892	Huiberts	after 14-9-2022 06:00	detections of a dropped off tag after 2022-09-14 06:00
2022	42315	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42315	4892	Huiberts	after 24-9-2022 00:00	detections of a dropped off tag after 2022-09-24 00:00
2022	42316	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42317	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42317	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42320	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42320	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42323	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42326	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42326	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42326	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42326	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42407	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42410	7351	17_Fedderwardersiel	all	numerous false positives of various tags from several countries
2022	42426	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42432	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards
2022	42434	8886	Borkum 1	all	numerous false positives of various tags from several countries from 1/10/2022 onwards

A2.3 Supplementary file 3: Arm length, Weight and Body Mass Index (BMI)

Females were slightly larger than males, as indicated by arm length, but no differences were observed among age classes within each sex (Table SF5-1 and Figure SF5-1). Adult bats were heavier than first-year bats within each sex. Among all groups, adult females were the heaviest, while first-year females and adult males had similar body weights (Table SF5-2 and Figure SF5-2). Calculating the residuals of the regression of Weight on Arm length per SexAge category (Figure SF5-4) resulted in the BMI, which did not differ among the SexAge categories, though the variation was a bit higher in adult females (Table SF5-4 and Figure SF5-5).

Table SF5-1 : Armlength per SexAge category

Category	Number of individuals	Arm length [mm]				
		median	mean	sd	min	max
F_adult	202	34.6	34.7	0.9	32.2	37.0
F_first	102	34.5	34.4	0.8	32.2	36.7
M_adult	167	33.6	33.6	0.8	31.7	35.1
M_first	90	33.6	33.7	0.9	31.8	36.8
All bats	561	34.2	34.1	1.0	31.7	37.0

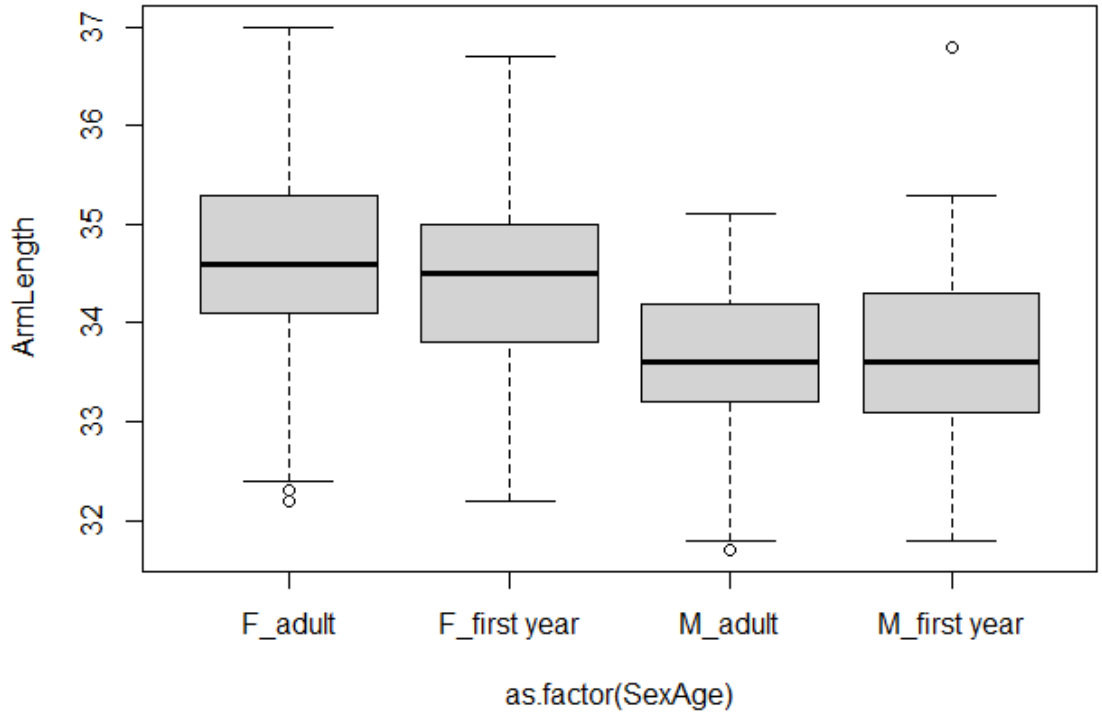


Figure SF5-1: Boxplot of armlength per SexAge category

Table SF5-2 : Weight per SexAge category

Category	Number of individuals	Weigth [g]				
		median	mean	sd	min	max
F_adult	202	8.8	8.9	1.1	6.2	12.2
F_first year	102	8.1	8.2	0.8	6.2	10.1
M_adult	167	8.1	8.1	0.9	5.2	10.8
M_first year	90	7.8	7.9	0.8	6.0	10.0
All bats	561	8.2	8.4	1.0	5.2	12.2

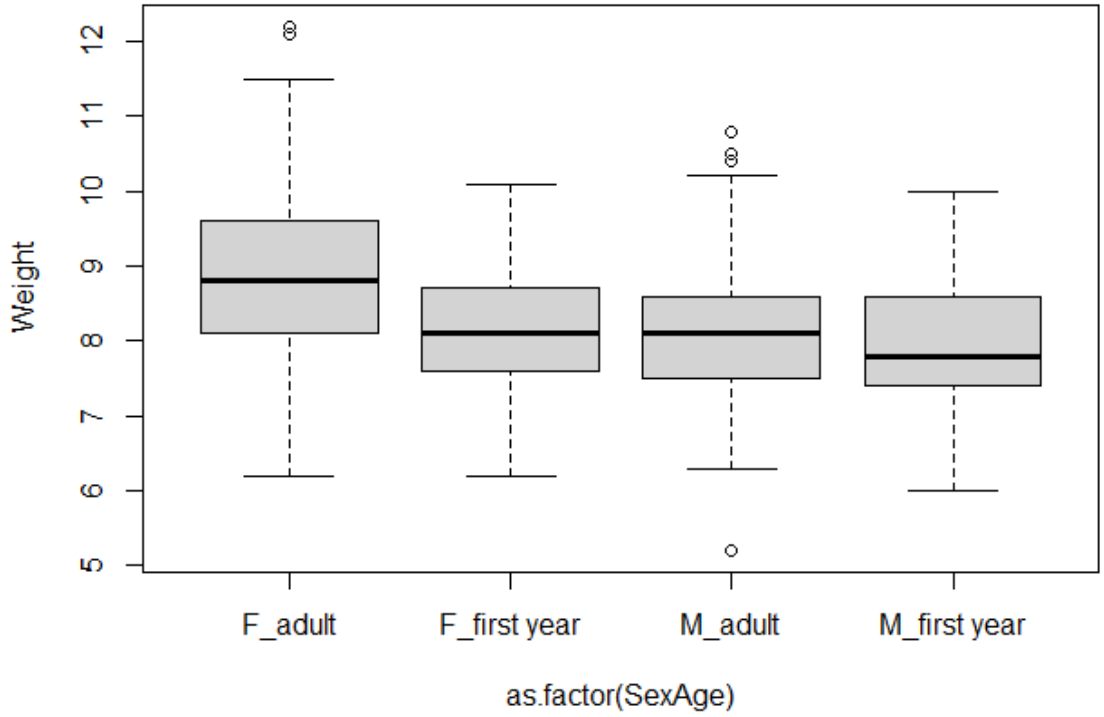


Figure SF5-2 Boxplot of weights per SexAge category

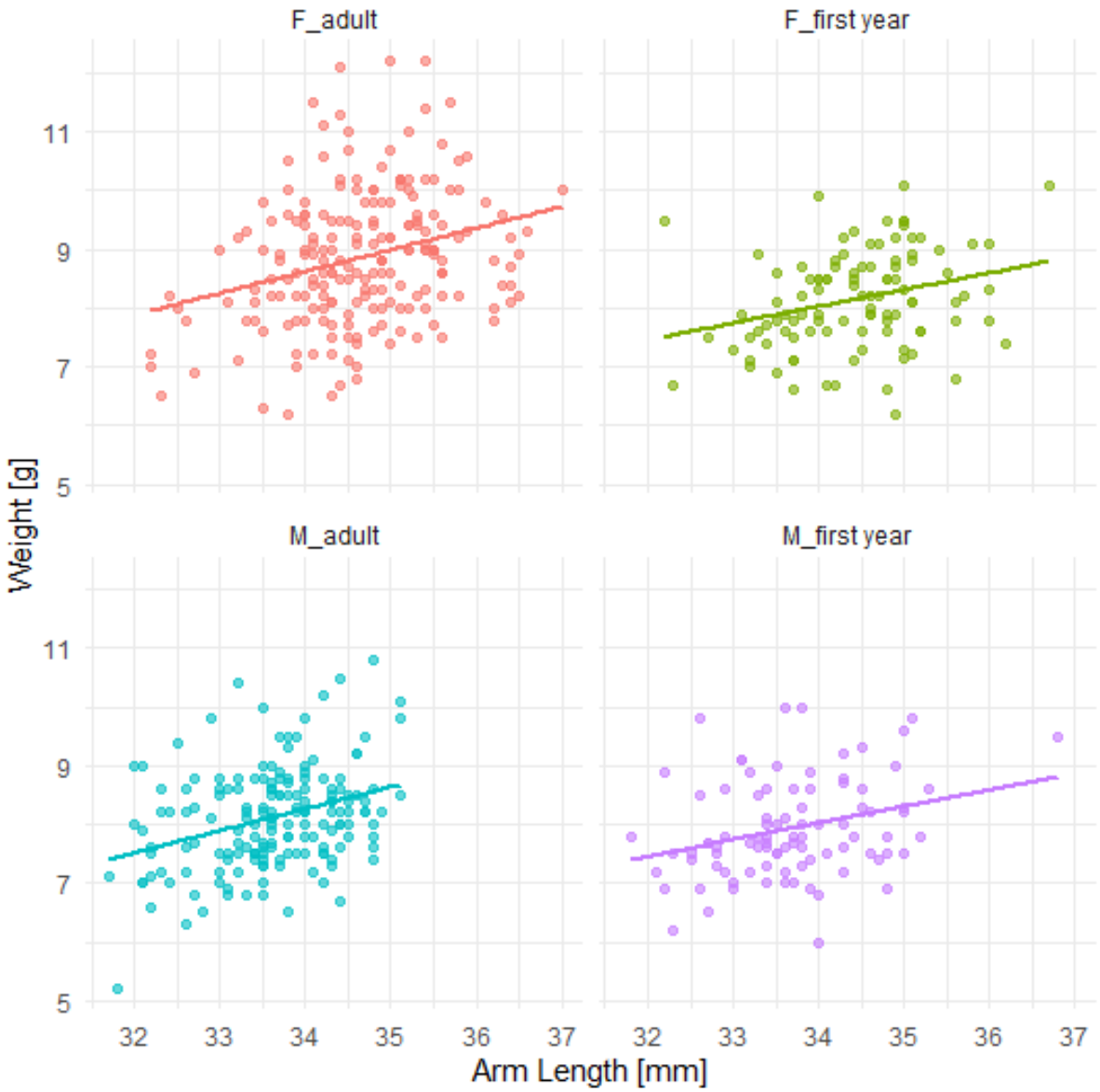


Figure SF5-3: Regression of Weight on Arm length per SexAge category

Table SF5-4 : BMI per SexAge category

Category	Number of individuals	Body Mass Index				
		median	mean	sd	min	max
F_adult	202	-0.12	-3.54E-18	1.09	-2.35	3.33
F_first year	102	-0.04	-2.44E-17	0.80	-2.08	1.99
M_adult	167	-0.06	1.78E-17	0.82	-2.24	2.44
M_first year	90	-0.10	-1.17E-17	0.81	-2.02	2.18
All bats	561	-0.09	-2.43E-18	0.92	-2.35	3.33

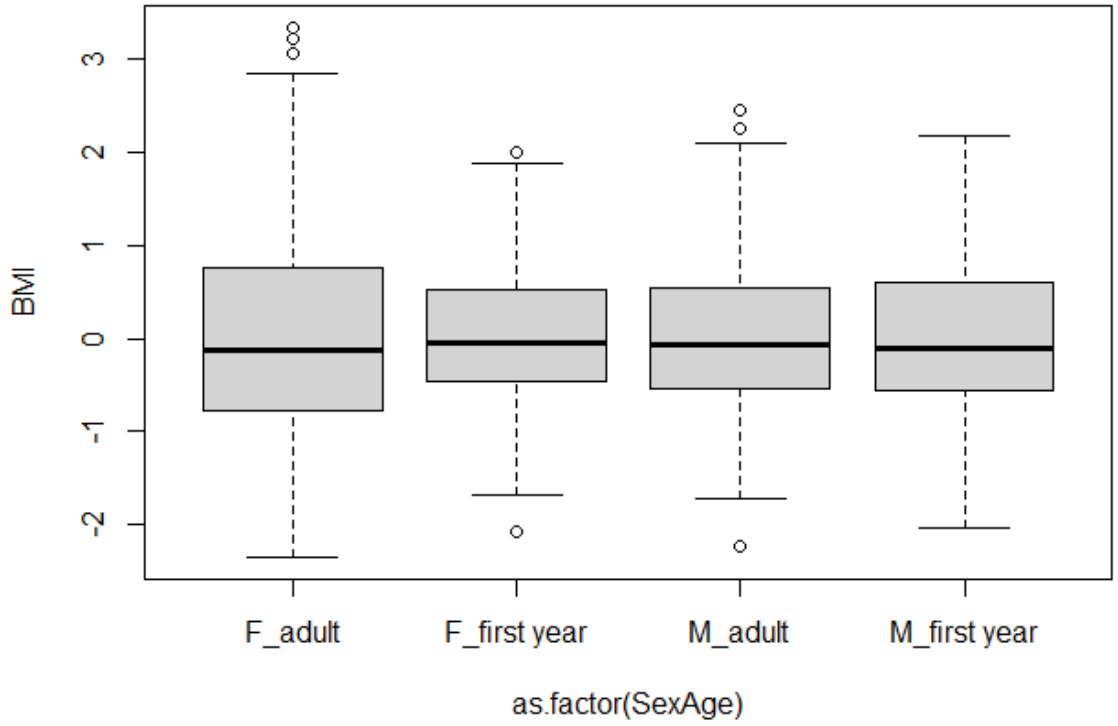
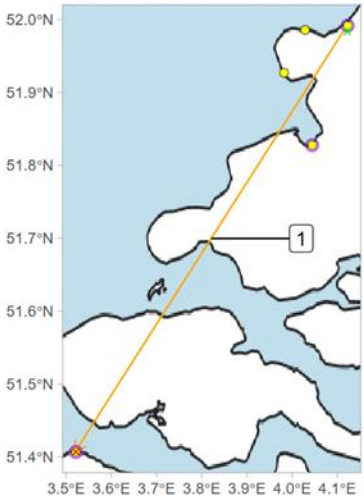


Figure SF5-5 : Body Mass Index per SexAge category

A2.4 Supplementary file 4: flights of all individuals

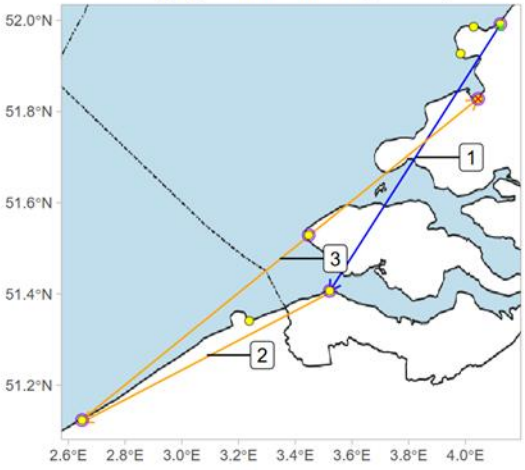
These figures shows the observed flights of individual bats over 30 km, with arrows indicating flight direction. Flights occurring within a single night are shown in blue, while movements spanning multiple nights are shown in orange. Each flight is annotated with start and end timestamps, along with the timestamps of tagging and last detection. MOTUS receivers are indicated by yellow dots.

Deployment ID 18816 (adult F)



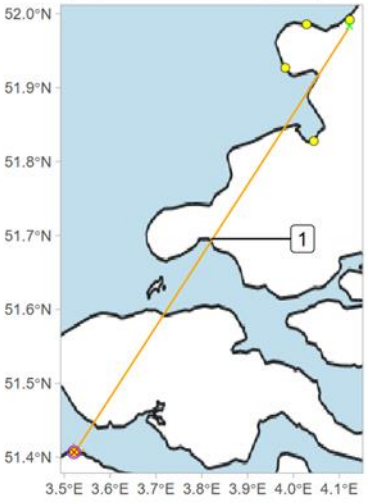
release: 2018-09-04 15:00
1) 2018-09-04 19:05 - 2018-09-05 21:11
final detection: 2018-09-05 21:12

Deployment ID 18817 (adult F)



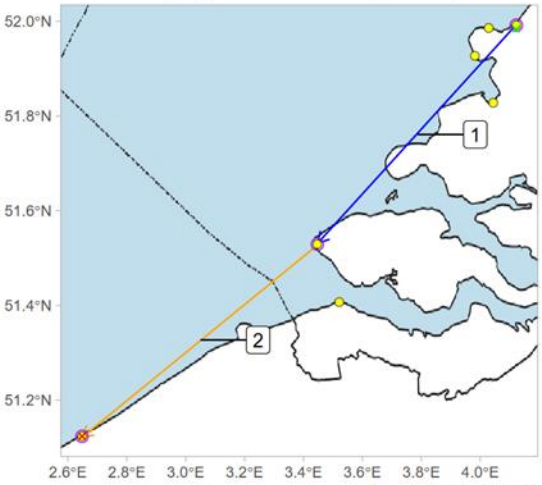
release: 2018-09-04 15:00
1) 2018-09-04 19:01 - 2018-09-04 22:25
2) 2018-09-04 22:25 - 2018-09-08 22:14
3) 2018-09-08 22:14 - 2018-11-18 00:54
final detection: 2018-11-18 00:54

Deployment ID 18822 (first year F)



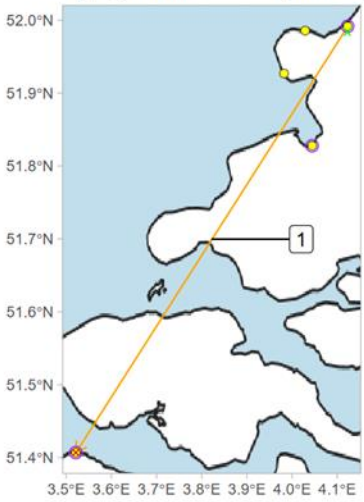
release: 2018-09-13 10:00
1) 2018-09-13 18:03 - 2018-09-16 22:35
final detection: 2018-09-16 22:36

Deployment ID 18824 (adult F)



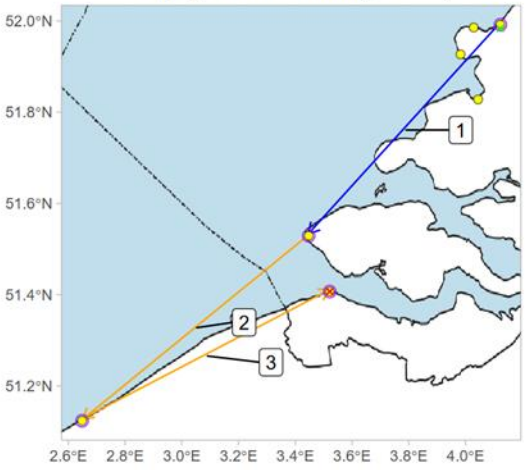
release: 2018-09-13 10:00
1) 2018-09-13 18:43 - 2018-09-13 22:16
2) 2018-09-13 22:16 - 2018-09-14 20:49
final detection: 2018-09-14 20:51

Deployment ID 18825 (adult F)



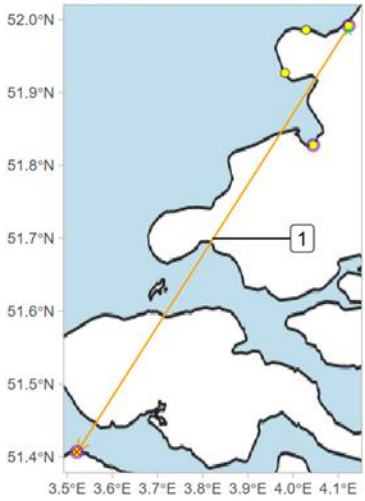
release: 2018-09-08 10:00
1) 2018-09-09 18:52 - 2018-09-17 23:23
final detection: 2018-09-17 23:25

Deployment ID 18828 (adult F)



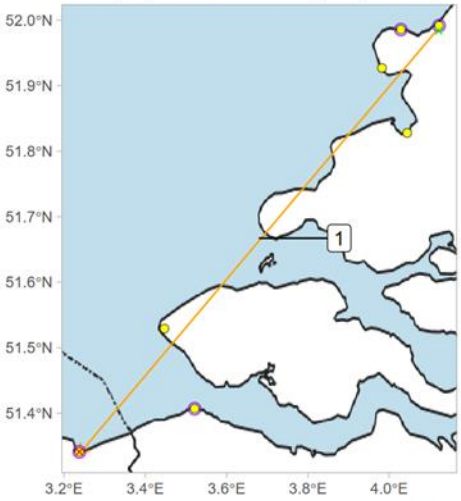
release: 2018-09-13 10:00
1) 2018-09-13 18:38 - 2018-09-13 21:59
2) 2018-09-13 21:59 - 2018-09-14 20:13
3) 2018-09-14 20:13 - 2018-09-19 00:28
final detection: 2018-09-19 18:32

Deployment ID 18829 (adult F)



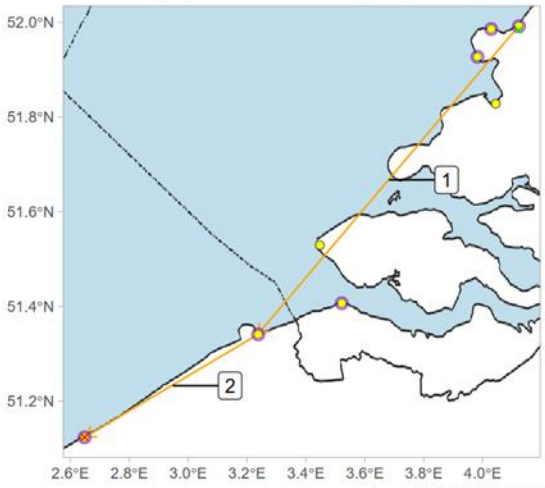
release: 2018-09-04 15:00
1) 2018-09-04 19:51 - 2018-09-05 21:33
final detection: 2018-09-05 21:38

Deployment ID 18831 (first year F)



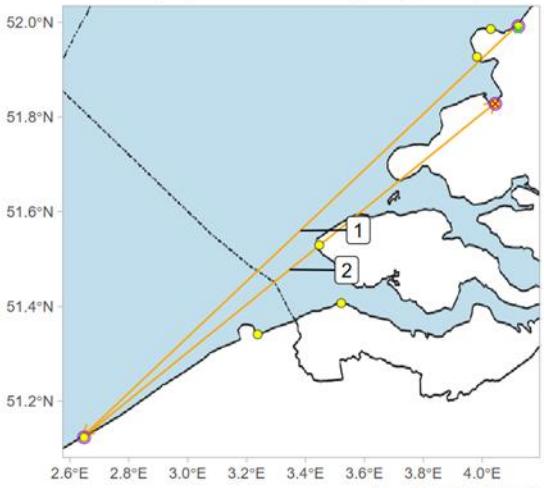
release: 2018-09-04 15:00
1) 2018-09-04 19:06 - 2018-09-05 20:34
final detection: 2018-09-05 20:35

Deployment ID 18832 (first year F)



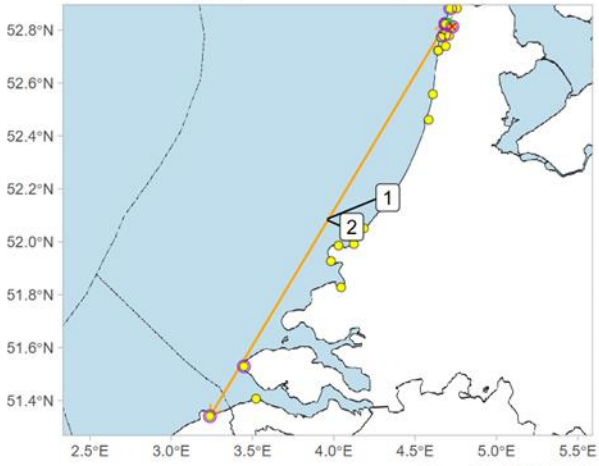
release: 2018-09-04 15:00
1) 2018-09-04 19:12 - 2018-09-05 20:04
2) 2018-09-05 20:04 - 2018-09-06 20:34
final detection: 2018-09-06 20:37

Deployment ID 18834 (first year F)



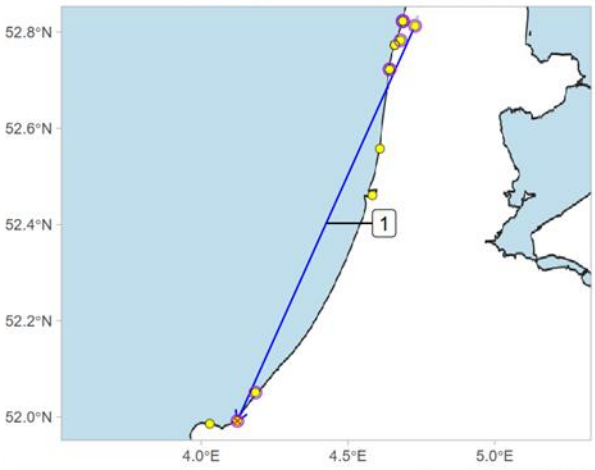
release: 2018-09-13 10:00
1) 2018-09-13 18:55 - 2018-09-14 22:05
2) 2018-09-14 22:05 - 2018-09-19 22:56
final detection: 2018-09-19 22:59

Deployment ID 18842 (adult F)

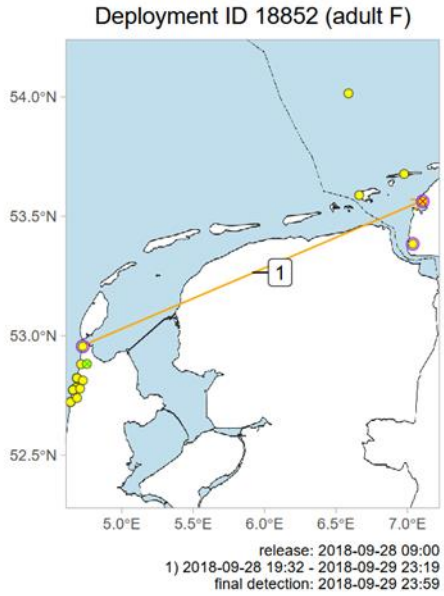


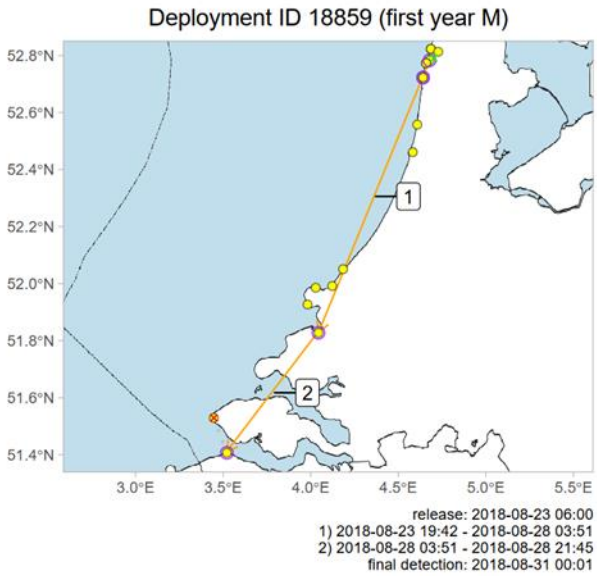
release: 2018-08-30 16:00
1) 2018-08-30 19:22 - 2018-09-01 00:59
2) 2018-09-01 00:59 - 2018-09-22 22:29
final detection: 2018-09-24 20:32

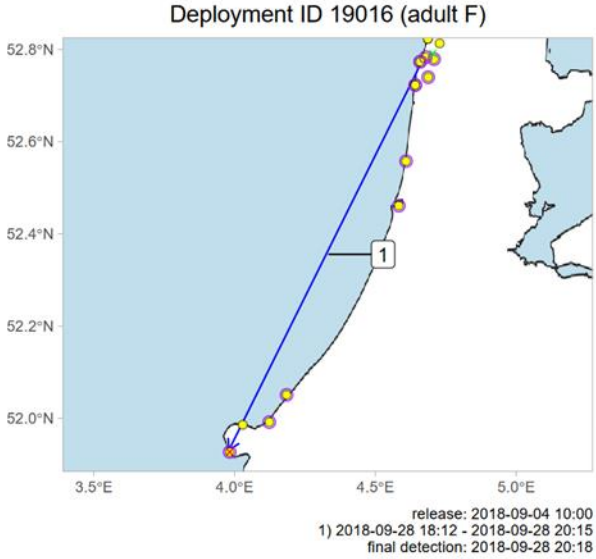
Deployment ID 18848 (first year F)

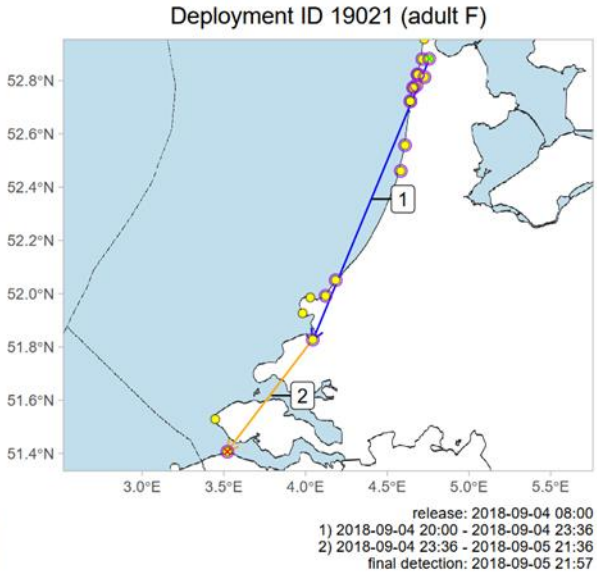


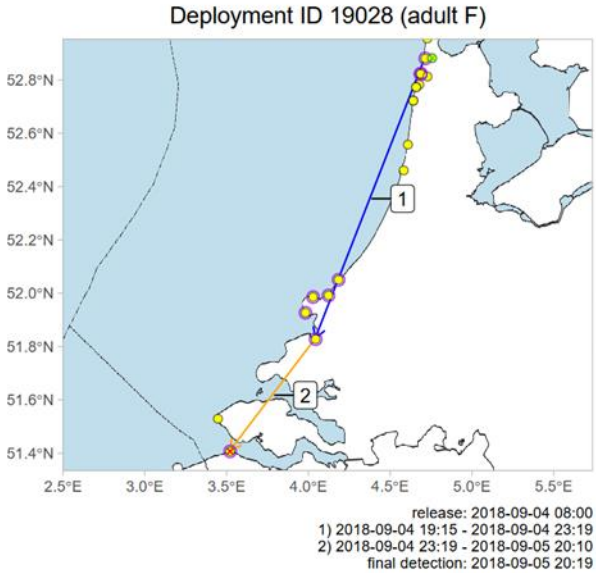
release: 2018-08-23 12:00
1) 2018-08-30 20:35 - 2018-08-30 23:47
final detection: 2018-08-31 00:10

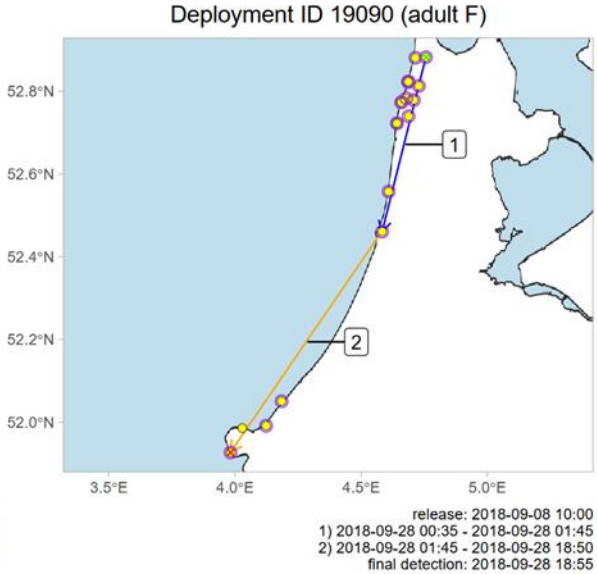

Deployment ID 18852 (adult F)
54.0°N
53.5°N
53.0°N
52.5°N
5.0°E
5.5°E
6.0°E
6.5°E
7.0°E
1
release: 2018-09-28 09:00
1) 2018-09-28 19:32 - 2018-09-29 23:19
final detection: 2018-09-29 23:59


Deployment ID 18859 (first year M)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
51.8°N
51.6°N
51.4°N
3.0°E
3.5°E
4.0°E
4.5°E
5.0°E
5.5°E
1
2
release: 2018-08-23 06:00
1) 2018-08-23 19:42 - 2018-08-28 03:51
2) 2018-08-28 03:51 - 2018-08-28 21:45
final detection: 2018-08-31 00:01

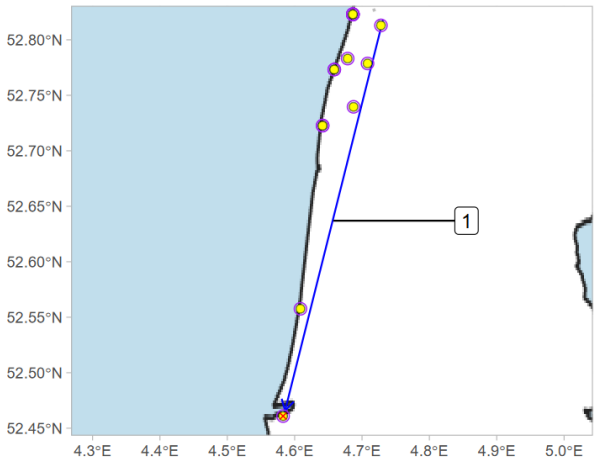

Deployment ID 19016 (adult F)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
3.5°E
4.0°E
4.5°E
5.0°E
1
release: 2018-09-04 10:00
1) 2018-09-28 18:12 - 2018-09-28 20:15
final detection: 2018-09-28 20:18


Deployment ID 19021 (adult F)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
51.8°N
51.6°N
51.4°N
3.0°E
3.5°E
4.0°E
4.5°E
5.0°E
5.5°E
1
2
release: 2018-09-04 08:00
1) 2018-09-04 20:00 - 2018-09-04 23:36
2) 2018-09-04 23:36 - 2018-09-05 21:36
final detection: 2018-09-05 21:57


Deployment ID 19028 (adult F)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
51.8°N
51.6°N
51.4°N
2.5°E
3.0°E
3.5°E
4.0°E
4.5°E
5.0°E
5.5°E
1
2
release: 2018-09-04 08:00
1) 2018-09-04 19:15 - 2018-09-04 23:19
2) 2018-09-04 23:19 - 2018-09-05 20:10
final detection: 2018-09-05 20:19

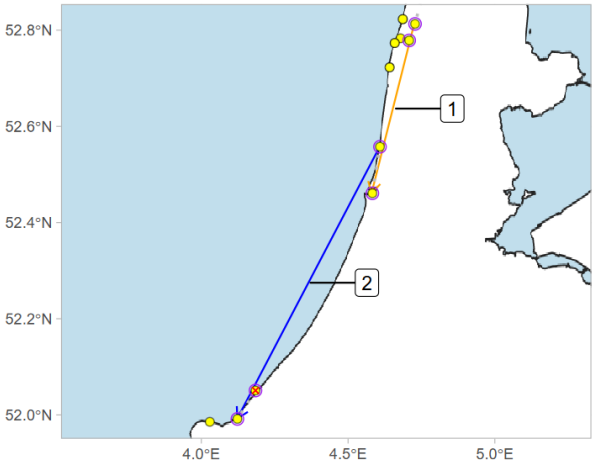

Deployment ID 19090 (adult F)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
3.5°E
4.0°E
4.5°E
5.0°E
1
2
release: 2018-09-08 10:00
1) 2018-09-28 00:35 - 2018-09-28 01:45
2) 2018-09-28 01:45 - 2018-09-28 18:50
final detection: 2018-09-28 18:55

Deployment ID 19092 (adult F)



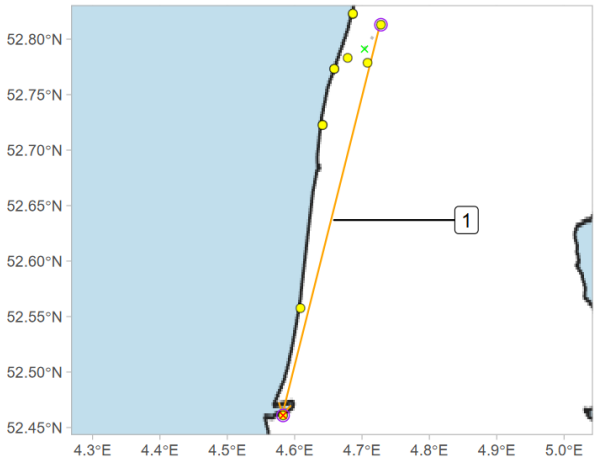
release: 2018-09-13 10:00
1) 2018-09-28 18:47 - 2018-09-28 19:40
final detection: 2018-09-28 19:43

Deployment ID 19094 (adult F)



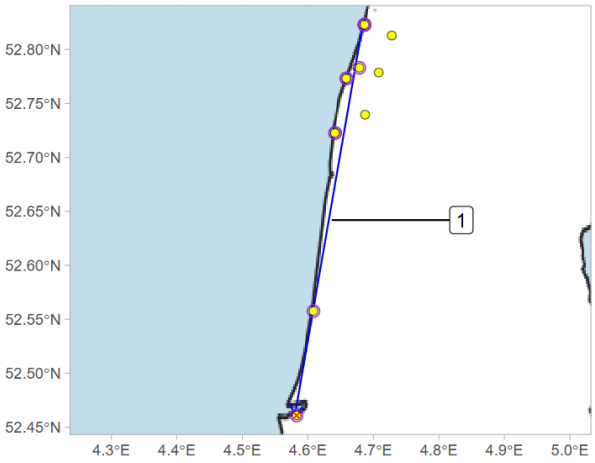
release: 2018-09-08 10:00
1) 2018-09-15 23:51 - 2018-09-16 23:08
2) 2018-09-17 22:03 - 2018-09-18 01:43
final detection: 2018-09-18 01:49

Deployment ID 19100 (adult F)



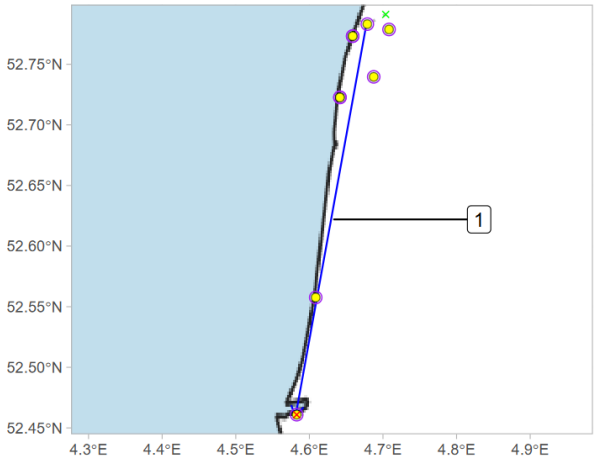
release: 2018-09-08 10:00
1) 2018-09-08 19:03 - 2018-09-19 00:43
final detection: 2018-09-19 00:44

Deployment ID 19110 (first year F)



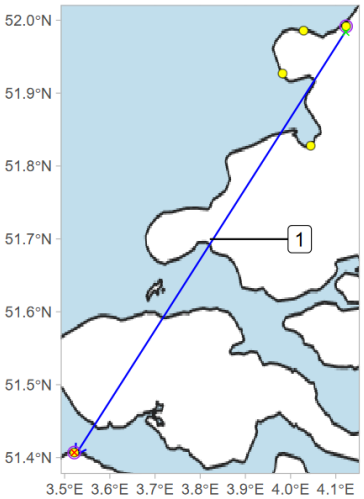
release: 2018-09-08 10:00
1) 2018-10-10 18:14 - 2018-10-10 20:15
final detection: 2018-10-10 20:19

Deployment ID 19119 (adult M)



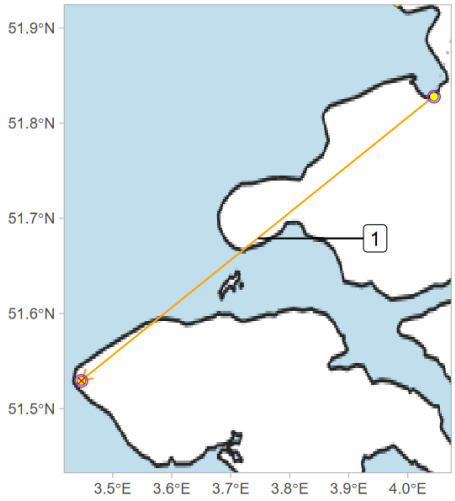
release: 2018-09-28 09:00
1) 2018-10-07 18:16 - 2018-10-07 20:05
final detection: 2018-10-07 20:10

Deployment ID 19125 (adult F)



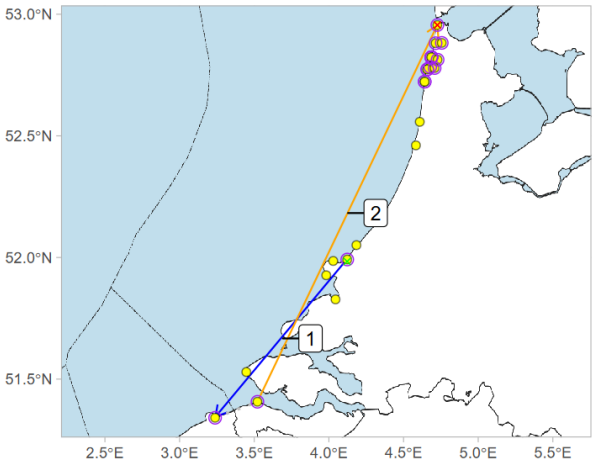
release: 2018-09-13 10:00
1) 2018-09-13 18:37 - 2018-09-13 22:50
final detection: 2018-09-13 22:51

Deployment ID 19126 (first year F)



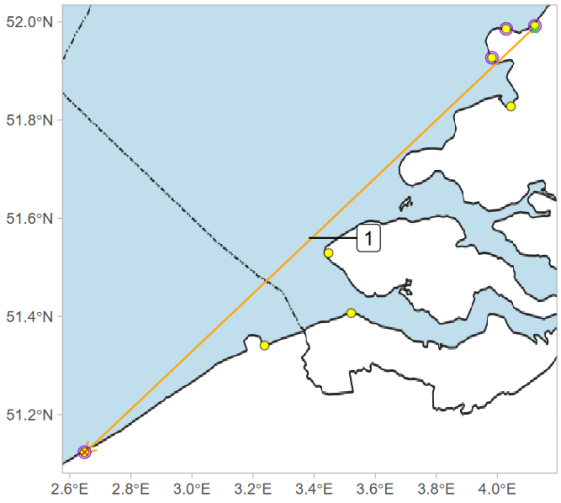
release: 2018-09-08 10:00
1) 2018-09-09 20:04 - 2018-09-12 20:39
final detection: 2018-09-12 20:45

Deployment ID 19129 (adult F)



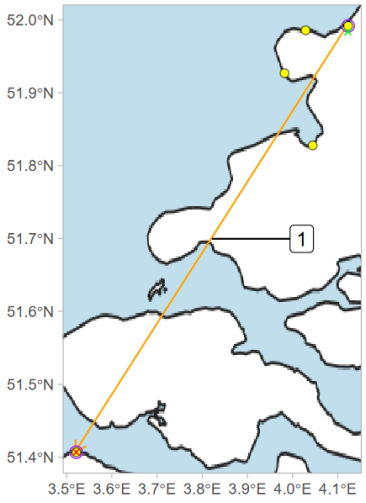
release: 2018-09-13 10:00
1) 2018-09-13 18:29 - 2018-09-13 23:19
2) 2018-09-14 22:21 - 2018-09-17 21:24
final detection: 2018-09-17 21:43

Deployment ID 19132 (adult F)



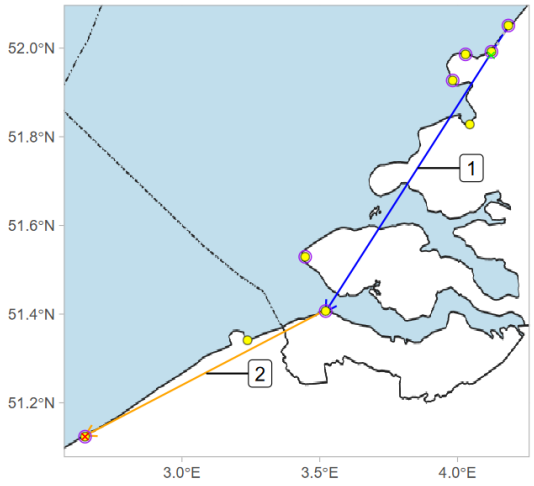
release: 2018-09-13 10:00
1) 2018-09-13 18:46 - 2018-09-14 20:26
final detection: 2018-09-14 20:28

Deployment ID 19133 (adult F)



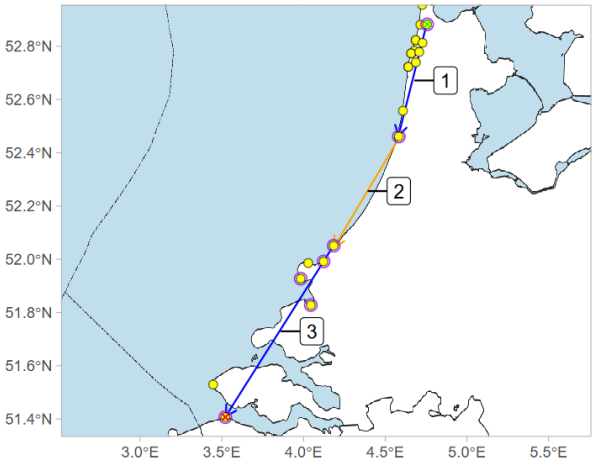
release: 2018-09-13 10:00
1) 2018-09-13 18:56 - 2018-09-14 22:23
final detection: 2018-09-14 22:25

Deployment ID 19138 (adult F)



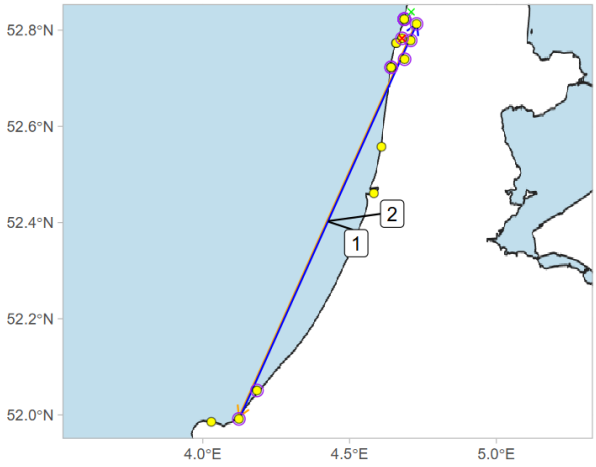
release: 2018-09-08 10:00
1) 2018-09-12 20:18 - 2018-09-12 22:39
2) 2018-09-12 22:39 - 2018-09-13 20:19
final detection: 2018-09-13 20:23

Deployment ID 19468 (adult F)



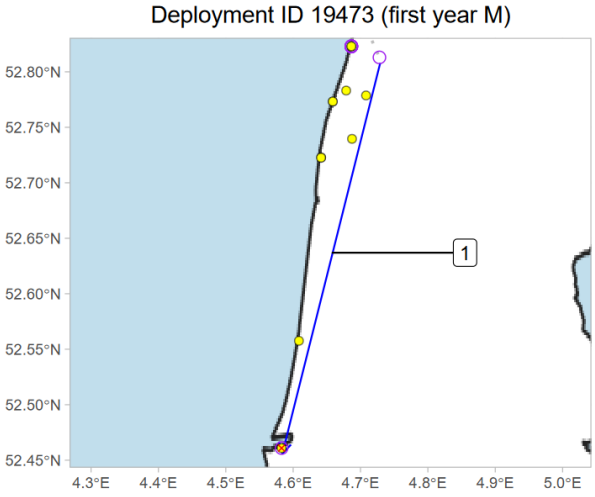
release: 2018-09-22 09:00
1) 2018-10-05 18:16 - 2018-10-05 21:06
2) 2018-10-05 22:27 - 2018-10-07 17:47
3) 2018-10-07 18:01 - 2018-10-07 21:20
final detection: 2018-10-07 21:37

Deployment ID 19470 (adult F)



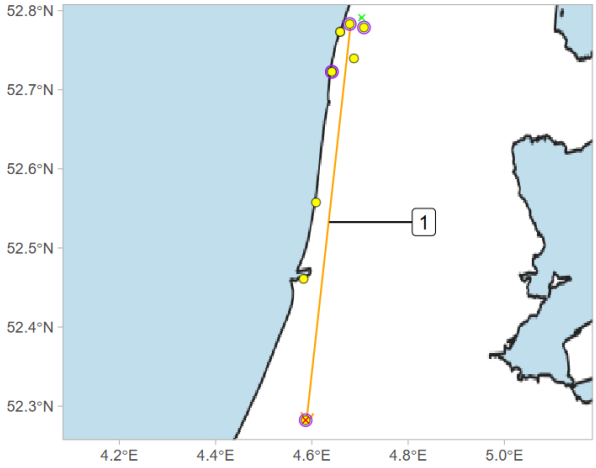
release: 2018-09-23 09:00
1) 2018-09-23 19:15 - 2018-09-25 23:37
2) 2018-09-25 23:37 - 2018-09-26 02:18
final detection: 2018-09-30 19:29

Deployment ID 19473 (first year M)



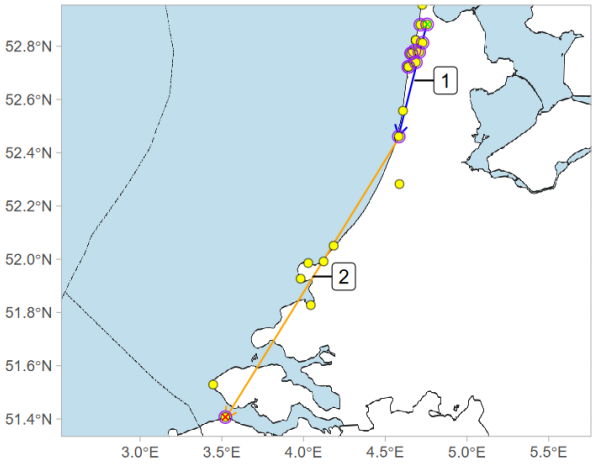
release: 2018-09-23 09:00
1) 2018-10-06 18:13 - 2018-10-06 19:31
final detection: 2018-11-06 04:42

Deployment ID 19479 (adult M)



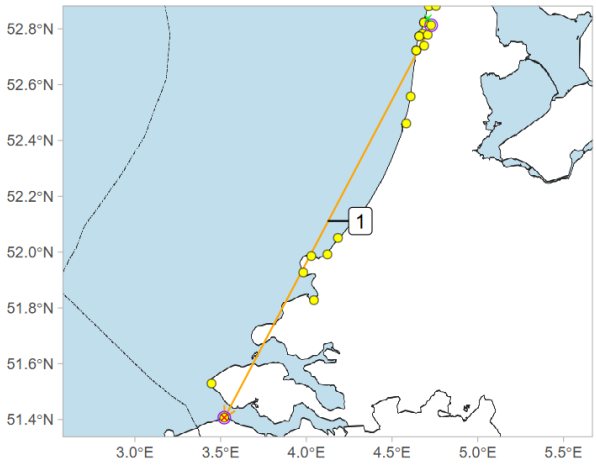
release: 2018-10-09 10:00
1) 2018-11-02 17:19 - 2018-11-05 17:49
final detection: 2018-11-05 17:50

Deployment ID 19487 (adult F)



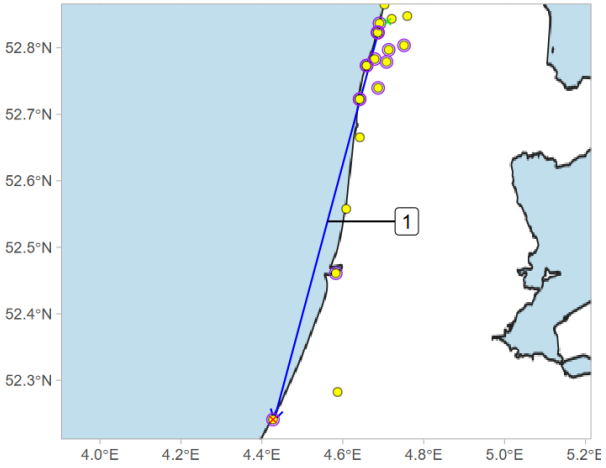
release: 2018-09-22 09:00
1) 2018-10-17 17:52 - 2018-10-17 19:24
2) 2018-10-17 19:24 - 2018-10-18 17:55
final detection: 2018-10-18 18:16

Deployment ID 19488 (adult F)



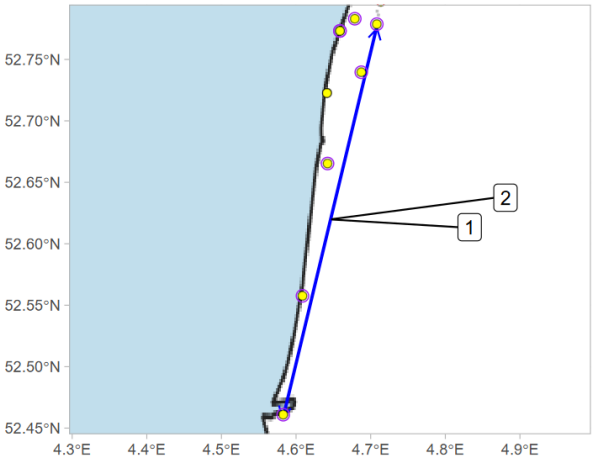
release: 2018-09-23 09:00
1) 2018-09-23 18:26 - 2018-09-28 22:16
final detection: 2018-09-28 22:18

Deployment ID 25088 (adult M)



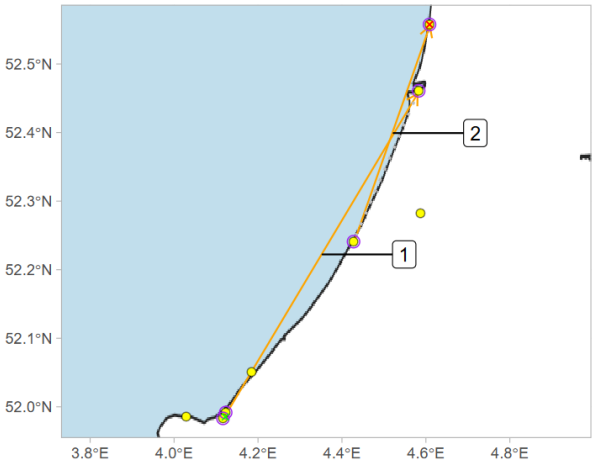
release: 2019-08-27 10:00
1) 2019-08-27 20:44 - 2019-08-28 02:40
final detection: 2019-08-28 02:40

Deployment ID 25090 (adult F)



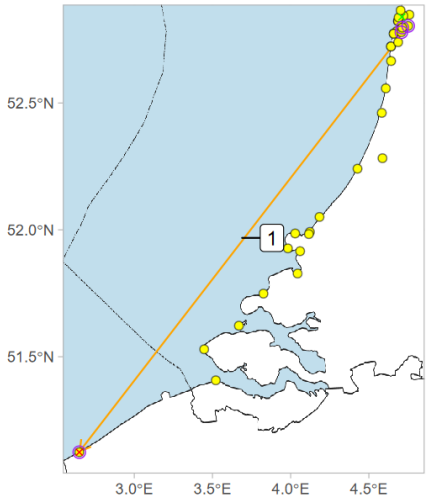
release: 2019-08-27 10:00
1) 2019-08-30 19:18 - 2019-08-30 21:54
2) 2019-08-30 23:34 - 2019-08-31 00:26
final detection: 2019-08-31 03:49

Deployment ID 25096 (first year F)



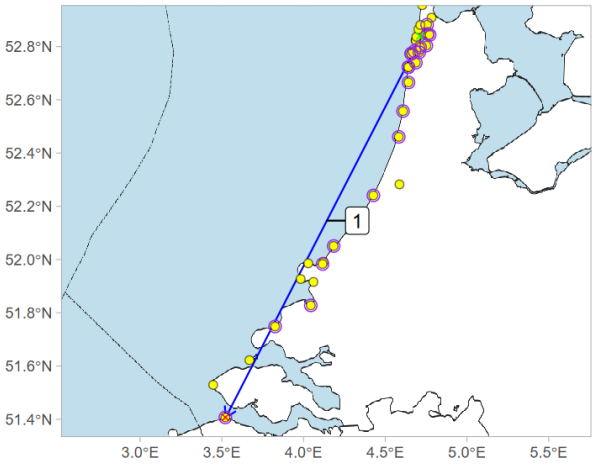
release: 2019-09-10 10:00
1) 2019-09-10 18:45 - 2019-09-13 20:33
2) 2019-09-13 21:22 - 2019-09-18 21:12
final detection: 2019-09-18 21:13

Deployment ID 25106 (adult F)



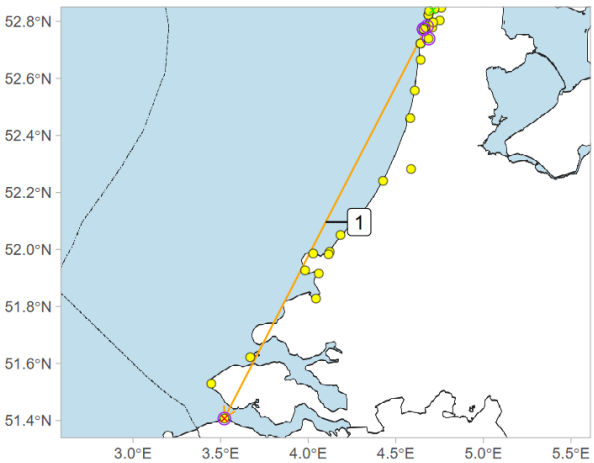
release: 2019-08-27 10:00
1) 2019-08-29 20:17 - 2019-09-09 23:36
final detection: 2019-09-09 23:36

Deployment ID 25115 (first year F)



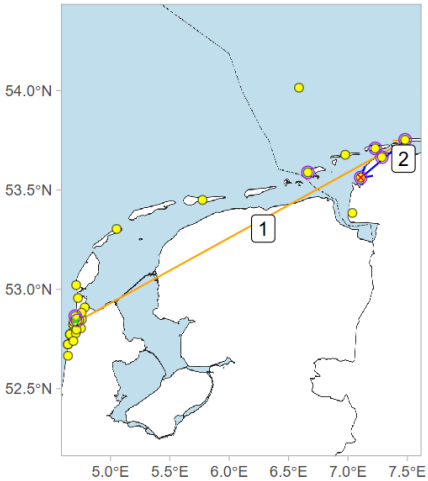
release: 2019-10-01 10:00
1) 2019-10-20 17:07 - 2019-10-20 21:19
final detection: 2019-10-20 21:32

Deployment ID 25118 (adult F)



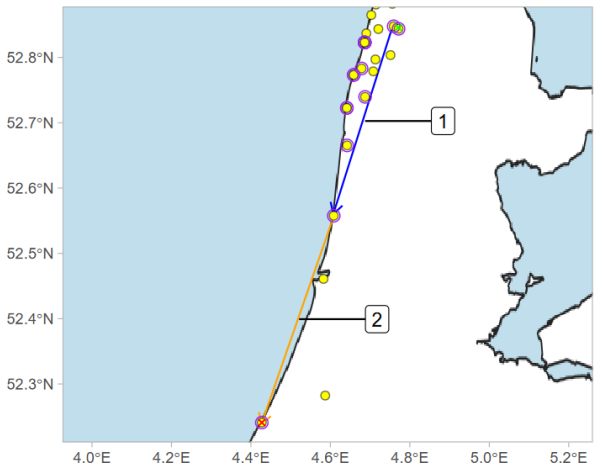
release: 2019-08-27 10:00
1) 2019-08-27 21:32 - 2019-09-04 21:29
final detection: 2019-09-04 21:31

Deployment ID 25119 (first year M)



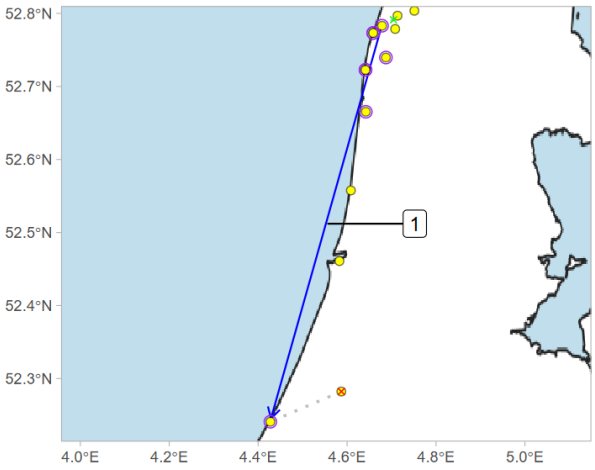
release: 2019-08-27 10:00
1) 2019-08-27 19:31 - 2019-08-30 01:22
2) 2019-08-30 19:13 - 2019-08-30 23:52
final detection: 2019-08-30 23:58

Deployment ID 25127 (adult F)



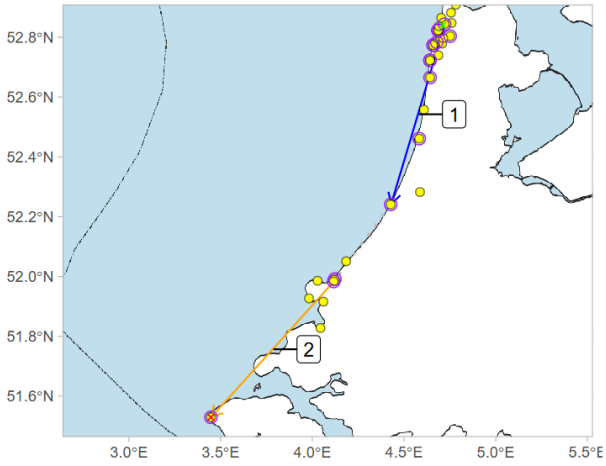
release: 2019-09-15 10:00
1) 2019-10-03 18:23 - 2019-10-03 20:18
2) 2019-10-03 20:18 - 2019-10-05 19:08
final detection: 2019-10-05 19:09

Deployment ID 25130 (adult F)



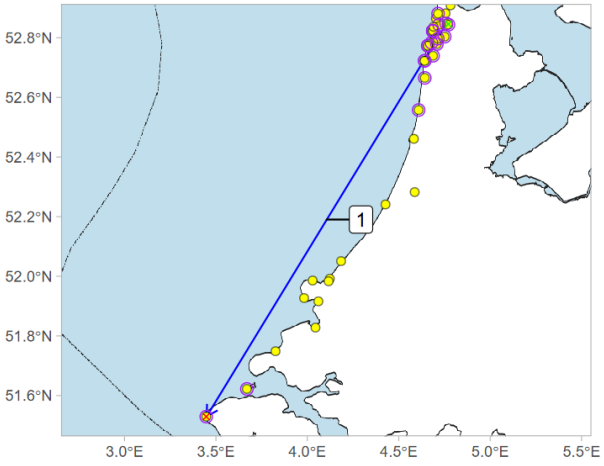
release: 2019-09-10 10:00
1) 2019-09-10 19:39 - 2019-09-10 22:56
final detection: 2019-09-11 21:43

Deployment ID 25136 (adult F)



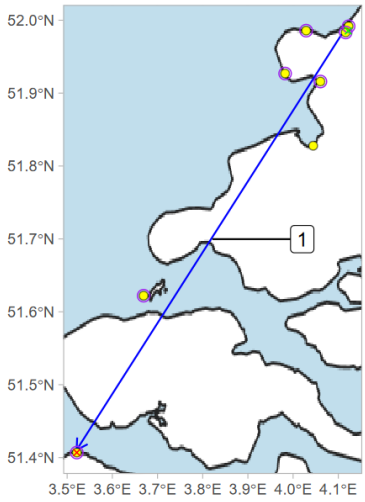
release: 2019-08-20 10:00
1) 2019-08-20 19:44 - 2019-08-21 00:18
2) 2019-08-21 21:20 - 2019-08-22 22:59
final detection: 2019-08-22 23:03

Deployment ID 25138 (first year F)



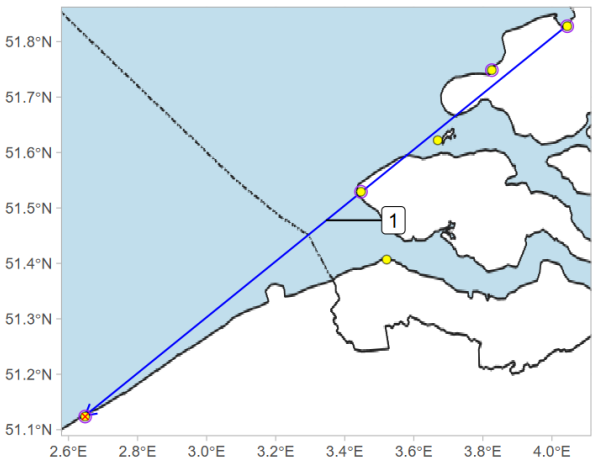
release: 2019-09-15 10:00
1) 2019-09-18 19:14 - 2019-09-19 02:29
final detection: 2019-09-19 02:42

Deployment ID 25140 (adult F)



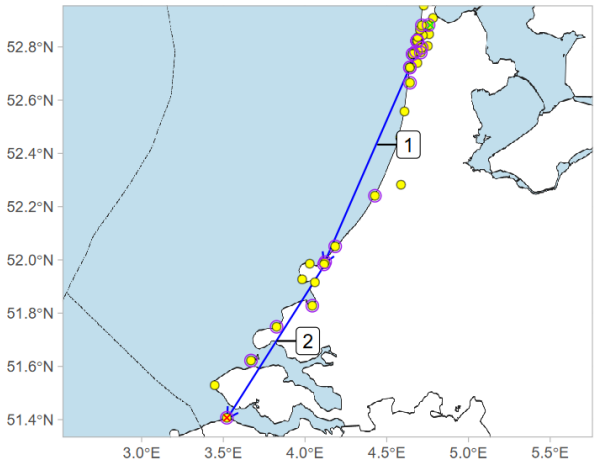
release: 2019-08-27 10:00
1) 2019-08-27 19:29 - 2019-08-27 23:18
final detection: 2019-08-27 23:44

Deployment ID 25145 (first year M)



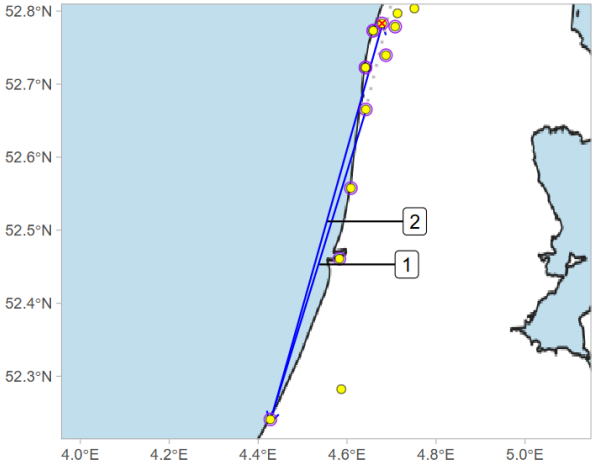
release: 2019-10-01 10:00
1) 2019-10-20 17:45 - 2019-10-20 20:35
final detection: 2019-10-20 20:35

Deployment ID 25146 (first year F)



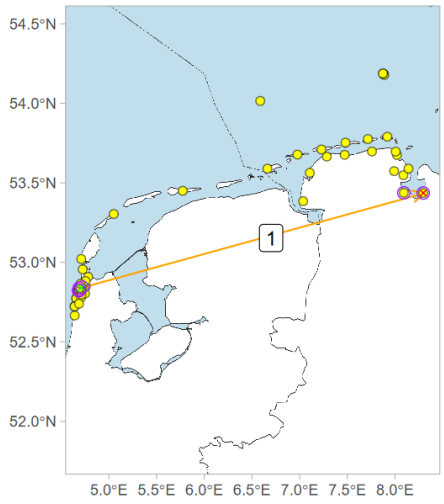
release: 2019-09-10 10:00
1) 2019-09-10 18:47 - 2019-09-11 01:04
2) 2019-09-13 18:59 - 2019-09-13 20:59
final detection: 2019-09-13 21:00

Deployment ID 25151 (adult F)



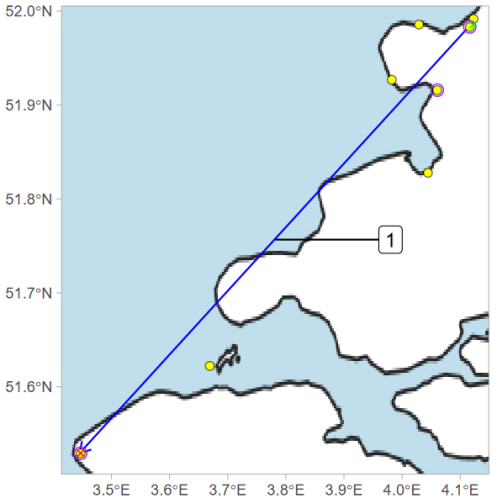
release: 2019-08-27 10:00
1) 2019-08-30 19:26 - 2019-08-30 23:33
2) 2019-08-30 23:43 - 2019-08-31 01:20
final detection: 2019-09-02 11:41

Deployment ID 25155 (adult F)



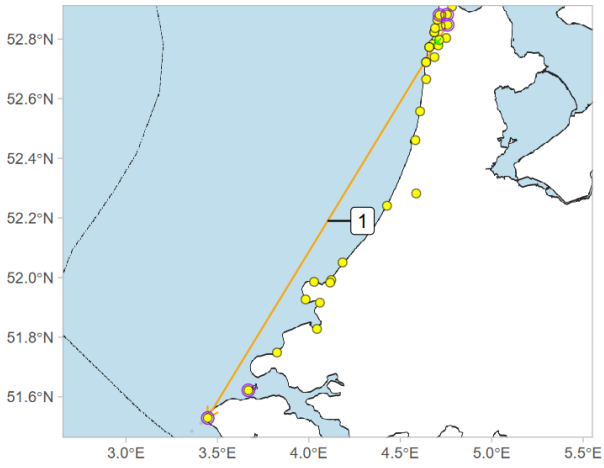
release: 2019-08-27 10:00
1) 2019-08-27 19:28 - 2019-08-30 01:19
final detection: 2019-08-30 01:19

Deployment ID 25170 (first year F)



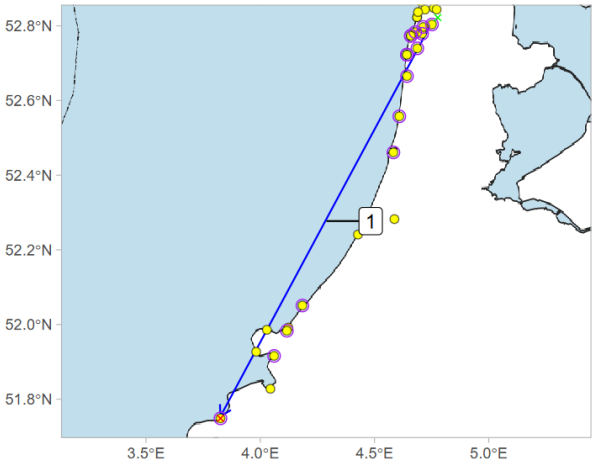
release: 2019-08-27 10:00
1) 2019-08-27 20:23 - 2019-08-28 00:41
final detection: 2019-08-28 01:02

Deployment ID 25180 (first year F)



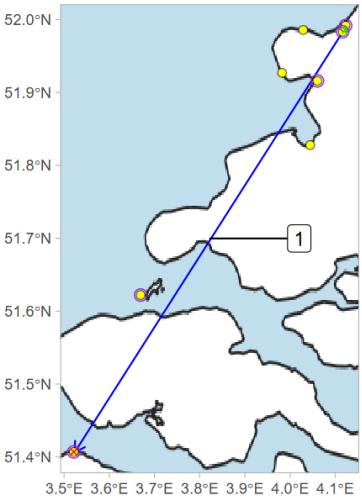
release: 2019-09-03 10:00
1) 2019-09-05 19:54 - 2019-09-09 21:57
final detection: 2019-09-10 21:45

Deployment ID 25221 (adult F)



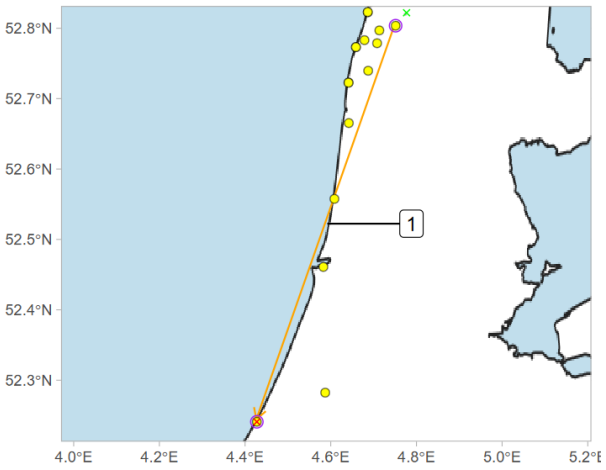
release: 2019-09-24 10:00
1) 2019-10-20 17:16 - 2019-10-20 20:48
final detection: 2019-10-20 20:58

Deployment ID 25226 (adult F)



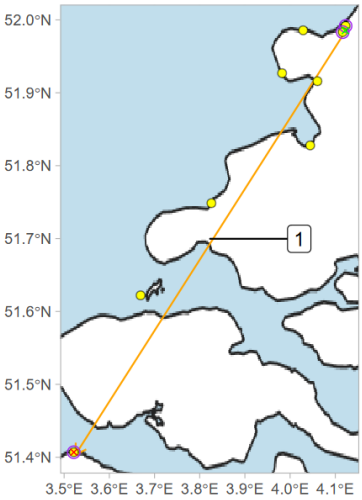
release: 2019-08-27 10:00
1) 2019-08-27 19:09 - 2019-08-27 23:47
final detection: 2019-08-27 23:53

Deployment ID 25958 (adult F)



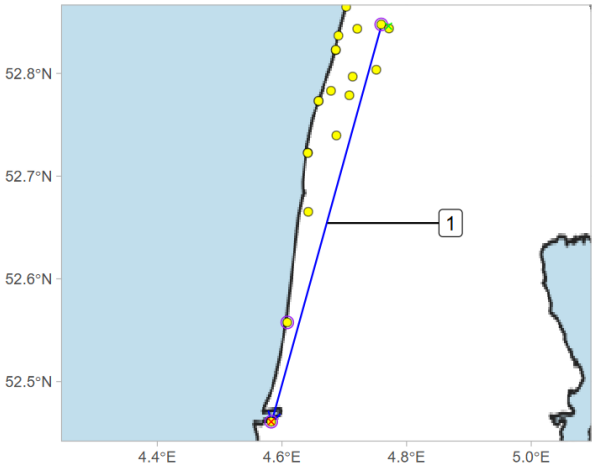
release: 2019-09-17 12:00
1) 2019-10-14 22:47 - 2019-10-24 01:26
final detection: 2019-10-24 01:29

Deployment ID 25968 (adult F)



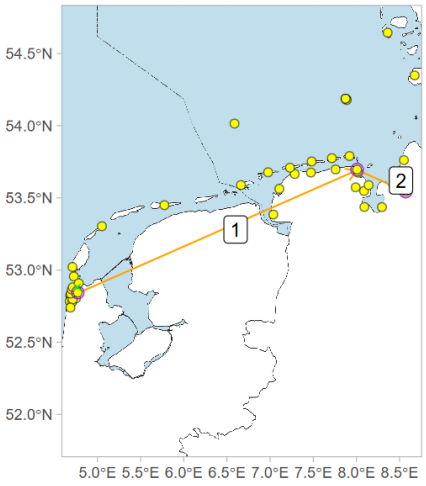
release: 2019-10-01 10:00
1) 2019-10-01 17:57 - 2019-10-05 20:44
final detection: 2019-10-05 20:44

Deployment ID 25970 (adult F)



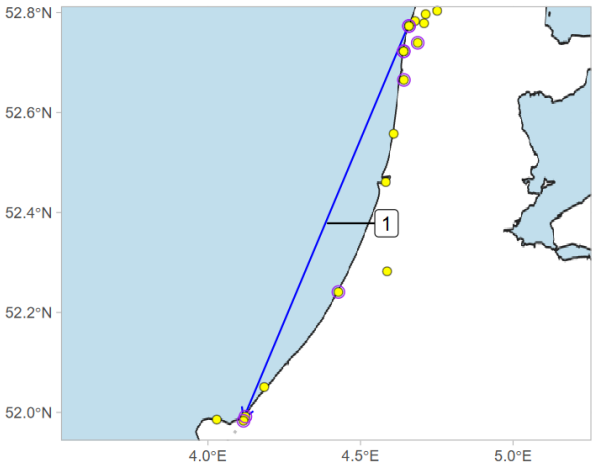
release: 2019-09-15 10:00
1) 2019-10-20 18:31 - 2019-10-20 20:57
final detection: 2019-10-20 20:58

Deployment ID 26140 (adult F)



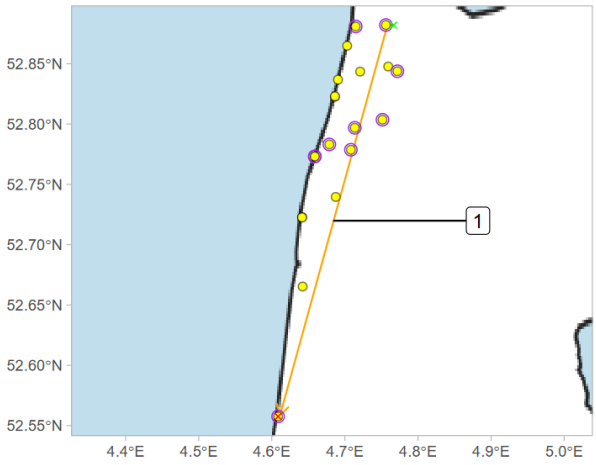
release: 2019-09-24 10:00
1) 2019-10-08 17:38 - 2019-10-10 19:42
2) 2019-10-10 19:42 - 2019-10-13 22:59
final detection: 2019-10-13 22:59

Deployment ID 26143 (adult F)



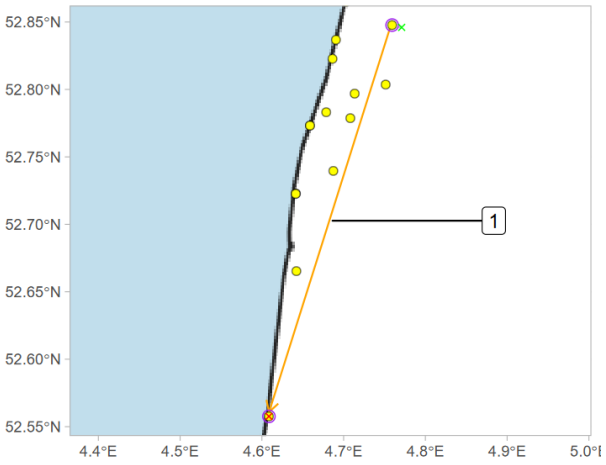
release: 2019-09-17 12:00
1) 2019-10-14 17:44 - 2019-10-14 22:41
final detection: 2019-10-17 19:45

Deployment ID 26147 (adult F)



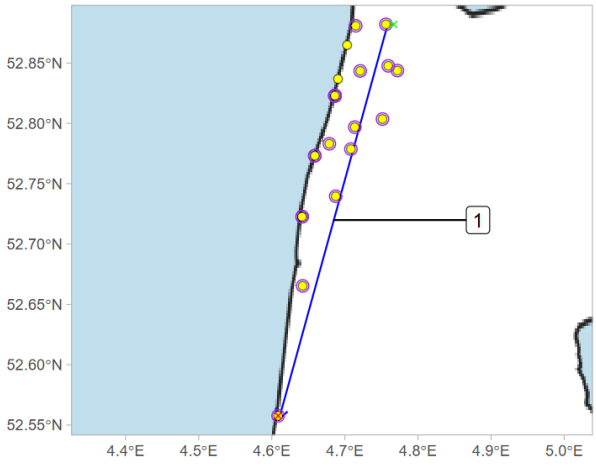
release: 2019-09-21 10:00
1) 2019-09-21 18:28 - 2019-10-05 19:44
final detection: 2019-10-05 20:49

Deployment ID 26155 (adult M)



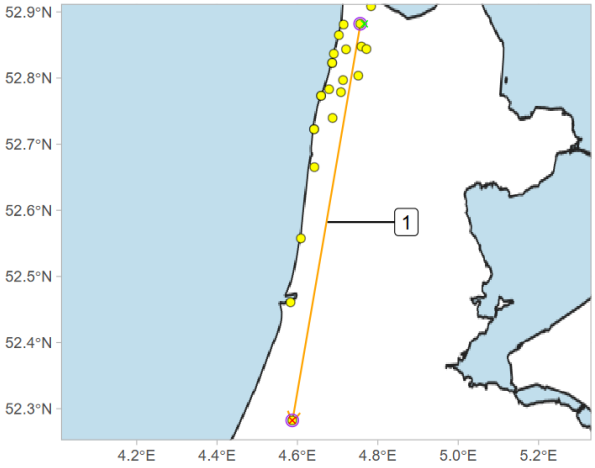
release: 2019-09-24 10:00
1) 2019-11-20 12:35 - 2019-11-29 19:33
final detection: 2019-11-29 19:35

Deployment ID 26159 (adult F)



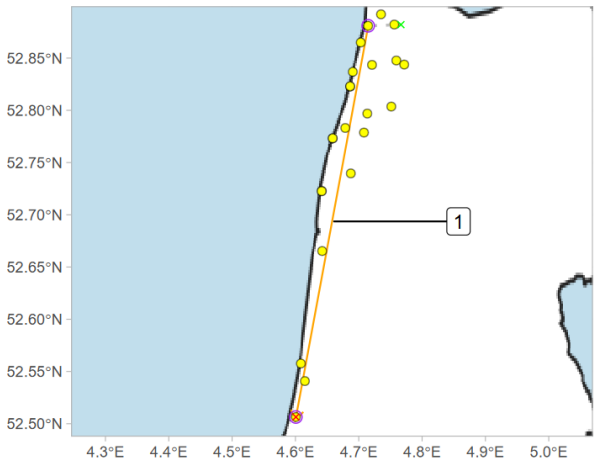
release: 2019-09-24 10:00
1) 2019-10-01 22:36 - 2019-10-01 23:25
final detection: 2019-10-01 23:27

Deployment ID 26641 (adult M)



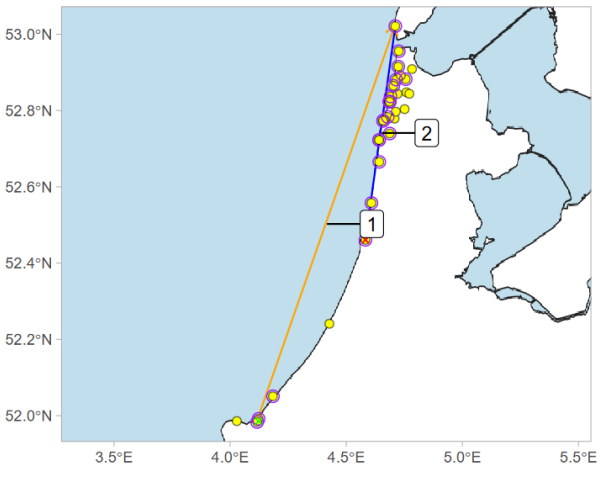
release: 2019-10-15 10:00
1) 2019-10-18 22:59 - 2019-10-27 21:12
final detection: 2019-10-27 21:12

Deployment ID 29172 (first year F)



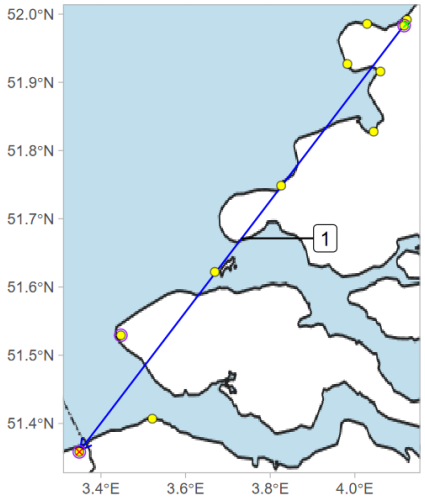
release: 2020-09-14 20:10
1) 2020-09-14 21:13 - 2020-10-13 18:52
final detection: 2020-10-13 18:54

Deployment ID 29174 (adult F)



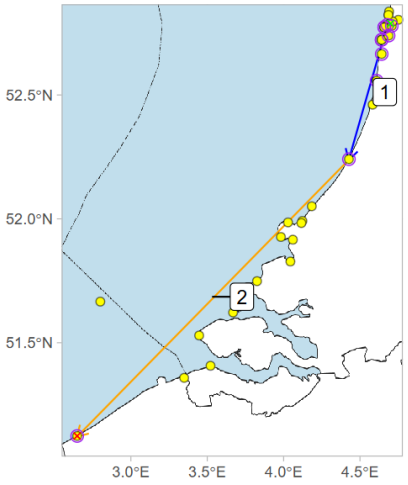
release: 2020-09-22 09:00
1) 2020-09-22 18:44 - 2020-09-27 21:19
2) 2020-09-29 18:20 - 2020-09-29 22:36
final detection: 2020-09-29 22:36

Deployment ID 29175 (first year F)



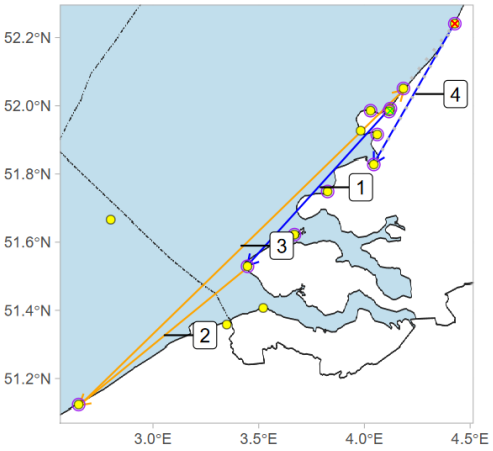
release: 2020-09-13 11:30
1) 2020-09-13 18:55 - 2020-09-14 01:39
final detection: 2020-09-14 01:40

Deployment ID 29176 (first year F)



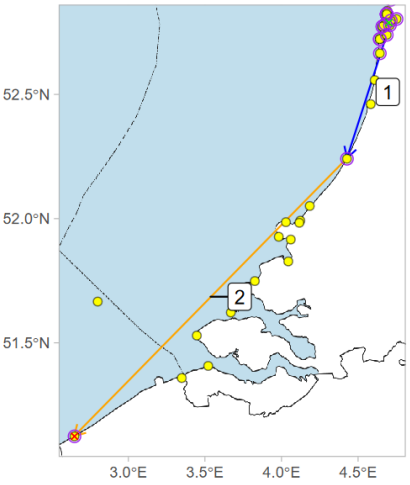
release: 2020-09-02 22:00
1) 2020-09-06 21:06 - 2020-09-07 00:01
2) 2020-09-08 22:04 - 2020-09-10 22:45
final detection: 2020-09-10 22:46

Deployment ID 29177 (adult F)



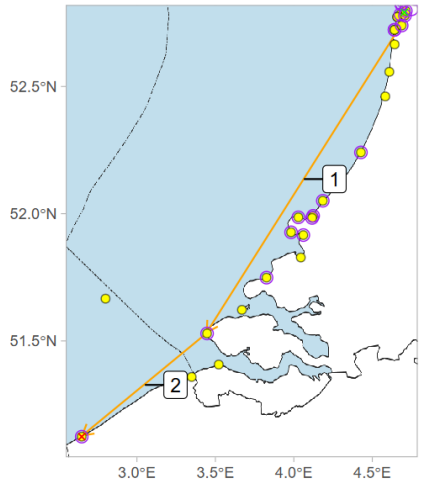
release: 2020-09-01 10:00
1) 2020-09-01 19:15 - 2020-09-01 22:10
2) 2020-09-01 22:10 - 2020-09-02 21:35
3) 2020-09-02 21:35 - 2020-09-07 22:16
4) 2020-09-09 21:12 - 2020-09-10 00:27
final detection: 2020-09-14 20:23

Deployment ID 29179 (adult F)



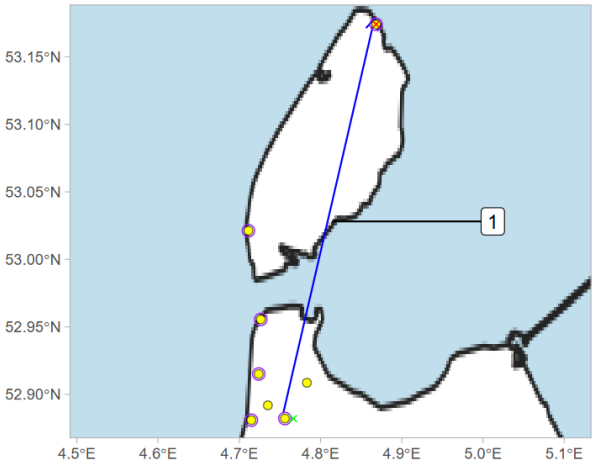
release: 2020-09-13 07:00
1) 2020-09-13 18:58 - 2020-09-13 23:20
2) 2020-09-13 23:20 - 2020-09-14 22:26
final detection: 2020-09-14 22:30

Deployment ID 29181 (first year F)



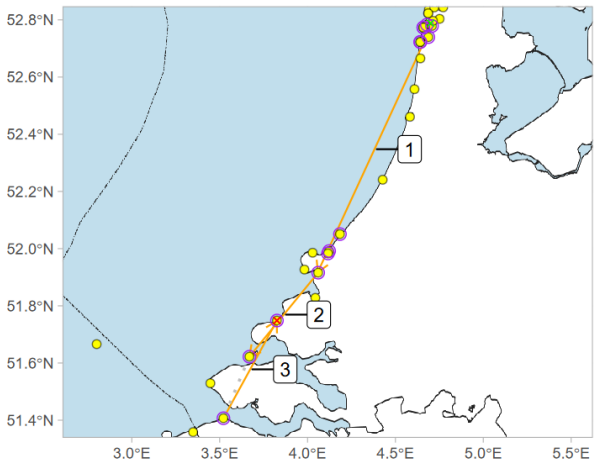
release: 2020-09-04 10:00
1) 2020-09-09 00:40 - 2020-09-10 01:57
2) 2020-09-10 01:57 - 2020-09-10 21:56
final detection: 2020-09-10 21:57

Deployment ID 29188 (first year F)



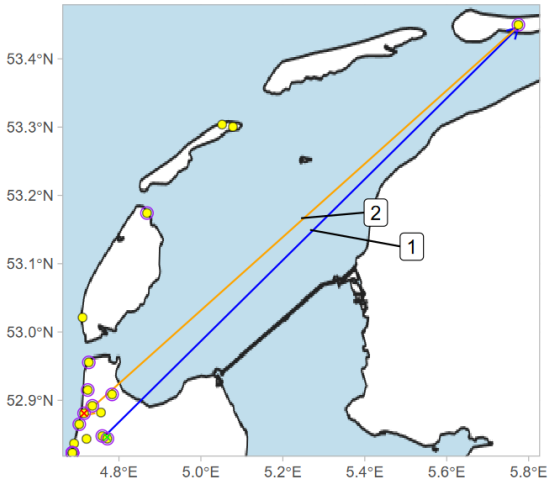
release: 2020-09-22 20:00
1) 2020-09-22 22:43 - 2020-09-22 23:39
final detection: 2020-09-22 23:40

Deployment ID 29191 (first year M)



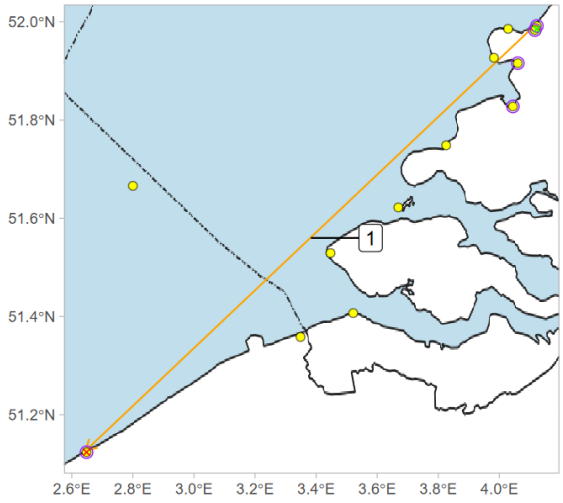
release: 2020-09-02 23:00
1) 2020-09-07 23:22 - 2020-09-10 02:10
2) 2020-09-10 02:10 - 2020-09-18 00:55
3) 2020-09-21 02:41 - 2020-09-21 20:38
final detection: 2020-09-21 20:40

Deployment ID 29194 (adult F)



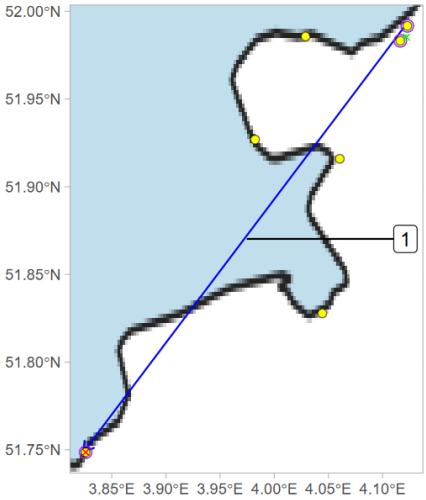
release: 2020-09-13 12:00
1) 2020-09-13 18:41 - 2020-09-13 23:07
2) 2020-09-13 23:07 - 2020-09-14 20:02
final detection: 2020-09-14 20:16

Deployment ID 29195 (first year F)



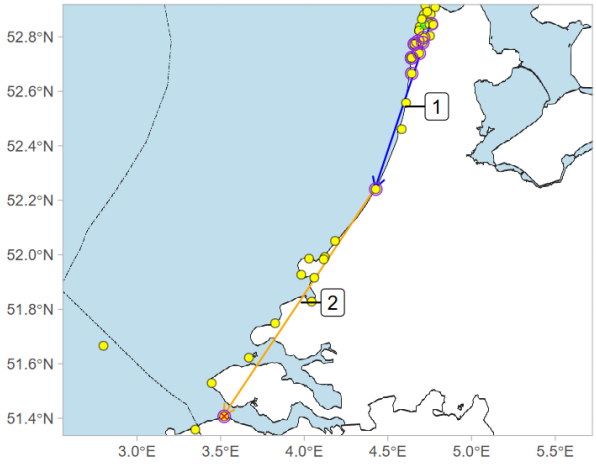
release: 2020-09-01 10:00
1) 2020-09-01 19:23 - 2020-09-02 21:57
final detection: 2020-09-02 21:58

Deployment ID 29200 (first year F)



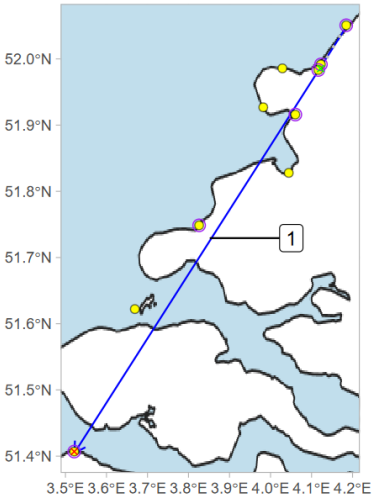
release: 2020-09-15 17:30
1) 2020-09-15 18:56 - 2020-09-15 21:23
final detection: 2020-09-15 21:24

Deployment ID 29201 (adult F)



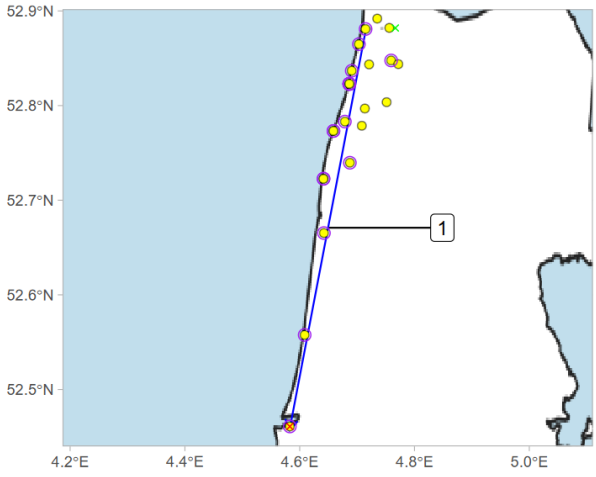
release: 2020-09-13 10:00
1) 2020-09-14 20:10 - 2020-09-14 23:36
2) 2020-09-14 23:36 - 2020-09-16 00:35
final detection: 2020-09-16 01:01

Deployment ID 29207 (adult M)



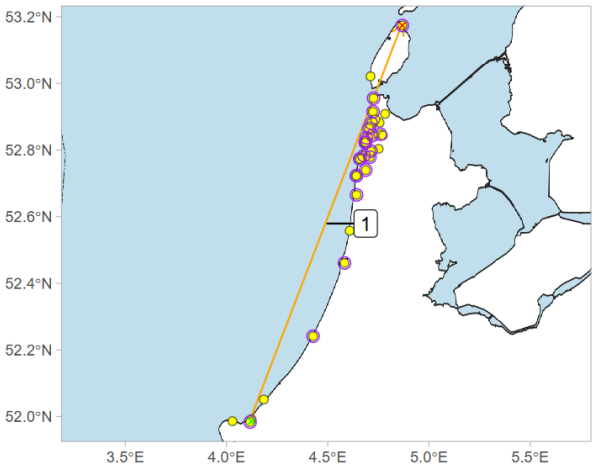
release: 2020-10-13 20:45
1) 2020-10-14 17:31 - 2020-10-14 19:15
final detection: 2020-10-14 19:17

Deployment ID 29210 (adult F)



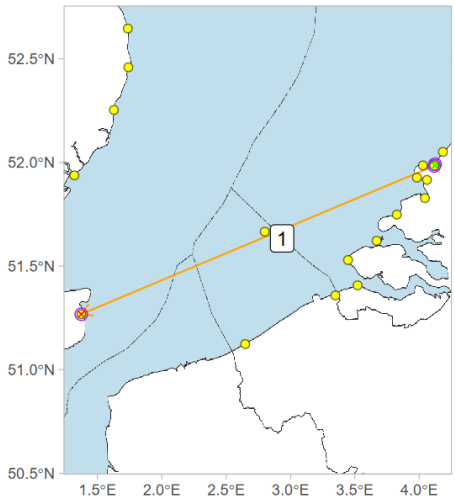
release: 2020-09-14 22:15
1) 2020-09-14 23:23 - 2020-09-15 01:36
final detection: 2020-09-15 01:37

Deployment ID 29212 (first year F)



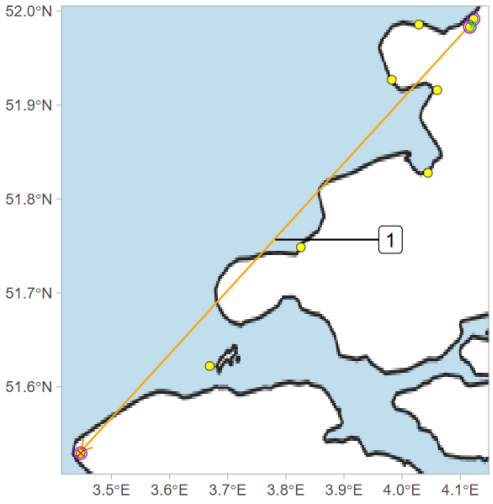
release: 2020-09-01 10:00
1) 2020-09-01 19:37 - 2020-09-14 00:21
final detection: 2020-09-14 00:30

Deployment ID 29213 (first year F)



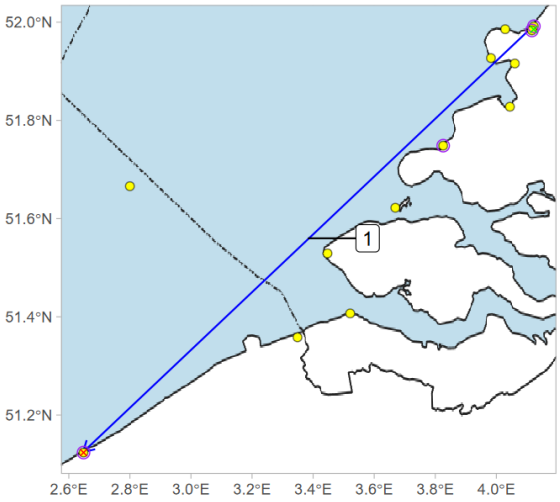
release: 2020-09-15 17:00
1) 2020-09-15 19:39 - 2020-09-22 04:45
final detection: 2020-09-22 04:45

Deployment ID 29219 (first year F)



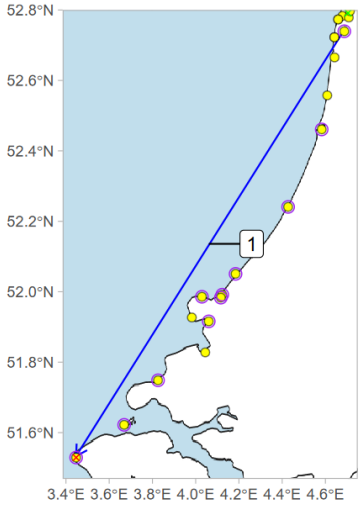
release: 2020-09-22 05:40
1) 2020-09-22 18:25 - 2020-09-29 23:55
final detection: 2020-09-29 23:56

Deployment ID 29233 (first year F)



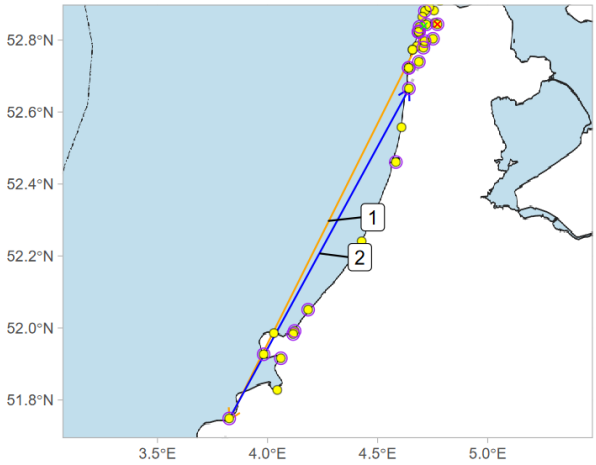
release: 2020-09-01 10:00
1) 2020-09-01 19:02 - 2020-09-02 02:16
final detection: 2020-09-02 21:50

Deployment ID 29234 (first year F)



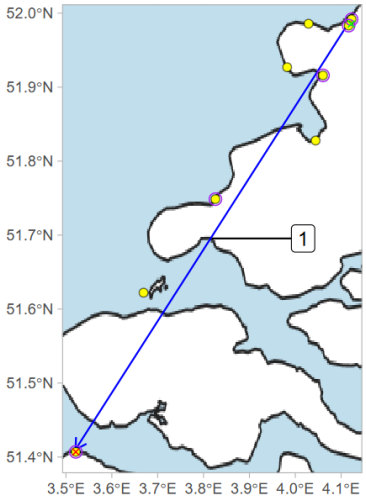
release: 2020-09-08 11:30
1) 2020-09-09 20:05 - 2020-09-10 01:31
final detection: 2020-09-10 01:36

Deployment ID 29259 (adult M)



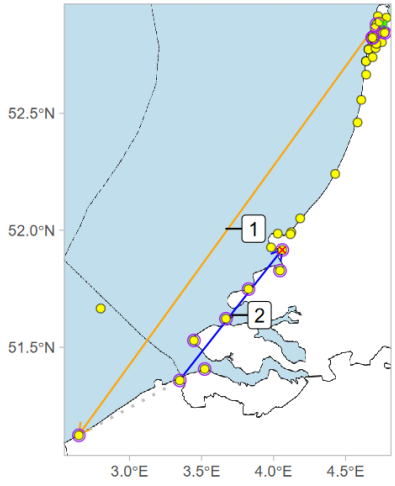
release: 2020-09-13 10:00
1) 2020-10-02 19:19 - 2020-10-03 21:03
2) 2020-10-05 17:43 - 2020-10-05 19:48
final detection: 2020-10-07 17:47

Deployment ID 29262 (first year F)



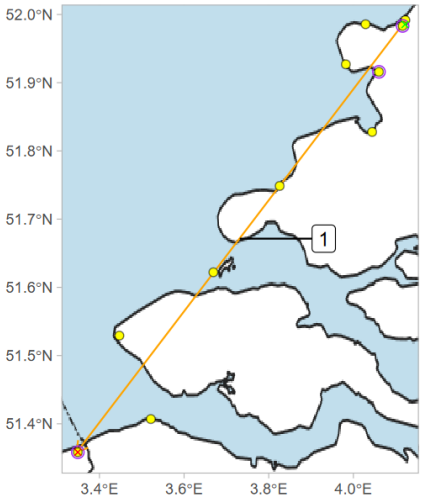
release: 2020-09-15 17:30
1) 2020-09-15 19:53 - 2020-09-16 02:14
final detection: 2020-09-16 02:18

Deployment ID 29263 (first year M)



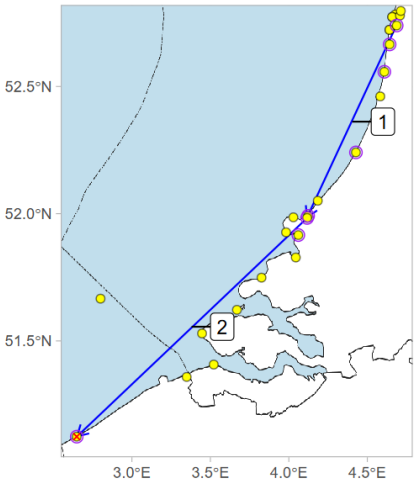
release: 2020-09-08 07:00
1) 2020-09-09 00:17 - 2020-09-11 00:25
2) 2020-09-23 23:00 - 2020-09-24 00:10
final detection: 2020-09-24 00:11

Deployment ID 29277 (first year F)



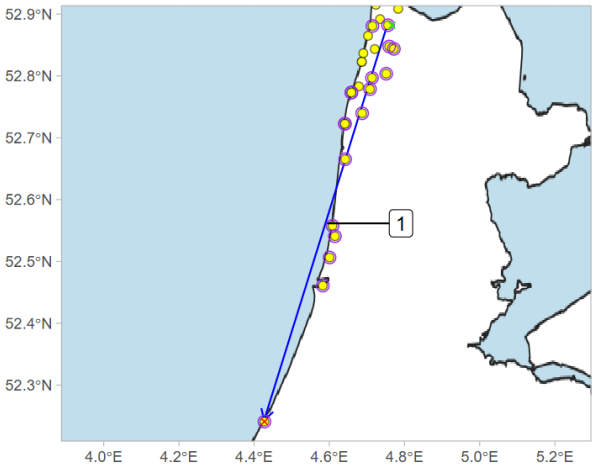
release: 2020-09-04 05:30
1) 2020-09-05 22:12 - 2020-09-09 23:20
final detection: 2020-09-09 23:23

Deployment ID 29280 (adult F)

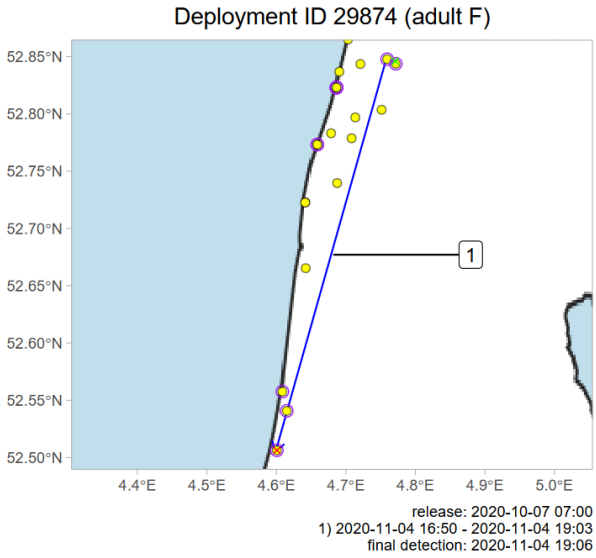


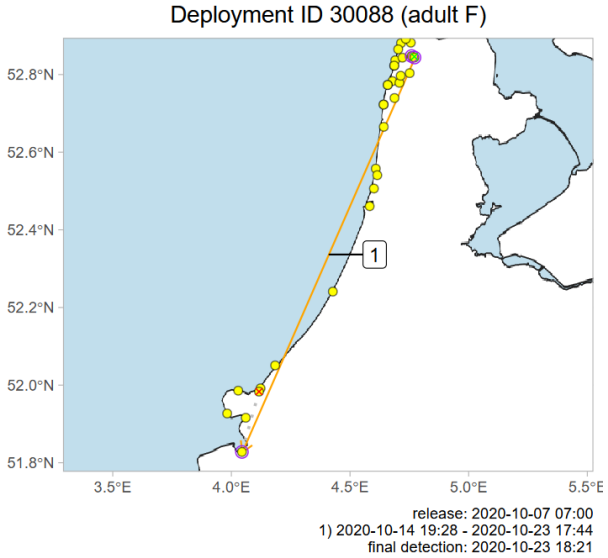
release: 2020-09-13 10:00
1) 2020-09-13 20:44 - 2020-09-14 02:13
2) 2020-09-14 19:14 - 2020-09-14 23:27
final detection: 2020-09-14 23:28

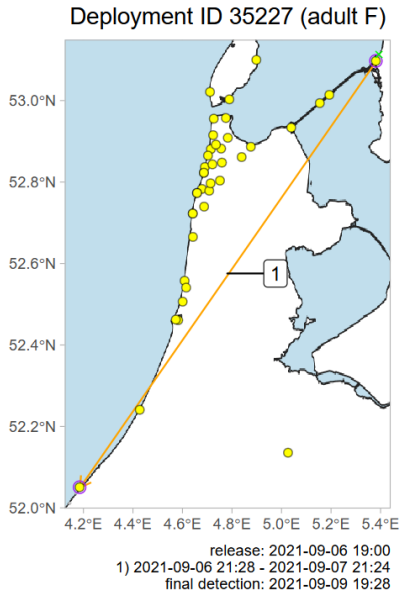
Deployment ID 29294 (first year F)

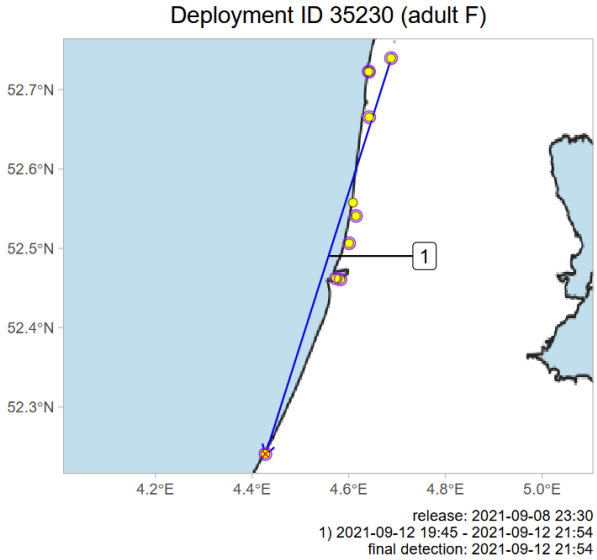


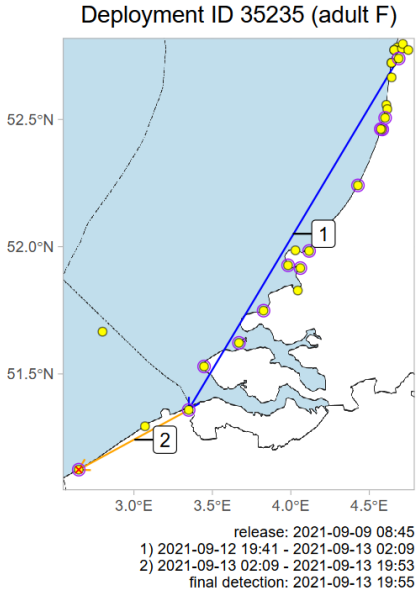
release: 2020-09-11 20:55
1) 2020-10-10 17:44 - 2020-10-10 19:58
final detection: 2020-10-10 20:01

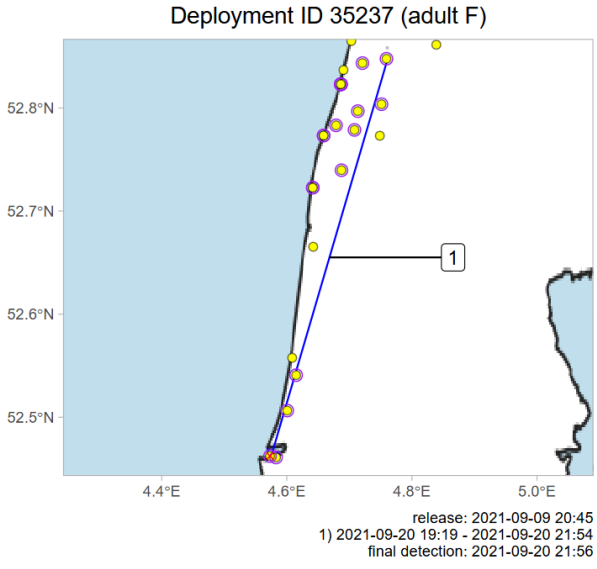

Deployment ID 29874 (adult F)
52.85°N
52.80°N
52.75°N
52.70°N
52.65°N
52.60°N
52.55°N
52.50°N
4.4°E
4.5°E
4.6°E
4.7°E
4.8°E
4.9°E
5.0°E
1
release: 2020-10-07 07:00
1) 2020-11-04 16:50 - 2020-11-04 19:03
final detection: 2020-11-04 19:06


Deployment ID 30088 (adult F)
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
51.8°N
3.5°E
4.0°E
4.5°E
5.0°E
5.5°E
1
release: 2020-10-07 07:00
1) 2020-10-14 19:28 - 2020-10-23 17:44
final detection: 2020-10-23 18:21

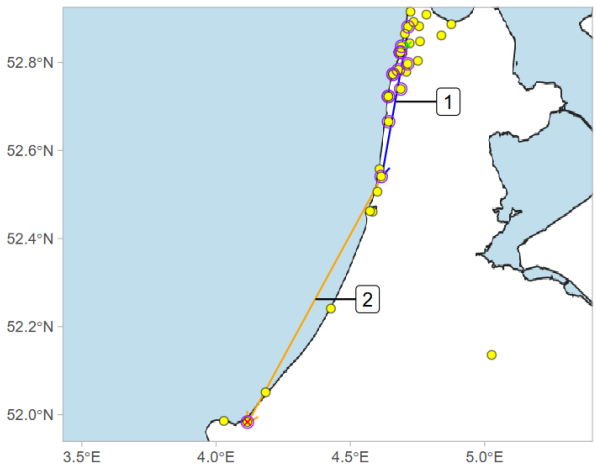

Deployment ID 35227 (adult F)
53.0°N
52.8°N
52.6°N
52.4°N
52.2°N
52.0°N
4.2°E
4.4°E
4.6°E
4.8°E
5.0°E
5.2°E
5.4°E
1
release: 2021-09-06 19:00
1) 2021-09-06 21:28 - 2021-09-07 21:24
final detection: 2021-09-09 19:28


Deployment ID 35230 (adult F)
52.7°N
52.6°N
52.5°N
52.4°N
52.3°N
4.2°E
4.4°E
4.6°E
4.8°E
5.0°E
1
release: 2021-09-08 23:30
1) 2021-09-12 19:45 - 2021-09-12 21:54
final detection: 2021-09-12 21:54


Deployment ID 35235 (adult F)
52.5°N
52.0°N
51.5°N
3.0°E
3.5°E
4.0°E
4.5°E
1
2
release: 2021-09-09 08:45
1) 2021-09-12 19:41 - 2021-09-13 02:09
2) 2021-09-13 02:09 - 2021-09-13 19:53
final detection: 2021-09-13 19:55

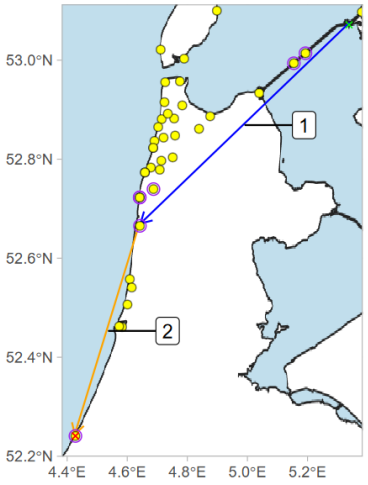

Deployment ID 35237 (adult F)
52.8°N
52.7°N
52.6°N
52.5°N
4.4°E
4.6°E
4.8°E
5.0°E
1
release: 2021-09-09 20:45
1) 2021-09-20 19:19 - 2021-09-20 21:54
final detection: 2021-09-20 21:56

Deployment ID 35239 (adult F)



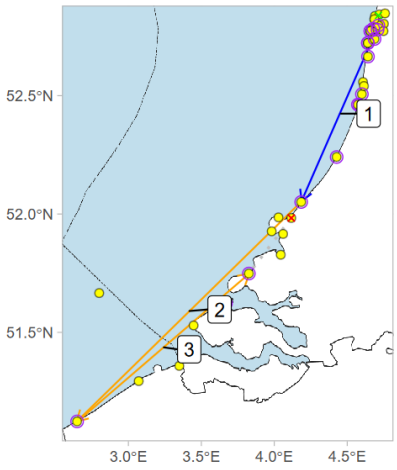
release: 2021-08-21 12:00
1) 2021-08-21 19:38 - 2021-08-21 21:13
2) 2021-08-21 21:13 - 2021-08-23 19:57
final detection: 2021-08-23 19:57

Deployment ID 35241 (adult F)



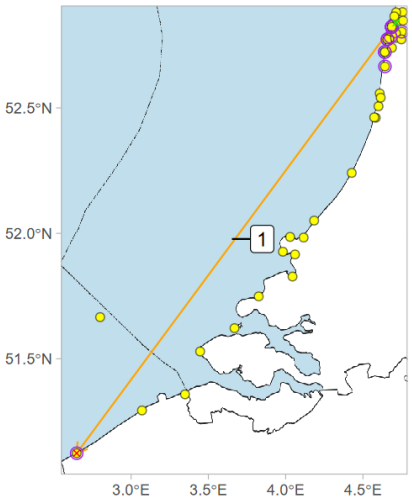
release: 2021-09-07 20:10
1) 2021-09-07 20:10 - 2021-09-08 01:00
2) 2021-09-08 01:00 - 2021-09-08 21:00
final detection: 2021-09-08 21:02

Deployment ID 35245 (adult F)



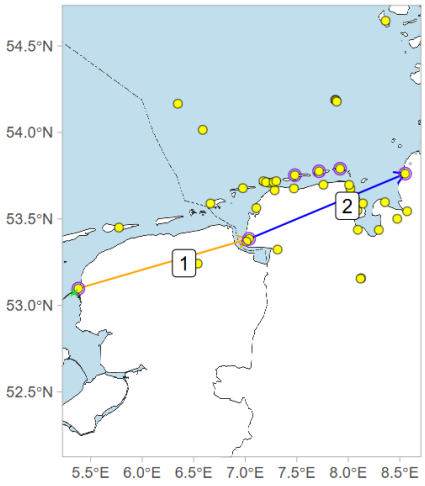
release: 2021-09-09 12:00
1) 2021-09-09 19:45 - 2021-09-10 00:36
2) 2021-09-10 00:36 - 2021-09-12 23:31
3) 2021-09-12 23:31 - 2021-09-18 21:57
final detection: 2021-09-21 19:44

Deployment ID 35247 (first year F)



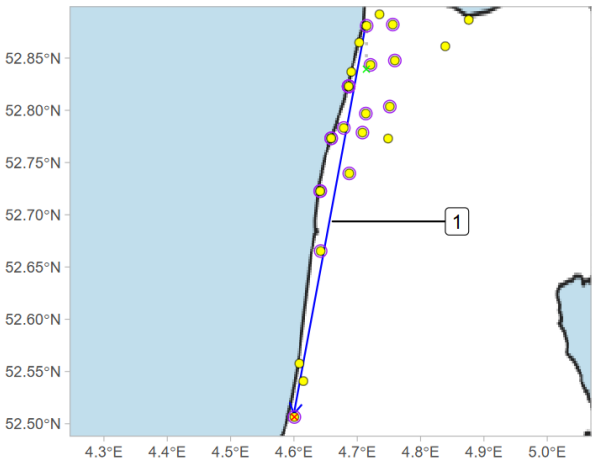
release: 2021-09-09 12:00
1) 2021-09-09 19:04 - 2021-09-14 00:11
final detection: 2021-09-14 00:12

Deployment ID 35251 (first year F)



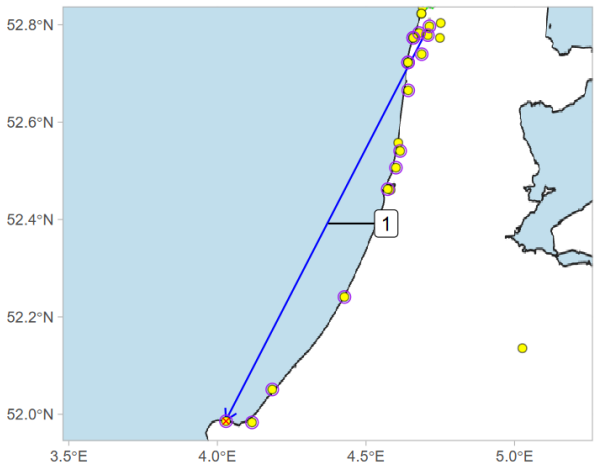
release: 2021-09-21 23:30
1) 2021-09-21 23:56 - 2021-09-22 19:19
2) 2021-09-22 19:19 - 2021-09-22 23:39
final detection: 2021-09-27 23:42

Deployment ID 35253 (adult F)



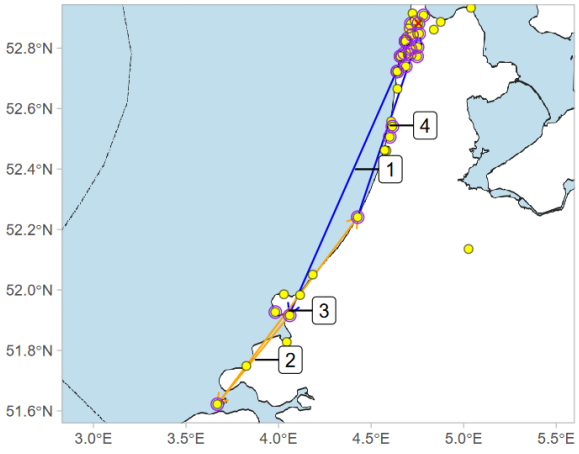
release: 2021-09-24 09:00
1) 2021-10-06 19:59 - 2021-10-06 20:55
final detection: 2021-10-06 21:02

Deployment ID 35254 (adult F)



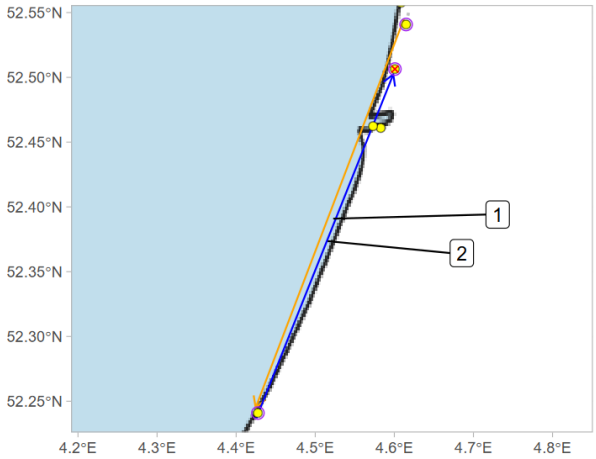
release: 2021-09-09 22:35
1) 2021-09-12 19:47 - 2021-09-13 00:18
final detection: 2021-09-13 00:18

Deployment ID 35255 (adult M)



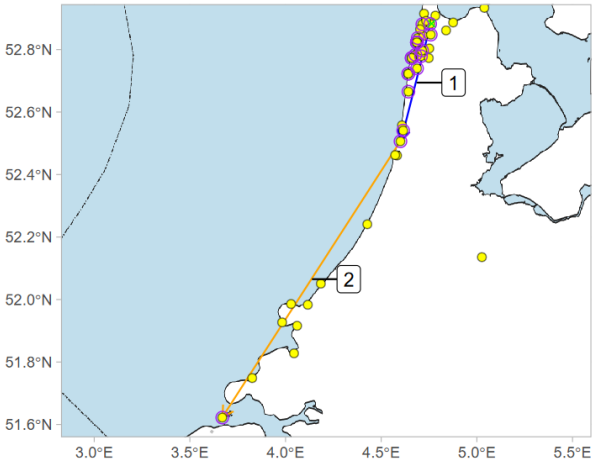
release: 2021-09-08 22:00
1) 2021-09-13 18:50 - 2021-09-14 02:41
2) 2021-09-14 18:42 - 2021-09-17 00:14
3) 2021-09-17 00:14 - 2021-09-24 02:22
4) 2021-09-24 02:22 - 2021-09-24 04:59
final detection: 2021-09-26 03:18

Deployment ID 35257 (adult M)



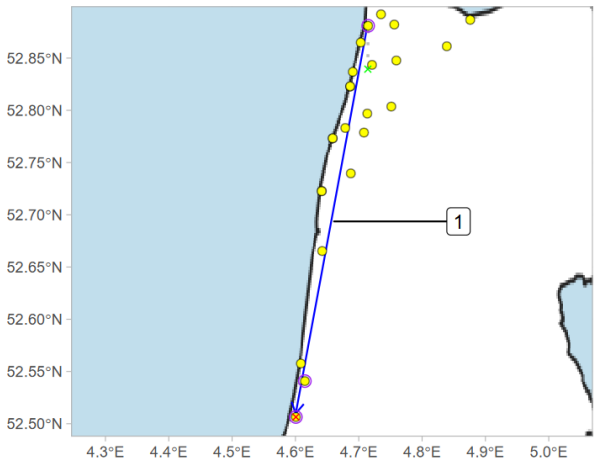
release: 2021-09-10 01:10
1) 2021-09-16 21:09 - 2021-09-17 21:24
2) 2021-09-17 21:24 - 2021-09-18 00:22
final detection: 2021-09-18 19:39

Deployment ID 35267 (adult M)



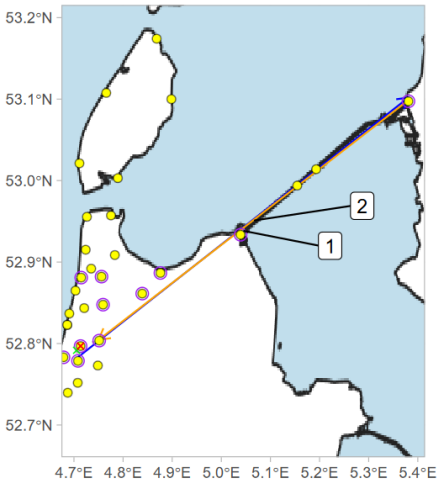
release: 2021-09-18 21:10
1) 2021-09-18 21:34 - 2021-09-19 01:31
2) 2021-09-19 19:24 - 2021-09-25 20:02
final detection: 2021-09-27 22:44

Deployment ID 35271 (adult F)



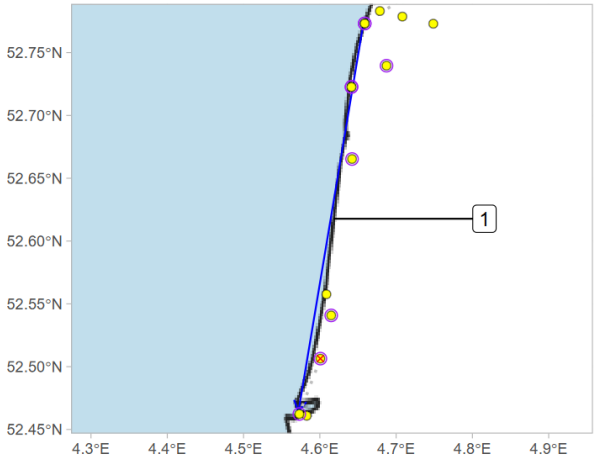
release: 2021-09-09 12:00
1) 2021-09-09 20:18 - 2021-09-09 23:26
final detection: 2021-09-09 23:41

Deployment ID 35272 (adult F)



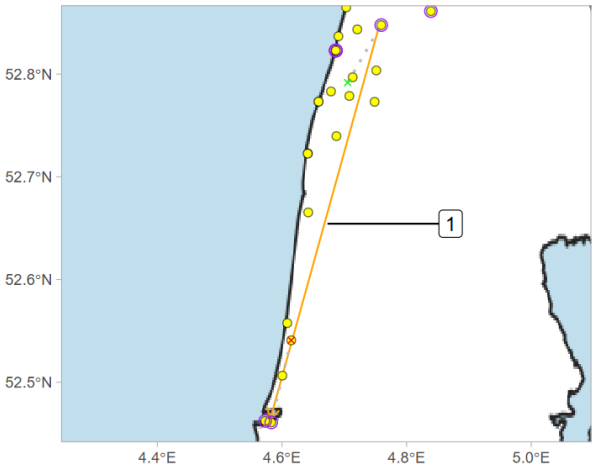
release: 2021-09-18 12:00
1) 2021-09-21 18:32 - 2021-09-21 21:11
2) 2021-09-21 23:46 - 2021-09-26 00:34
final detection: 2021-11-16 11:59

Deployment ID 35275 (adult F)



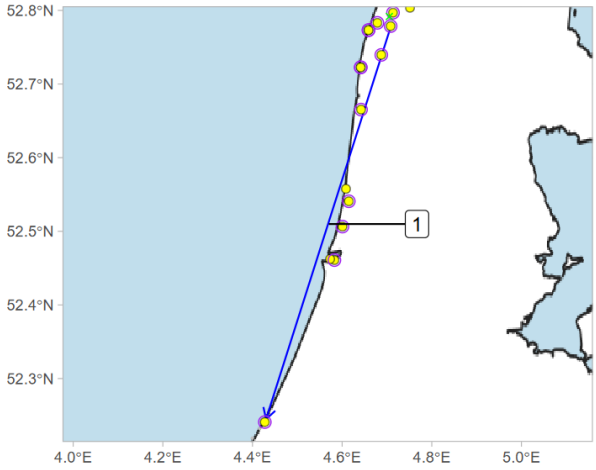
release: 2021-09-08 21:25
1) 2021-09-13 20:00 - 2021-09-13 20:55
final detection: 2021-09-13 21:02

Deployment ID 35276 (first year M)



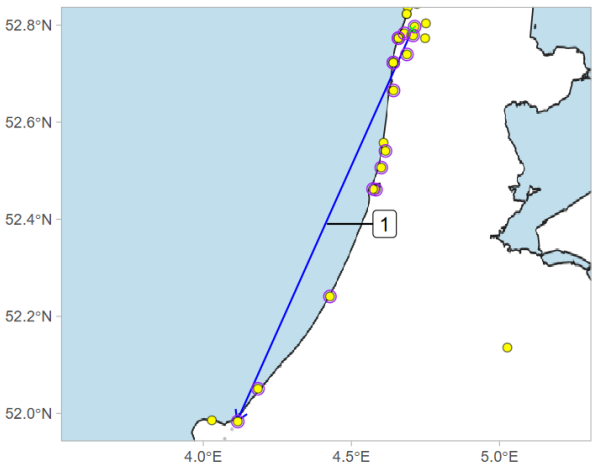
release: 2021-09-08 20:55
1) 2021-09-12 19:30 - 2021-09-17 20:31
final detection: 2021-09-17 20:58

Deployment ID 35277 (first year M)



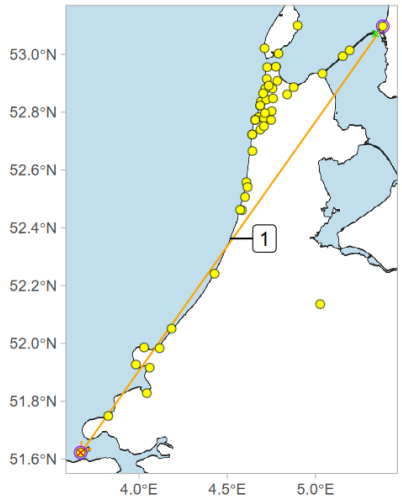
release: 2021-09-08 20:50
1) 2021-09-08 21:06 - 2021-09-09 00:28
final detection: 2021-09-09 22:03

Deployment ID 35280 (first year M)



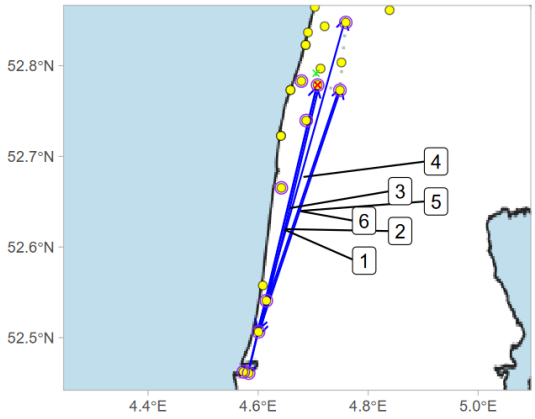
release: 2021-09-08 20:10
1) 2021-09-12 18:52 - 2021-09-12 22:57
final detection: 2021-09-13 21:24

Deployment ID 35349 (adult F)



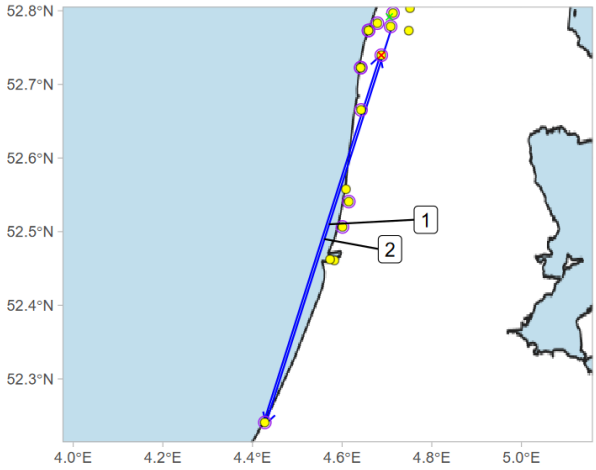
release: 2021-09-07 19:50
1) 2021-09-07 21:55 - 2021-10-08 00:20
final detection: 2021-10-08 00:21

Deployment ID 35362 (first year F)



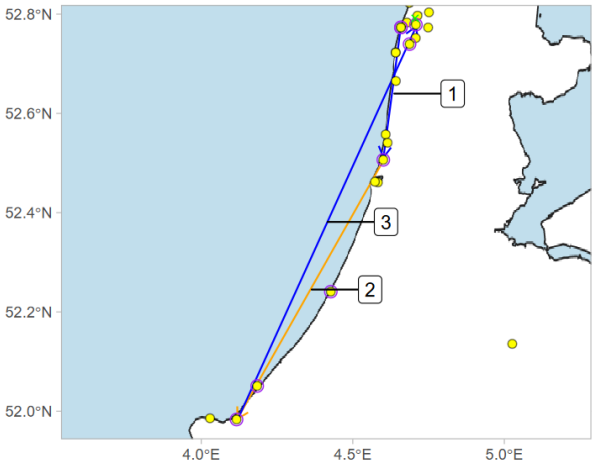
release: 2021-09-08 23:50
1) 2021-09-09 19:30 - 2021-09-09 21:16
2) 2021-09-09 21:16 - 2021-09-10 02:42
3) 2021-09-12 18:57 - 2021-09-12 20:24
4) 2021-09-12 20:24 - 2021-09-13 03:03
5) 2021-09-13 18:57 - 2021-09-13 20:53
6) 2021-09-13 21:57 - 2021-09-14 00:24
final detection: 2021-09-28 18:21

Deployment ID 35366 (first year F)



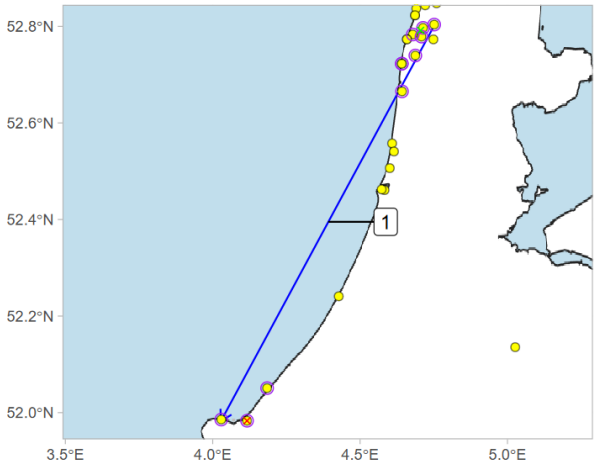
release: 2021-09-09 12:30
1) 2021-09-09 19:01 - 2021-09-09 22:53
2) 2021-09-10 00:21 - 2021-09-10 03:08
final detection: 2021-09-12 19:01

Deployment ID 35372 (first year M)



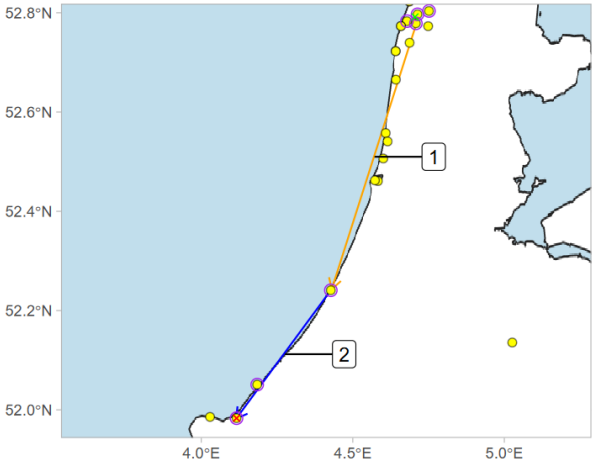
release: 2021-09-08 23:10
1) 2021-09-13 19:29 - 2021-09-13 20:46
2) 2021-09-13 20:46 - 2021-09-19 22:15
3) 2021-09-19 22:15 - 2021-09-20 02:53
final detection: 2021-10-09 21:29

Deployment ID 35561 (first year M)



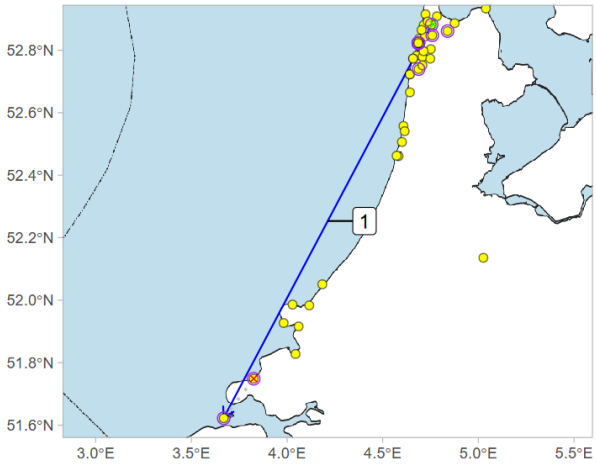
release: 2021-09-17 16:00
1) 2021-09-17 18:52 - 2021-09-18 00:02
final detection: 2021-09-18 00:21

Deployment ID 35562 (adult F)



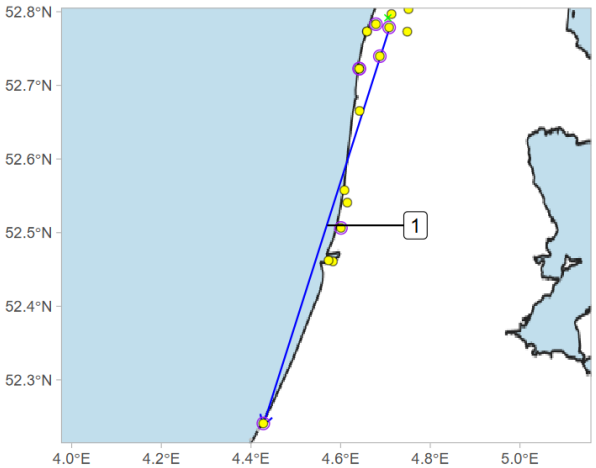
release: 2021-09-09 19:25
1) 2021-09-09 19:43 - 2021-09-17 22:46
2) 2021-09-17 22:46 - 2021-09-18 00:31
final detection: 2021-09-18 00:31

Deployment ID 35570 (adult F)



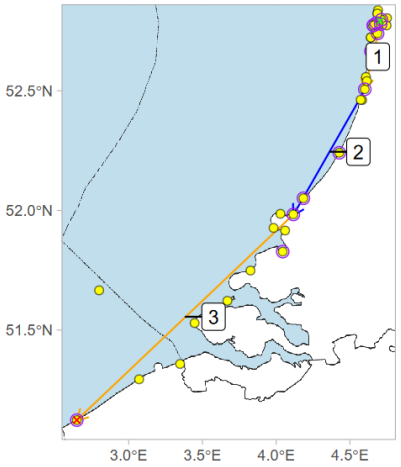
release: 2021-10-12 08:30
1) 2021-10-12 17:30 - 2021-10-13 01:54
final detection: 2021-10-13 17:58

Deployment ID 35571 (first year M)



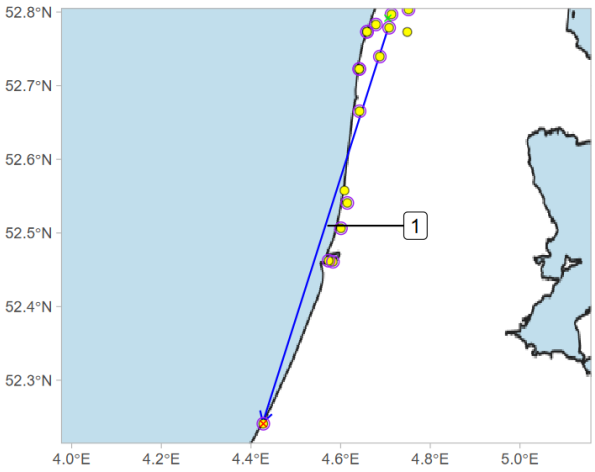
release: 2021-09-09 22:20
1) 2021-09-12 18:50 - 2021-09-12 22:02
final detection: 2021-09-16 20:17

Deployment ID 35572 (first year M)



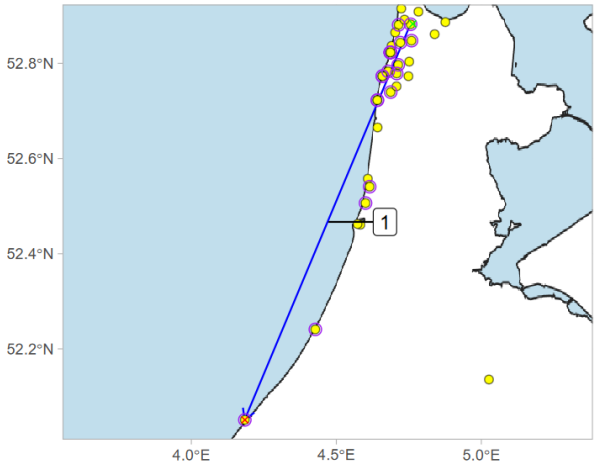
release: 2021-09-09 22:40
1) 2021-09-09 23:18 - 2021-09-12 19:39
2) 2021-09-12 19:39 - 2021-09-12 23:14
3) 2021-09-12 23:14 - 2021-09-20 00:11
final detection: 2021-09-20 00:12

Deployment ID 35578 (adult F)



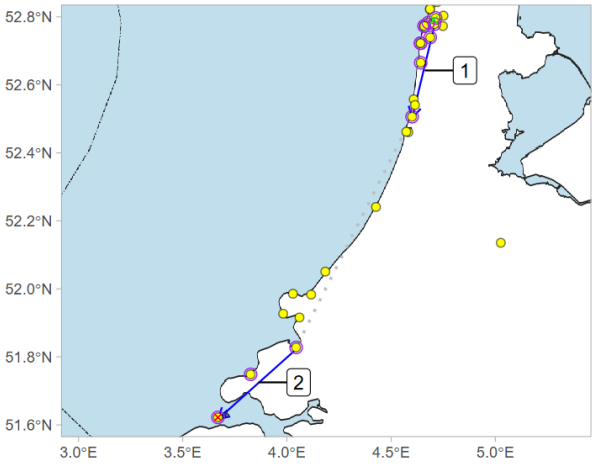
release: 2021-09-09 12:30
1) 2021-09-20 19:08 - 2021-09-20 22:36
final detection: 2021-09-20 22:37

Deployment ID 35580 (adult M)



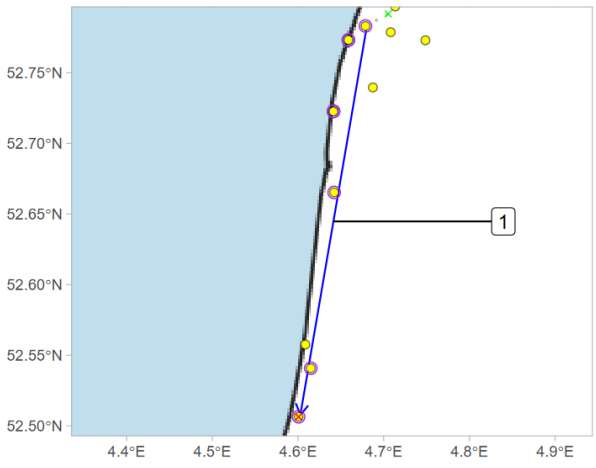
release: 2021-10-12 07:35
1) 2021-10-12 18:10 - 2021-10-12 20:29
final detection: 2021-10-12 20:30

Deployment ID 35585 (first year F)



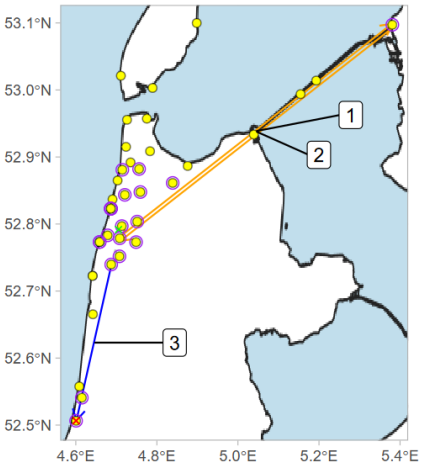
release: 2021-09-18 12:52
1) 2021-09-18 18:41 - 2021-09-18 20:26
2) 2021-09-19 19:29 - 2021-09-19 20:49
final detection: 2021-09-19 23:38

Deployment ID 35586 (first year M)



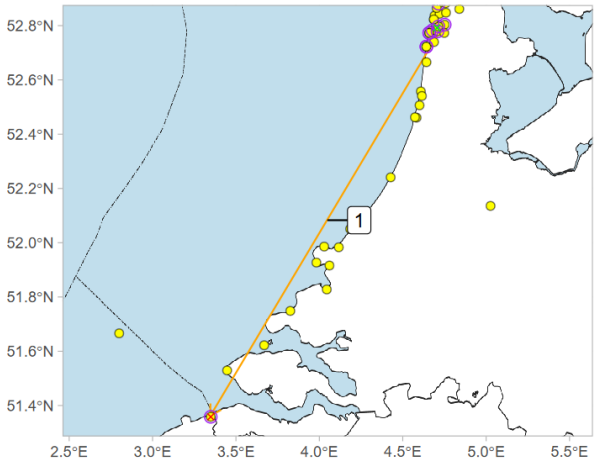
release: 2021-09-18 21:00
1) 2021-09-18 21:24 - 2021-09-18 23:12
final detection: 2021-09-18 23:14

Deployment ID 35587 (first year F)



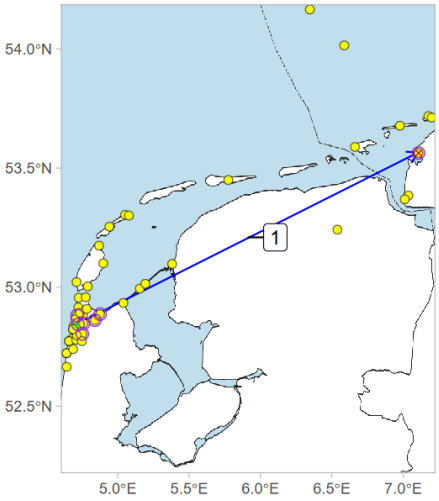
release: 2021-09-18 13:10
1) 2021-09-22 18:34 - 2021-09-25 21:20
2) 2021-09-25 21:20 - 2021-09-26 22:07
3) 2021-10-10 18:17 - 2021-10-10 19:18
final detection: 2021-10-10 19:21

Deployment ID 35588 (first year F)



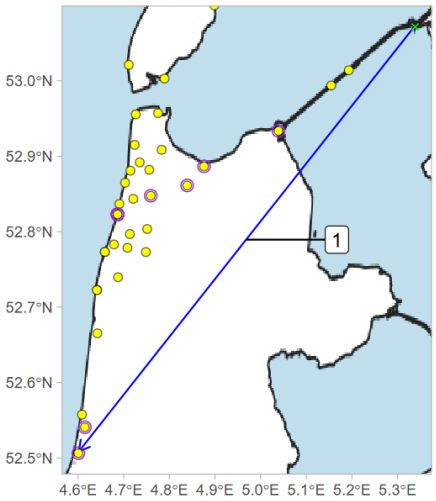
release: 2021-09-09 12:30
1) 2021-09-09 19:02 - 2021-09-18 21:17
final detection: 2021-09-18 21:17

Deployment ID 36029 (first year M)



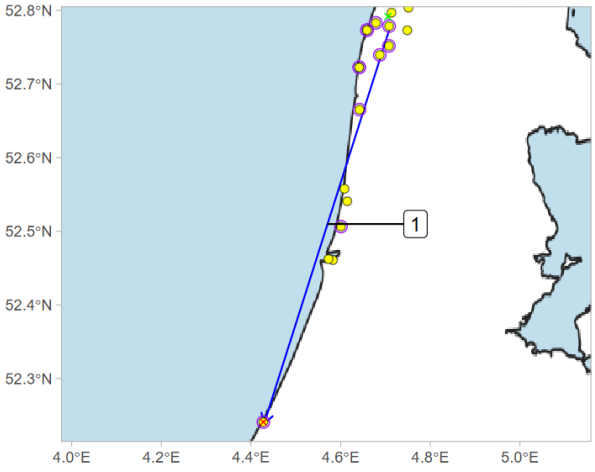
release: 2021-09-18 21:20
1) 2021-09-21 18:47 - 2021-09-22 00:22
final detection: 2021-09-22 00:34

Deployment ID 36045 (first year M)



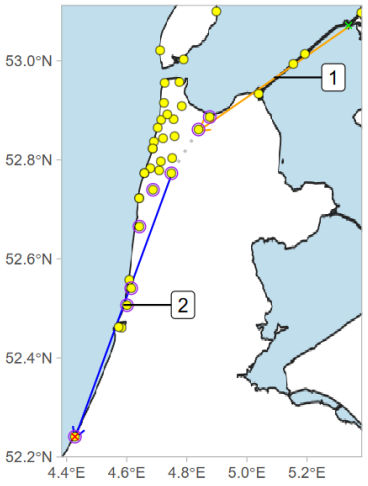
release: 2021-09-26 19:00
1) 2021-09-26 19:00 - 2021-09-27 02:58
final detection: 2021-09-27 23:49

Deployment ID 36234 (adult F)



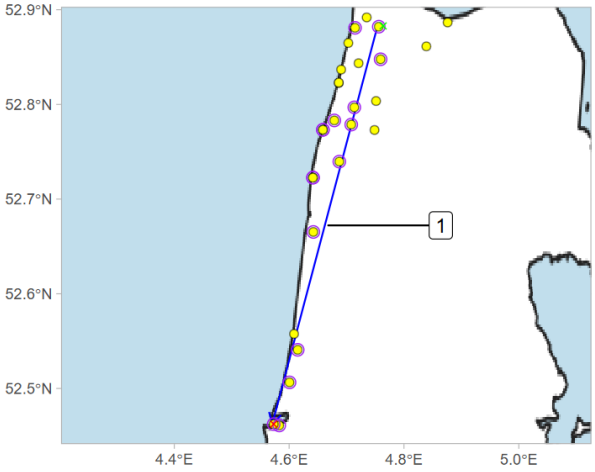
release: 2021-09-24 11:55
1) 2021-10-15 17:38 - 2021-10-15 19:15
final detection: 2021-10-15 19:16

Deployment ID 36236 (first year F)



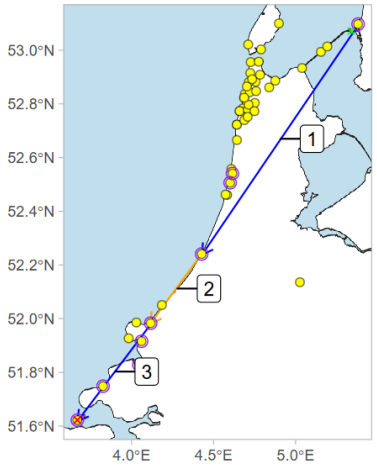
release: 2021-09-21 20:40
1) 2021-09-21 22:40 - 2021-09-26 22:23
2) 2021-09-27 19:47 - 2021-09-28 00:39
final detection: 2021-09-28 00:43

Deployment ID 36237 (first year F)



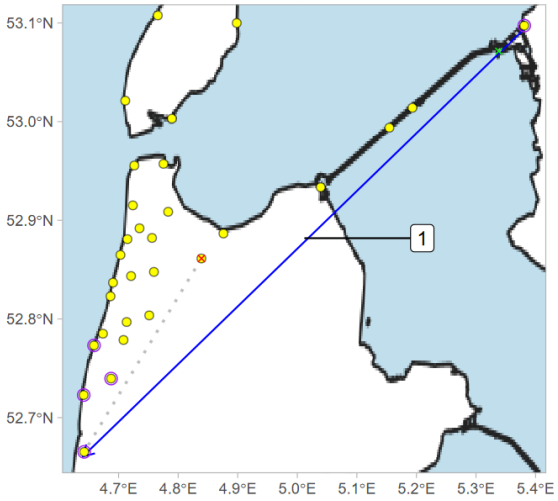
release: 2021-09-23 09:00
1) 2021-10-06 17:39 - 2021-10-06 19:53
final detection: 2021-10-06 19:57

Deployment ID 36241 (first year M)



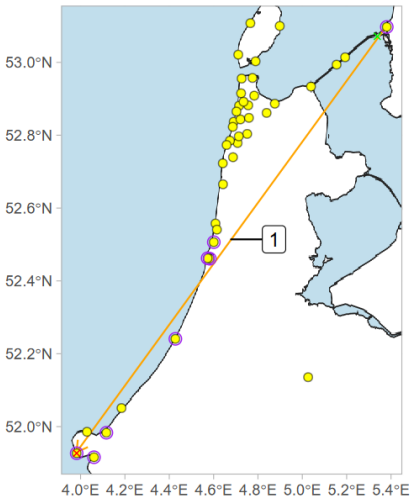
release: 2021-09-26 22:40
1) 2021-10-08 18:35 - 2021-10-08 23:25
2) 2021-10-08 23:25 - 2021-10-09 18:48
3) 2021-10-09 18:48 - 2021-10-09 20:17
final detection: 2021-10-09 20:20

Deployment ID 36331 (first year F)



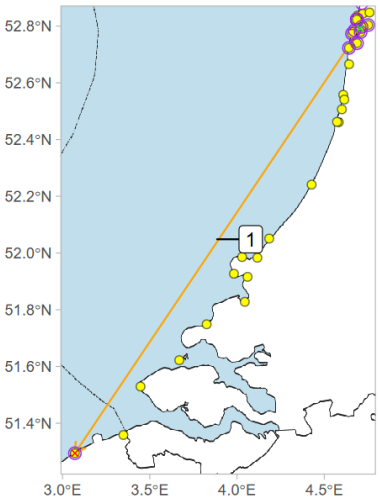
release: 2022-10-11 20:46
1) 2022-10-18 17:44 - 2022-10-18 23:02
final detection: 2022-10-24 05:35

Deployment ID 36333 (adult F)



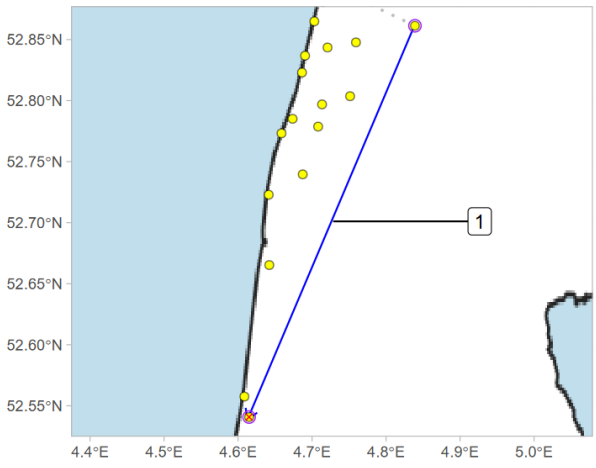
release: 2022-10-11 20:37
1) 2022-10-30 17:26 - 2022-11-13 22:30
final detection: 2022-11-13 22:31

Deployment ID 42200 (first year M)



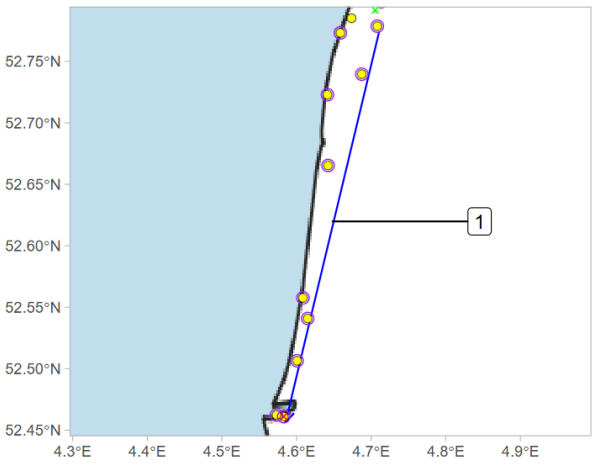
release: 2022-08-31 15:00
1) 2022-08-31 19:19 - 2022-09-04 20:36
final detection: 2022-09-04 20:39

Deployment ID 42202 (adult F)



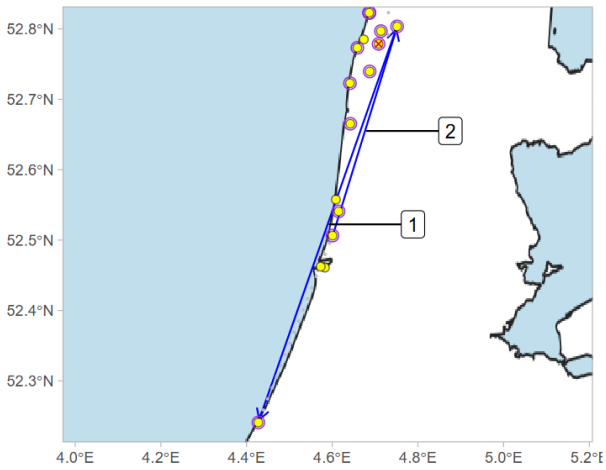
release: 2022-09-14 11:00
1) 2022-09-24 20:22 - 2022-09-24 21:00
final detection: 2022-09-24 21:01

Deployment ID 42203 (first year M)



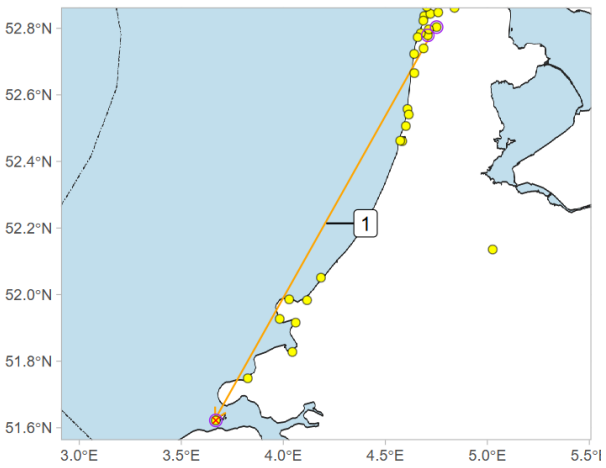
release: 2022-08-31 23:55
1) 2022-09-03 19:58 - 2022-09-03 21:34
final detection: 2022-09-03 21:35

Deployment ID 42204 (first year M)



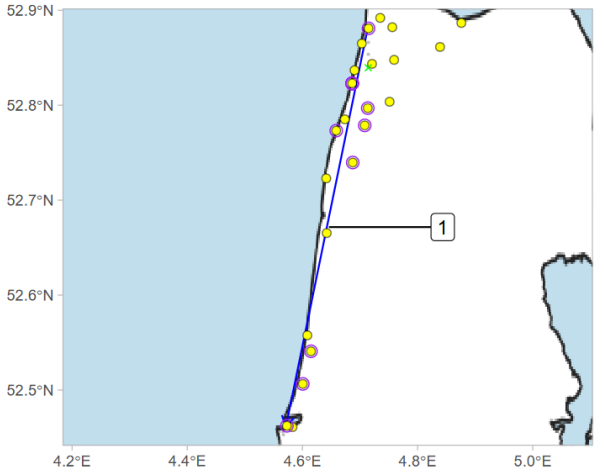
release: 2022-09-12 15:00
1) 2022-09-24 18:55 - 2022-09-24 20:12
2) 2022-09-25 20:38 - 2022-09-25 22:44
final detection: 2022-10-31 17:19

Deployment ID 42206 (first year M)



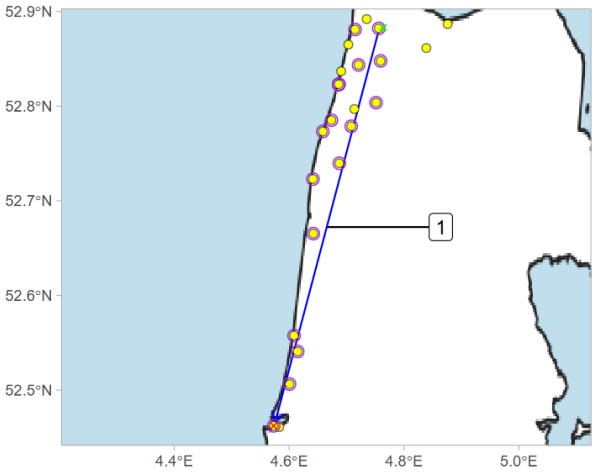
release: 2022-09-06 08:30
1) 2022-09-12 21:30 - 2022-09-14 20:45
final detection: 2022-09-14 20:47

Deployment ID 42209 (adult F)



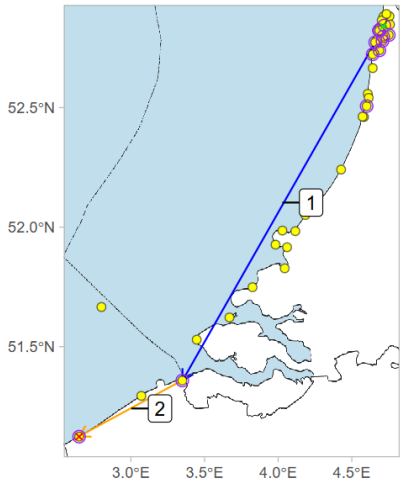
release: 2022-09-06 15:15
1) 2022-09-06 19:05 - 2022-09-06 21:07
final detection: 2022-09-08 20:42

Deployment ID 42214 (first year F)



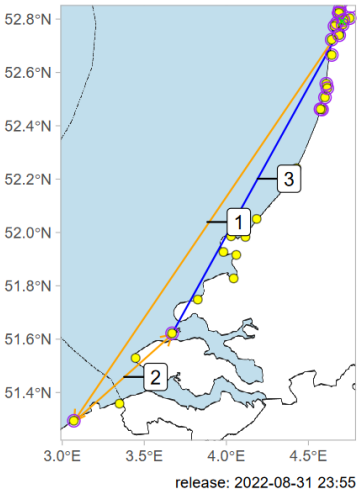
release: 2022-09-01 01:00
1) 2022-09-01 19:25 - 2022-09-01 21:21
final detection: 2022-09-01 21:22

Deployment ID 42215 (adult F)



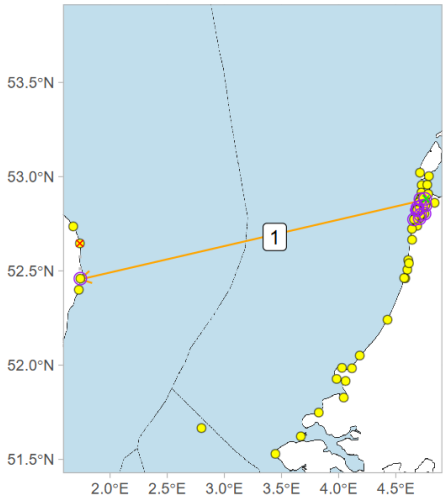
release: 2022-09-06 15:15
1) 2022-09-10 18:54 - 2022-09-11 01:50
2) 2022-09-11 01:50 - 2022-09-11 20:39
final detection: 2022-09-11 20:39

Deployment ID 42216 (first year M)



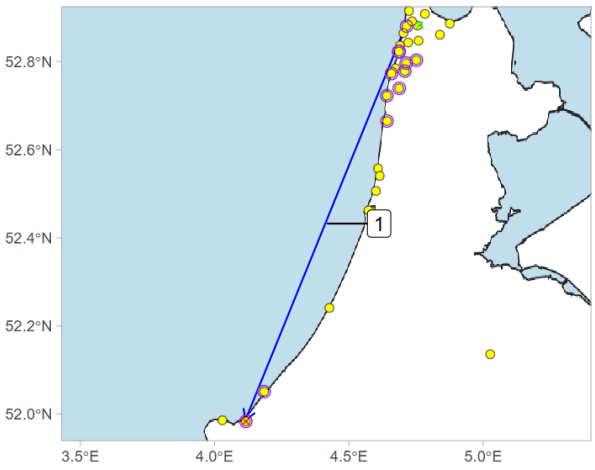
release: 2022-08-31 23:55
1) 2022-09-01 19:26 - 2022-09-02 19:59
2) 2022-09-02 20:09 - 2022-09-03 19:07
3) 2022-09-03 19:07 - 2022-09-04 01:55
final detection: 2022-09-05 20:28

Deployment ID 42220 (first year F)



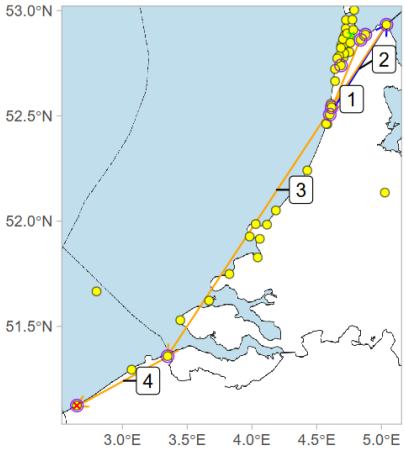
release: 2022-09-01 01:40
1) 2022-09-01 19:21 - 2022-09-09 19:48
final detection: 2022-09-10 22:27

Deployment ID 42221 (first year F)



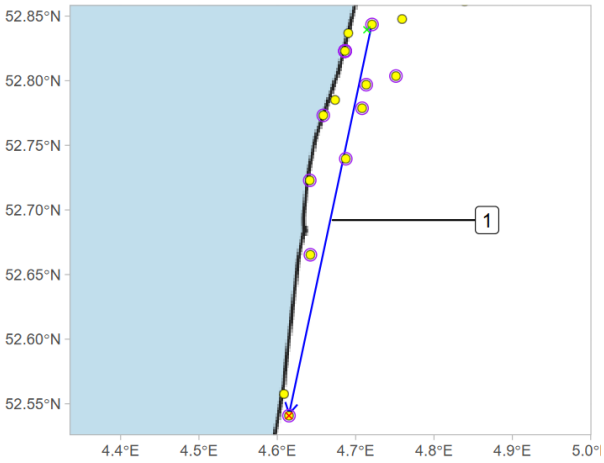
release: 2022-09-06 08:30
1) 2022-09-13 19:47 - 2022-09-13 22:24
final detection: 2022-09-13 22:36

Deployment ID 42222 (first year M)



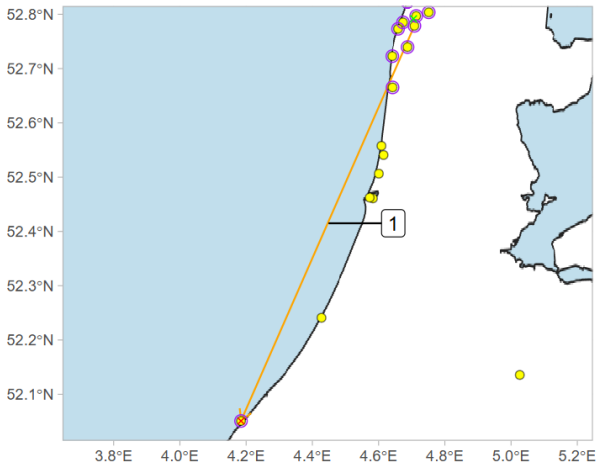
release: 2022-09-01 21:30
1) 2022-09-01 22:38 - 2022-09-04 21:23
2) 2022-09-04 21:23 - 2022-09-04 23:23
3) 2022-09-08 22:46 - 2022-09-11 01:30
4) 2022-09-11 01:30 - 2022-09-11 19:19
final detection: 2022-09-11 19:19

Deployment ID 42226 (first year F)



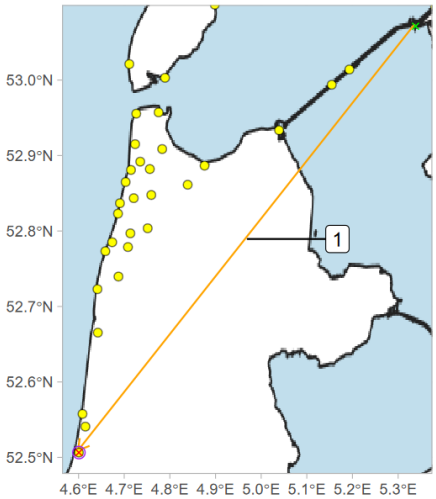
release: 2022-09-06 15:15
1) 2022-09-06 18:52 - 2022-09-06 20:31
final detection: 2022-09-06 20:32

Deployment ID 42227 (first year M)



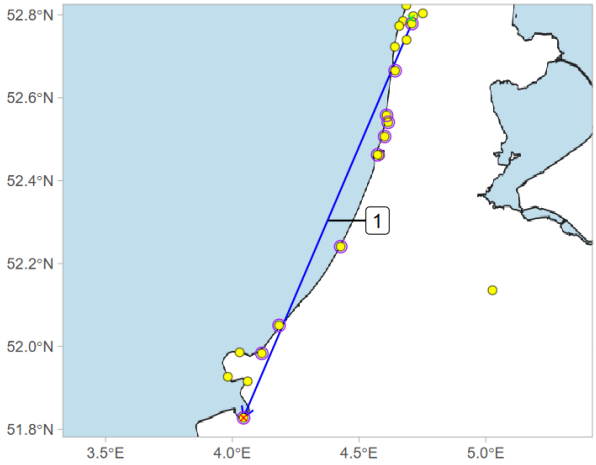
release: 2022-09-05 16:15
1) 2022-09-05 19:00 - 2022-09-08 19:45
final detection: 2022-09-08 20:42

Deployment ID 42228 (first year M)



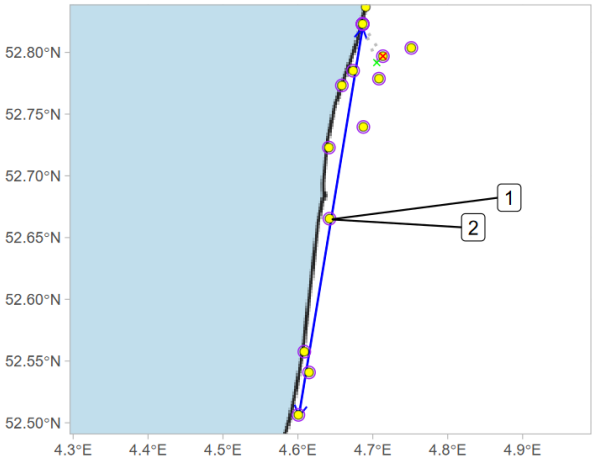
release: 2022-09-04 20:00
1) 2022-09-04 20:00 - 2022-09-06 21:58
final detection: 2022-09-07 20:20

Deployment ID 42232 (adult F)



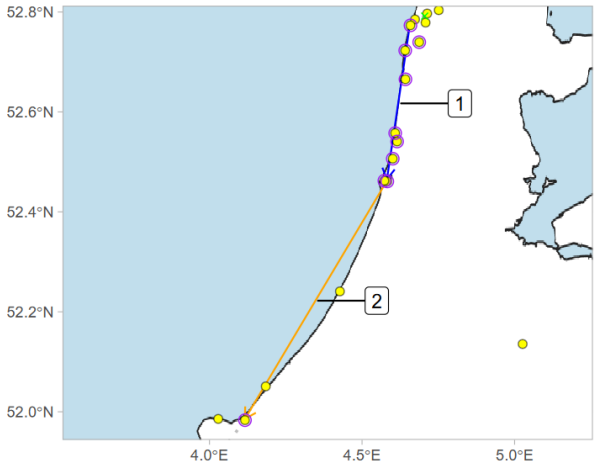
release: 2022-08-31 22:00
1) 2022-09-03 20:01 - 2022-09-04 01:22
final detection: 2022-09-04 02:02

Deployment ID 42235 (first year F)



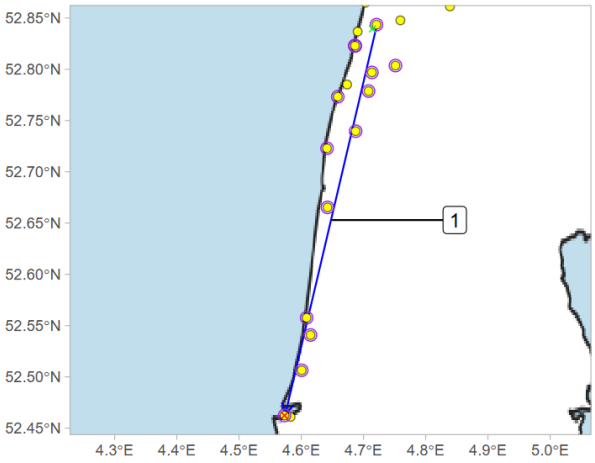
release: 2022-08-31 16:00
1) 2022-09-01 19:38 - 2022-09-01 21:18
2) 2022-09-01 21:50 - 2022-09-01 23:33
final detection: 2022-09-04 19:58

Deployment ID 42236 (first year M)



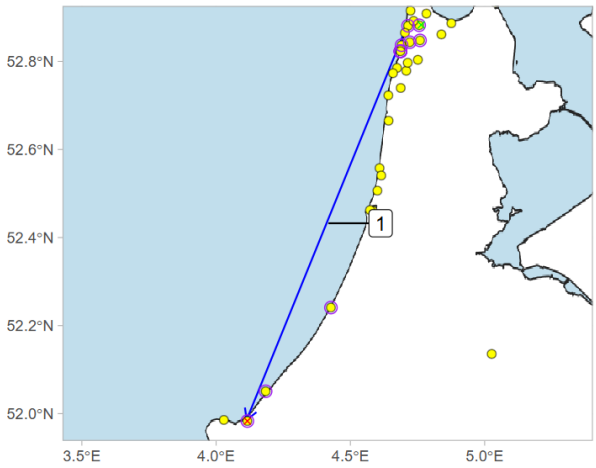
release: 2022-08-31 23:55
1) 2022-09-02 19:22 - 2022-09-02 21:25
2) 2022-09-02 21:25 - 2022-09-03 23:50
final detection: 2022-09-04 02:21

Deployment ID 42246 (adult F)



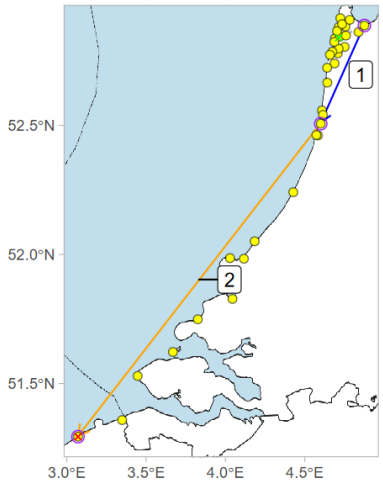
release: 2022-09-01 12:00
1) 2022-09-01 19:22 - 2022-09-01 21:18
final detection: 2022-09-01 21:20

Deployment ID 42247 (first year F)



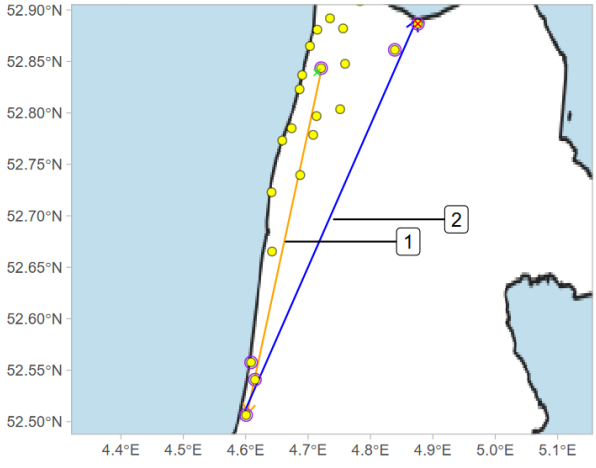
release: 2022-09-01 20:00
1) 2022-09-03 19:50 - 2022-09-04 01:36
final detection: 2022-09-04 01:37

Deployment ID 42248 (first year F)



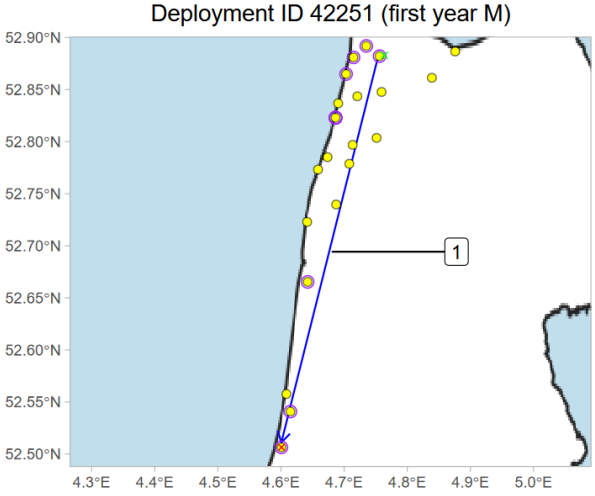
release: 2022-09-01 12:00
1) 2022-09-03 19:20 - 2022-09-03 21:10
2) 2022-09-03 21:10 - 2022-09-13 20:09
final detection: 2022-09-13 20:10

Deployment ID 42249 (adult F)



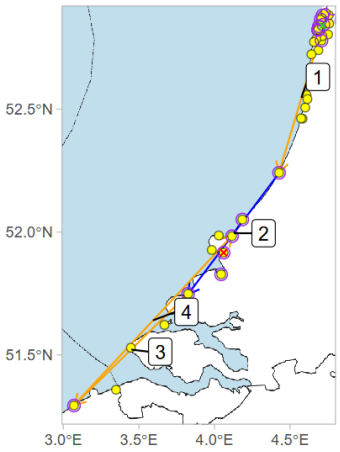
release: 2022-08-31 22:50
1) 2022-08-31 23:15 - 2022-09-01 20:30
2) 2022-09-01 21:01 - 2022-09-02 00:28
final detection: 2022-09-02 23:45

Deployment ID 42251 (first year M)



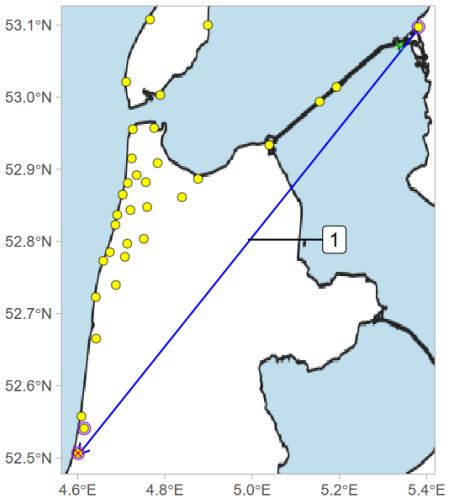
release: 2022-08-31 21:00
1) 2022-08-31 23:25 - 2022-09-01 03:06
final detection: 2022-09-01 03:13

Deployment ID 42252 (first year F)



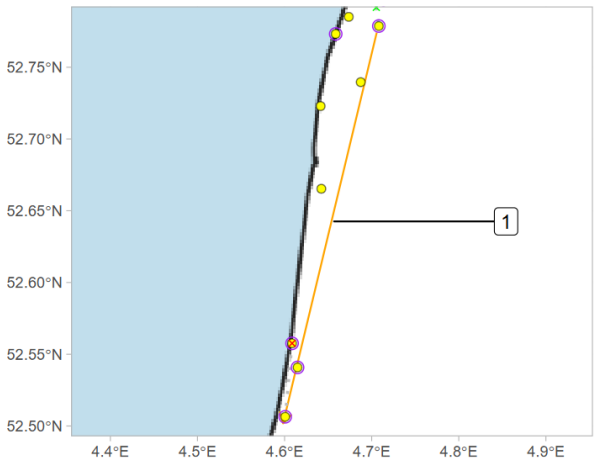
release: 2022-09-01 12:00
1) 2022-09-01 19:21 - 2022-09-03 22:21
2) 2022-09-03 22:21 - 2022-09-04 02:54
3) 2022-09-04 02:54 - 2022-09-05 23:45
4) 2022-09-05 23:45 - 2022-09-13 22:16
final detection: 2022-09-13 22:31

Deployment ID 42256 (adult F)



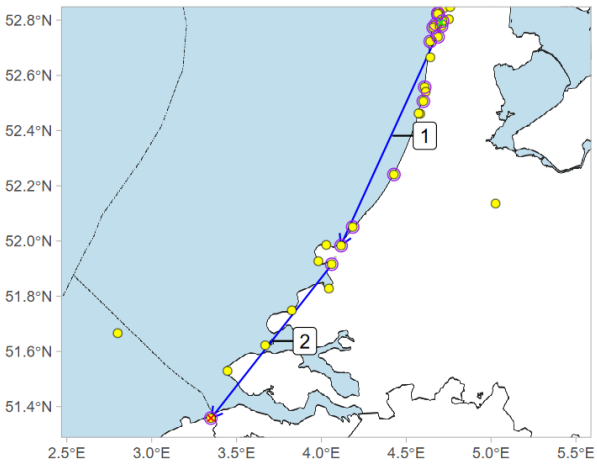
release: 2022-10-11 22:25
1) 2022-11-04 17:27 - 2022-11-04 22:58
final detection: 2022-11-04 23:00

Deployment ID 42259 (first year M)



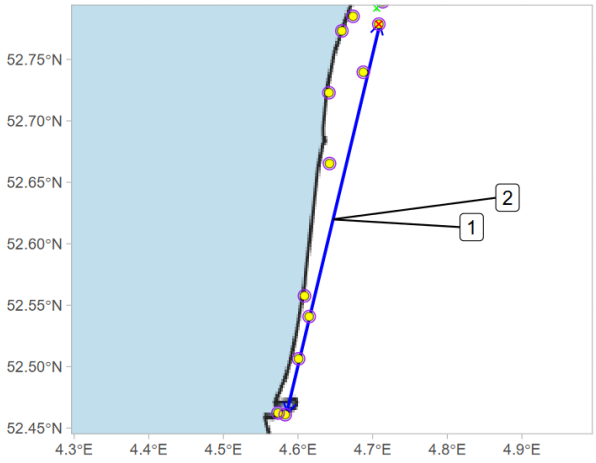
release: 2022-09-01 23:15
1) 2022-09-01 23:41 - 2022-09-02 21:22
final detection: 2022-09-02 21:24

Deployment ID 42260 (first year M)



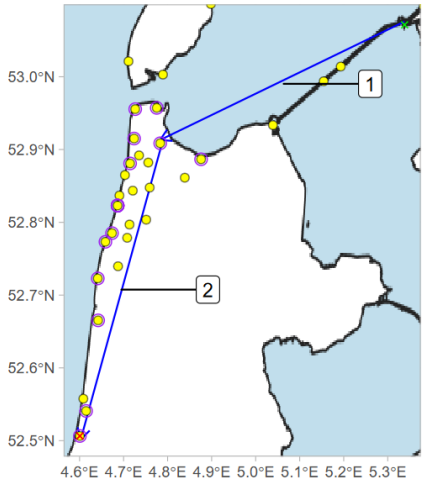
release: 2022-09-01 22:40
1) 2022-09-02 19:56 - 2022-09-03 00:26
2) 2022-09-03 19:05 - 2022-09-03 23:04
final detection: 2022-09-03 23:05

Deployment ID 42266 (first year M)



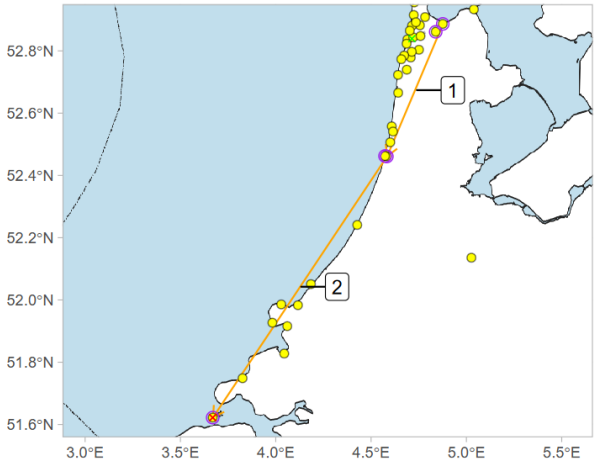
release: 2022-09-01 21:30
1) 2022-09-03 20:07 - 2022-09-03 21:52
2) 2022-09-03 21:52 - 2022-09-04 00:50
final detection: 2022-09-04 20:18

Deployment ID 42269 (adult F)



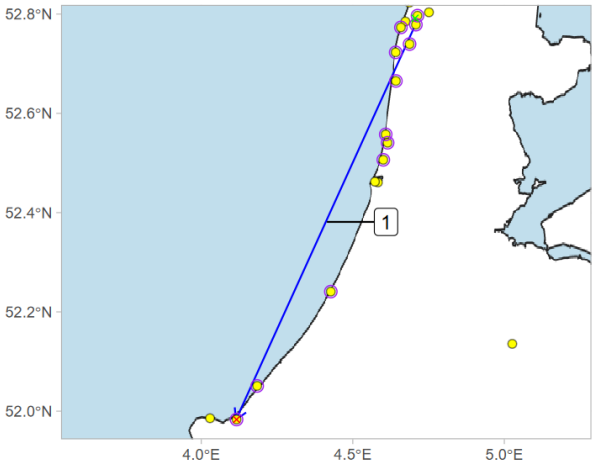
release: 2022-10-11 22:39
1) 2022-10-11 22:39 - 2022-10-12 00:24
2) 2022-10-12 17:45 - 2022-10-12 22:22
final detection: 2022-10-12 22:24

Deployment ID 42271 (first year F)



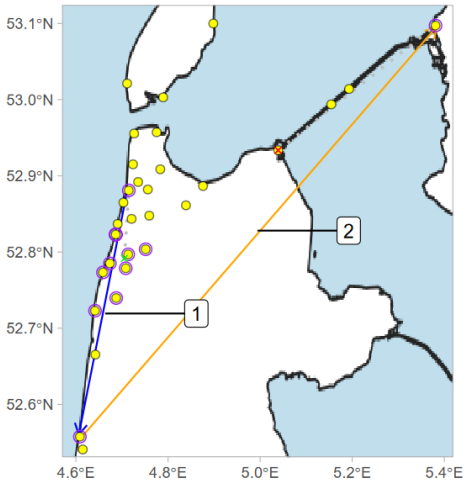
release: 2022-09-22 20:35
1) 2022-10-03 18:47 - 2022-10-16 20:12
2) 2022-10-16 20:12 - 2022-10-18 19:54
final detection: 2022-10-18 19:55

Deployment ID 42274 (first year F)



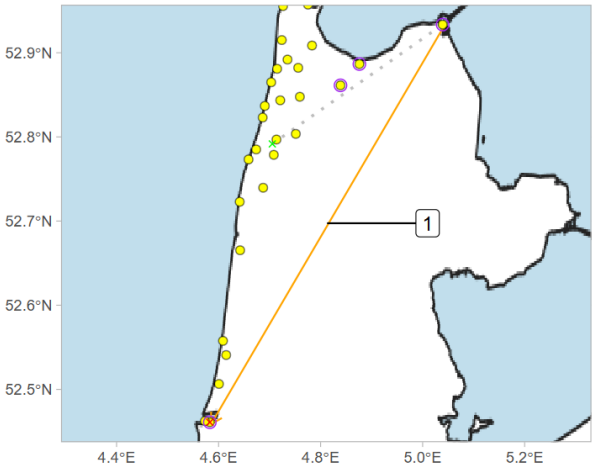
release: 2022-09-01 21:40
1) 2022-09-24 18:52 - 2022-09-24 20:26
final detection: 2022-09-24 20:26

Deployment ID 42276 (first year M)



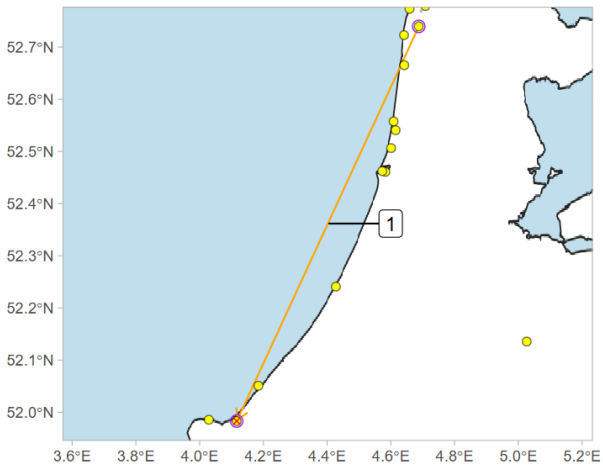
release: 2022-09-01 23:45
1) 2022-09-02 20:28 - 2022-09-02 23:23
2) 2022-09-02 23:23 - 2022-09-04 21:20
final detection: 2022-09-09 02:32

Deployment ID 42278 (first year F)



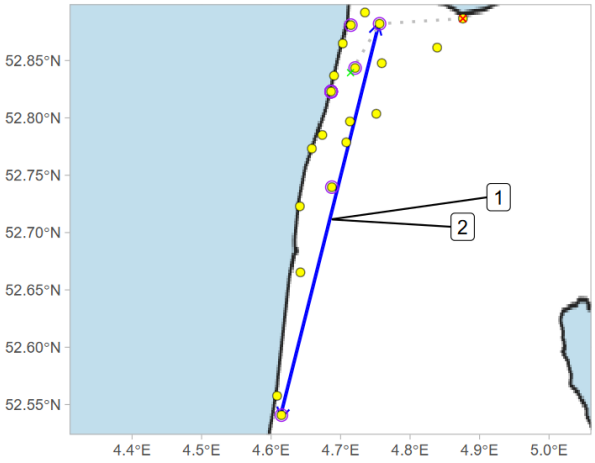
release: 2022-09-01 22:00
1) 2022-09-06 20:43 - 2022-09-08 00:08
final detection: 2022-09-08 00:09

Deployment ID 42290 (first year F)



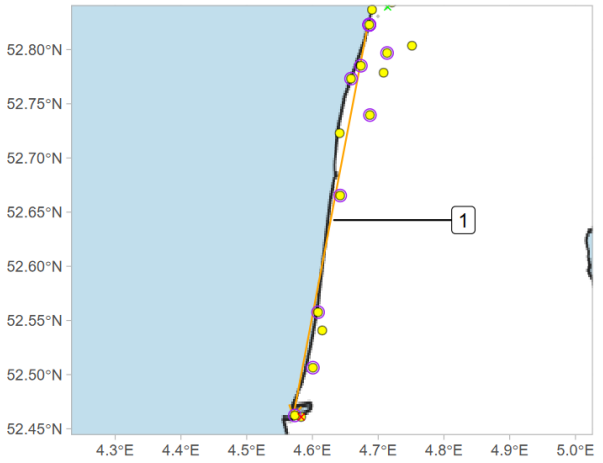
release: 2022-09-21 21:15
1) 2022-09-22 23:06 - 2022-09-24 21:58
final detection: 2022-09-24 21:59

Deployment ID 42292 (first year F)



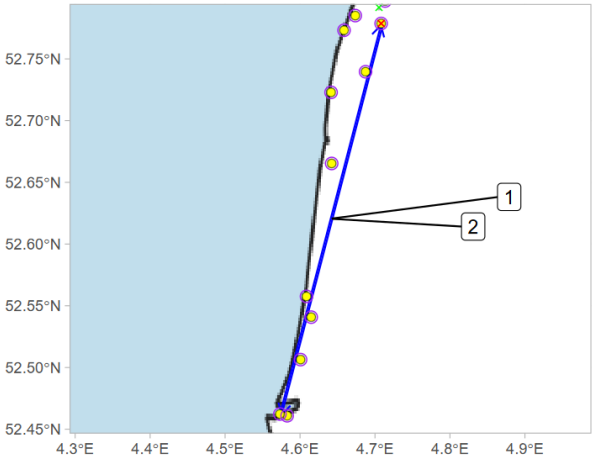
release: 2022-09-02 00:30
1) 2022-09-02 19:55 - 2022-09-02 23:48
2) 2022-09-02 23:48 - 2022-09-03 02:33
final detection: 2022-09-04 20:55

Deployment ID 42296 (first year M)



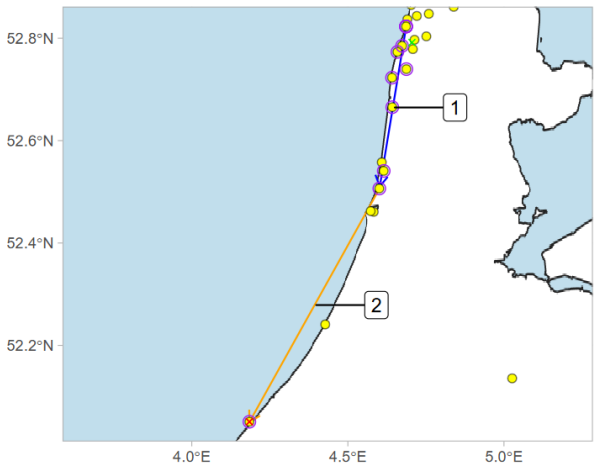
release: 2022-09-01 21:40
1) 2022-09-01 22:00 - 2022-09-02 20:34
final detection: 2022-09-02 20:39

Deployment ID 42300 (first year M)



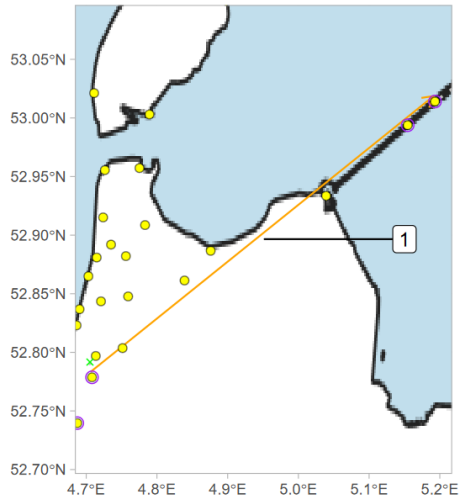
release: 2022-09-14 21:30
1) 2022-09-24 18:45 - 2022-09-24 19:29
2) 2022-09-24 19:29 - 2022-09-25 01:31
final detection: 2022-10-07 00:59

Deployment ID 42301 (first year M)



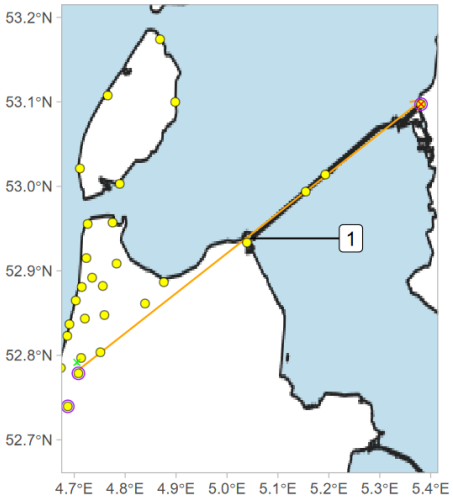
release: 2022-09-20 20:20
1) 2022-10-03 18:36 - 2022-10-03 20:34
2) 2022-10-03 20:34 - 2022-10-08 19:51
final detection: 2022-10-08 19:59

Deployment ID 42306 (adult M)



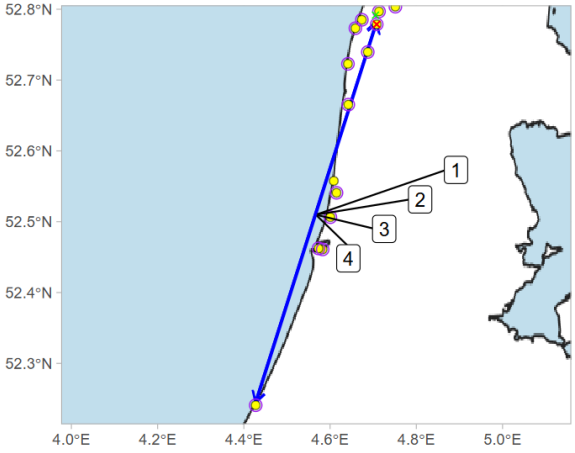
release: 2022-09-20 23:00
1) 2022-09-20 23:16 - 2022-09-21 20:46
final detection: 2022-09-30 19:35

Deployment ID 42307 (first year M)



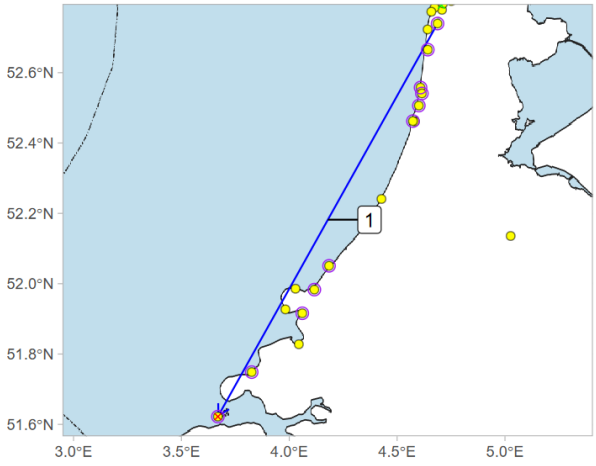
release: 2022-09-20 21:40
1) 2022-09-20 22:03 - 2022-09-21 20:20
final detection: 2022-10-09 17:50

Deployment ID 42315 (first year M)



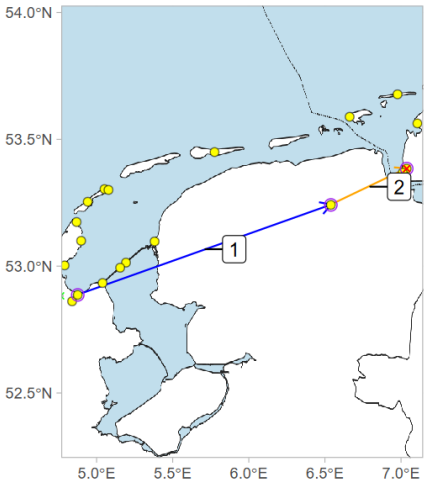
release: 2022-09-07 22:42
1) 2022-09-10 19:15 - 2022-09-10 22:40
2) 2022-09-10 22:40 - 2022-09-11 01:22
3) 2022-09-13 19:24 - 2022-09-13 21:34
4) 2022-09-13 21:34 - 2022-09-14 02:35
final detection: 2022-09-23 17:26

Deployment ID 42316 (first year F)



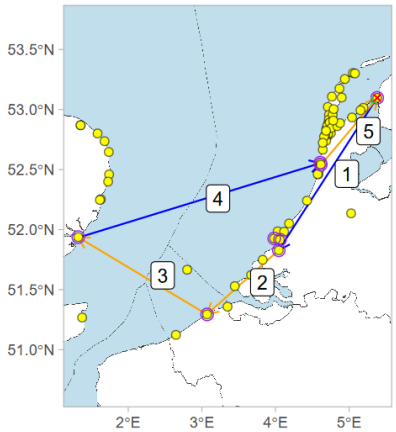
release: 2022-09-07 21:30
1) 2022-09-10 20:15 - 2022-09-11 01:11
final detection: 2022-09-11 01:12

Deployment ID 42327 (adult F)



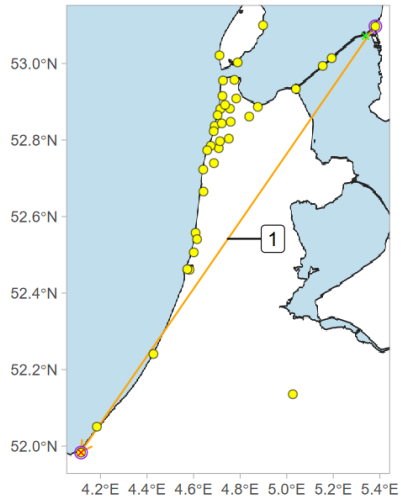
release: 2022-09-22 20:45
1) 2022-09-25 19:38 - 2022-09-25 23:27
2) 2022-09-25 23:27 - 2022-10-02 18:58
final detection: 2022-10-02 18:59

Deployment ID 42408 (adult F)



release: 2022-09-11 19:55
1) 2022-09-13 18:51 - 2022-09-14 00:34
2) 2022-09-14 00:34 - 2022-09-15 01:19
3) 2022-09-15 01:19 - 2022-10-03 19:09
4) 2022-10-03 19:09 - 2022-10-04 03:31
5) 2022-10-04 18:08 - 2022-10-06 17:56
final detection: 2022-10-11 17:41

Deployment ID 42412 (adult M)



release: 2022-09-22 22:45
1) 2022-09-22 23:10 - 2022-09-24 21:37
final detection: 2022-09-24 21:38

A2.5 Supplementary file 5: output of the models

Night-to-night departures

	mean	sd	0.0250	0.5000	0.9750	Rhat	n.eff	overlap0	f
beta0	0.2290	0.4438	-0.6922	0.2480	1.0358	1.0031	2410	1	0.712961
sigma_ind	1.0962	0.3009	0.5376	1.0824	1.7266	1.0041	1871	0	1
beta_jdate_c	0.0161	0.0141	-0.0136	0.0170	0.0415	1.0009	9677	1	0.87515
beta_jdate_c_sq	-0.0022	0.0005	-0.0032	-0.0021	-0.0013	1.0040	1663	0	1
beta_crosswind_200	-0.0412	0.0306	-0.1016	-0.0409	0.0183	1.0008	7911	1	0.911472
beta_crosswind_200_sq	0.0262	0.0049	0.0169	0.0260	0.0363	1.0009	6966	0	1
beta_tailwind_200	-0.1739	0.0300	-0.2357	-0.1727	-0.1182	1.0102	648	0	1
beta_tailwind_200_sq	0.0093	0.0033	0.0033	0.0092	0.0161	1.0079	841	0	0.999522
beta_dryness	-1.1506	0.4091	-1.9507	-1.1499	-0.3441	1.0013	4951	0	0.997394
beta_cloud_by_dryness	1.2625	0.6181	0.0707	1.2545	2.4983	1.0009	7426	0	0.981122
beta_temp	-0.1188	0.0906	-0.2998	-0.1176	0.0559	1.0026	2500	1	0.907661
beta_Male	0.7474	0.4132	-0.0071	0.7284	1.6154	1.0006	13476	1	0.9739
beta_Adult	0.5382	0.3589	-0.1341	0.5268	1.2740	1.0018	3803	1	0.941289
beta_Male_jdate_c	0.0491	0.0226	0.0063	0.0485	0.0955	1.0017	3820	0	0.987933
deviance	455.5168	22.6779	411.1207	455.5765	500.1475	1.0025	2794	0	1

DIC = 711.663

Within-night departures

	mean	sd	0.0250	0.5000	0.9750	Rhat	n.eff	overlap0	f
beta0	-3.2302	3.1440	-9.7436	-3.0670	2.5576	1.0047	1561	1	0.858422
sigma_ind	13.9426	4.0645	6.7736	13.6892	22.6126	1.0068	1166	0	1
beta_time_since_sunset	-24.0768	6.5363	-37.6485	-23.7750	-12.2344	1.0072	1104	0	1
beta_crosswind_200	0.4877	0.4031	-0.2289	0.4545	1.3784	1.0020	4489	1	0.906783
beta_tailwind_200	-0.7979	0.4061	-1.6997	-0.7584	-0.1239	1.0022	3809	0	0.991033
beta_dryness	1.4130	3.7934	-6.0642	1.3708	9.0674	1.0027	2570	1	0.648578
beta_cloud_by_dryness	-0.9919	4.7340	-10.4476	-1.0070	8.4862	1.0018	3843	1	0.589211
beta_moon_illumination	-3.2637	4.3505	-12.0546	-3.1433	5.1129	1.0041	1695	1	0.782272
beta_hrly_temp	0.4696	0.6614	-0.7606	0.4378	1.8870	1.0026	2863	1	0.7732
deviance	29.3451	12.7512	10.4479	27.3782	59.6913	1.0033	2502	0	1

DIC = 110.2892

Both models successfully converged based on Rhat values (all < 1.01).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

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